Colour misbinding during motion rivalry

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When two dissimilar colours are displayed to the two eyes at overlapping retinal locations, binocular rivalry typically results: a fluctuating struggle for perceptual dominance of each eye’s stimulus. We found instead that isoluminant counter-rotating patterns consisting of coloured and achromatic portions can promote an illusory colour ‘misbinding’, where the colours from both eyes were perceived within a single rotating pattern. The achromatic portion of one rotating pattern thus appeared to take on the colour of the other, oppositely rotating pattern. The results suggest that the neural mechanisms of colour binding can operate even while representations of the same patterns’ motions are undergoing rivalry, and support the idea that rivalry can occur in isolation within the motion system.

1. Introduction

Several decades of investigation into the primate visual system has shown that different visual attributes are processed along relatively independent parallel pathways. This functional division, which begins in the retina and continues on to visual cortex, is perhaps most apparent in terms of the inputs to the magnocellular (M) and parvocellular (P) layers of the lateral geniculate nucleus, together forming the dominant pathways in primate vision. The M-pathway is crucial for motion processing, showing high-temporal and low-spatial frequency tuning and no selectivity for wavelength, whereas the P-pathway shows lower-temporal and higher-spatial frequency tuning than the M-pathway, and strong colour-opponent responses [1]. An enduring puzzle in the neuroscience of perception is how information carried across such distributed neural representations leads to our typically coherent perceptual experiences—a conundrum known as ‘the binding problem’.

Though binding is anatomically and computationally a problem, the neurologically normal brain is remarkably good at it, and demonstrations of erroneous binding (‘misbinding’) of object features are rare. One approach to studying binding is the binocular rivalry (BR) paradigm. In BR, conflicting monocular images are presented at corresponding locations in the two retinae. Typically, the observer experiences periods of perceptual dominance of the image presented to one eye with concomitant suppression of the other eye’s image from awareness, and these periods of dominance and suppression fluctuate stochastically over time. BR thus provides a powerful tool for probing the neural strategies of resolving competition between signals from the two eyes when they differentially stimulate the P- and M-pathways.

He et al. [2] propose that the parallel pathways might determine whether competing stimulus information undergoes rivalry or is combined across the eyes, depending on their relative activation. In their synthesis of the available evidence, He et al. argue that conflicting information carried predominantly by the P-stream (e.g. colour) is more likely to engage in rivalry, whereas conflicting information carried predominantly by the M-stream (e.g. motion) is more likely to be combined interocularly. They note that, generally, stimuli of opponent colours or high luminance contrast provide good rivalry stimuli, whereas those low in contrast or differing only in temporal frequency are more likely to be combined across the eyes to produce a single percept.
Recent work has, however, revealed a type of misbinding of stimulus features in BR that is seemingly at odds with He et al.’s [2] view. Hong & Shevell [3] presented isoluminant square-wave gratings to the two eyes. Each eye’s stimulus consisted of coloured and achromatic portions alternating over space—such as a red and grey grating in one eye and a green and grey grating in the other eye. In addition to rivalry of the two monocular images (as might be expected for such stimuli), participants also reported a perceptual misbinding of the two colours across the eyes. The colour from one eye’s stimulus appeared to replace the achromatic region in the other eye’s stimulus—such that a two-colour grating (e.g. with red and green portions) was perceived. This colour misbinding phenomenon has since been observed under a variety of conditions [4–6], but only where the relevant stimuli have less than 10–20% luminance contrast [3]. Colour misbinding appears counter to He et al.’s [2] theory because instead of promoting rivalry, the isoluminant colours (which should primarily stimulate P’ neurons) are misbound such that the dominant percept consists of colours sourced from both eyes.

