

Background

A fundamental question for visual neuroscience is whether the brain separately analyses basic visual attributes, such as colour, motion and shape (e.g., Zeki, 1993). Among various forms of cross-attribute interactions, extensive investigations have been made on the effects of colour information on motion perception (see Dobkins & Albright, 2004 for review). In contrast, only a few studies have been made on the effects of motion information on colour perception (Cicerone *et al.*, 1995; Nijhawan, 1997; Moller & Hurlburt, 1997), and it remains open whether motion information is effectively used for colour perception. Here we report two phenomena that demonstrate that the human brain integrates colour signals over time along the trajectory of motion, in order to recover veridical colours of moving objects without motion blur or intrusion from background colours.

Motion-induced colour mixture (Nishida *et al.*, VSS'04)

Phenomenon

Different colours presented at separate retinal locations, but along the same trajectory of a moving object, are perceptually mixed.

Methods (Watanabe *et al.*, ECV'04)

Observers: Five (three of the authors, two naives)

Apparatus: GDM-F520 CRT (Sony) + VSG2/5 (CRS), 160 Hz refresh, 800 × 600 pixels (1.5 min/pixel)

Colour specification: A linear scale of colour mixture was made by modulating the intensities of red ($x=0.625, y=0.341$) and green ($x=0.290, y=0.606$) phosphors: $M=1$, a pair of red and green (perfect segregation); $M=3$, a pair of reddish yellow and greenish yellow (partial mixture); $M=5$, a pair of the same yellows (perfect mixture). When $M=1$, each phosphor was driven at maximum intensities of the monitor (maxluminance condition: $I_{red}=28 \text{ cd/m}^2$ and $I_{green}=84 \text{ cd/m}^2$).

Motion stimulus: Bars continuously jumped with a step equal to the bar width ($3^\circ\text{-}12^\circ$). At every jump, the colour of all bars was synchronously changed.

Flash stimulus (control): Colour stripes were flashed for 6.25 ms, two times with an interval of 125 ms