Traditionally, BR has been explained in terms of either ‘eye-rivalry’ or ‘stimulus-rivalry’, whereby eye-rivalry entails a low-level suppression of an entire monocular channel while stimulus-rivalry is considered a higher-level process involving competition between more abstract cortical representations of the stimulus (reviewed in [7]). An emerging alternative to these theories has come from evidence that suppression in BR targets only the rivalving features. During motion rivalry, for instance, an image of a face is spared from suppression when presented to the eye whose motion stimulus is being suppressed (and vice versa [8]), suggesting an independence of feature channels during rivalry [9–11]. Here, we considered whether isoluminant colour misbinding could occur across rivalrous moving patterns. Our results indicated that, surprisingly, it can. Unlike traditional views of eye- or stimulus-rivalry, this implies that rivalry can occur independently within the parallel processing streams, involving only those features carried within the same channel [12].

2. Material and methods

Five experienced psychophysicists (first author (R.T.M.) and four naive; ages 24–42, two females), participated in the experiment. All had normal or corrected-to-normal visual acuity and were tested for normal trichromacy and normal stereopsis. Stimuli were square-wave radial gratings (12 cycles), one presented to each eye, rotating in opposite directions (figure 1a). The gratings, or ‘windmills’, consisted of alternating achromatic (grey) and coloured sectors, where the coloured sectors were different in the two eyes’ stimuli. Four different colours (red, green, red and yellowish/orange) were paired across the eyes in both an opponent (red with green, blue with yellowish/orange) and a non-opponent sense (red with blue, green with yellowish/orange). The windmills (isoluminant at 8 cd m⁻²) rotated (0.25 rotations per second or 3 Hz) behind a circular aperture (3° diameter) against a black background. Stimuli were matched for luminance and chromaticity according to previous specifications [3–5]. In CIE coordinates, chromaticities were grey (x = 0.331, y = 0.331), red (x = 0.307, y = 0.160), green (x = 0.261, y = 0.561), blue (x = 0.180, y = 0.200) and yellowish/orange (x = 0.497, y = 0.385). Rings and nonius lines surrounded the windmills to aid in binocular fusion (figure 1a). Presented above and below each dichoptical stimulus were non-rivalrous stationary windmills (one of each of the colours present in the dichoptic stimuli) that served as a colour reference. Stimuli were generated using the psychophysics toolbox [13,14] within MATLAB (2010a, The MathWorks, Inc.) and were displayed on a gamma-corrected Sony Trinitron CRT (75 Hz; resolution 1024 × 768). Stimuli were viewed dichoptically (distance 57 cm) using a mirror stereoscope mounted on a chin rest. Mirrors were front-surfaced with flat reflectance spectra and a luminance attenuation of 49 per cent (the reported stimulus luminance accounts for this attenuation).

During each dichoptic viewing period (duration 90 s), participants continuously monitored their perception and reported, by holding down one of two buttons on a response pad (RB-730; Cedrus), when their dominant percept rotated in a clockwise or counter-clockwise direction. They were instructed to report the exclusive dominance of a single rotation direction, and to withhold their response if they perceived both motions simultaneously, if they perceived mixed or ‘piecemeal’ rivalry, or if their percept was ambiguous. Participants also reported (by holding down a third button) whether both colours (as indicated in the reference stimuli) were perceived within the dominant windmill stimulus: the colour misbinding effect. This particular response methodology was selected based on a prior experiment employing a different strategy, in which a binocular ‘mixture’ of the monocular colours/motions was found to be rare and colour misbinding occurred just as often as the exclusive dominance of the monocular stimuli (see the electronic supplementary material). Because it is possible that simultaneous colour contrast might induce something resembling the misbinding effect (i.e. a red stimulus might make adjacent achromatic sectors appear green, and vice versa), a control condition was included in which the counter-rotating windmills presented to the two eyes were actually of the same colour. For these single-colour control conditions, one reference stimulus was the opponent colour of that presented centrally. The different colour pairing conditions were randomly interleaved, with colour and direction of rotation counterbalanced across the eyes within testing sessions. Testing was repeated in three separate sessions. Data are available at the Dryad repository (http://dx.doi.org/10.5061/dryad.sn42f).

3. Results

Figure 1b (grey bars) shows the mean proportion of the viewing time in which a single direction of rotation (clockwise or anticlockwise) was reported as dominant in the dichoptic colour pairings as well as the single-colour controls. On average, participants experienced dominance of a single direction of motion for the majority of the display period across all conditions. Importantly, colour misbinding (figure 1b, coloured bars) was reported for all dichoptic colour pairings (figure 1b, four rightmost panels) during these periods of motion dominance, though less frequently for the non-opponent colour pairings (figure 1b, two rightmost panels).

To rule out the possibility that the misbinding reported in the dichoptic dual-colour conditions was simply due to chromatic contrast, Bonferroni-corrected, paired t-tests (two-tailed) were performed on the (arc sine-transformed) average proportions of misbinding for the opponent colour pairings and the appropriate single-colour controls (where the reported ‘misbinding’ is most likely attributable to chromatic contrast). Thus, the red–green colour pairing was compared with the red–red (t₄ = 6.48, p = 0.003) and green–green (t₄ = 4.48, p = 0.01) conditions, while the blue–yellowish/orange colour pairing was compared with the blue–blue (t₄ = 9.73, p < 0.001) and yellowish/orange–yellowish/orange (t₄ = 4.43, p = 0.01) conditions. All tests indicated...
that the ‘true’ misbinding observed in the dichoptic opponent-colour pairings significantly outweighed any ‘false’ misbinding owing to chromatic contrast. For the non-opponent colour pairings, the reported misbinding was reliably greater than zero for the green–yellowish/orange pairing (one-sample t-test; $t_4 = 3.6$, $p = 0.02$) but not the red–blue pairing ($t_4 = 2.29$, $p = 0.08$).

4. Discussion
When two radial grating ‘windmill’ stimuli of different colours and opposing directions of rotation were presented to the two eyes, robust periods of motion rivalry were generated. Surprisingly, during these bouts of rivalry the achromatic sectors of the windmills were frequently replaced by a second colour, such that two colours, one from each eye, were perceived. The colours from the two eyes’ stimuli were thus misbound into a percept of a single, dual-coloured rotating pattern (figure 1a). In addition to highlighting the importance of luminance contrast in the correct assignment of colour information to object contours [3] within moving stimuli, the results also have implications for the distributed neural processing of ambiguous motion and colour inputs.

Previous investigations indicate that colour misbinding reflects an integration of features across the eyes and not merely monocular chromatic contrast effects [4,5], and for two reasons this is likely to be the case here also. Firstly, the misbinding observed in the opponent colour pairings reliably exceeded any ‘false’ misbinding as measured in the single-colour control conditions. Secondly, colour misbinding still occurred with non-opponent colour pairings, at least for

Figure 1. Methods and results. (a) Schematic of the binocular rivalry set-up, with example stimuli (here a green windmill rotating clockwise and a red windmill rotating anticlockwise) and examples of possible misbound colour percepts (here a red–green windmill rotating clockwise or anticlockwise). (b) Mean (across-participant) proportions of motion dominance and colour misbinding for single-colour control conditions (four leftmost panels) and dichoptic colour pairings (four rightmost panels). Grey bars: mean proportion of viewing time where clockwise or anticlockwise motion was dominant. Coloured bars: mean proportion of these dominance periods where colour misbinding was also reported (expressed as proportion of total viewing time). Error bars: ± 1 s.e.m.
green and yellowish/orange. In this condition, the misbinding could not be due to chromatic contrast because the colours that may have been induced by each monocular stimulus were different to those reported in the misbound percept.

That the colours from two counter-rotating patterns could be misbound into a single feature-integrated percept, even while their motions were rivalling, was unexpected. While the independence of motion and colour in rivalry has been demonstrated previously [10], in that instance, it was luminance information that was misbound into a single motion percept, while colour underwent rivalry. Here, it was the colours that were combined interocularly while the motions rivalled, suggesting that rivalry can occur in isolation within the motion-processing system [8,12]. Moreover, our results show that under certain circumstances, colour can be misbound into a pattern moving in the opposite direction even at the centre of vision, complementing a previous account of colour-motion misbinding in the periphery [15]. Colour misbinding probably occurs early [3,4] and in parallel [10] in rivalry, and suggests the underlying neural binding processes are separate, yet similar, for motion and colour inputs.

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References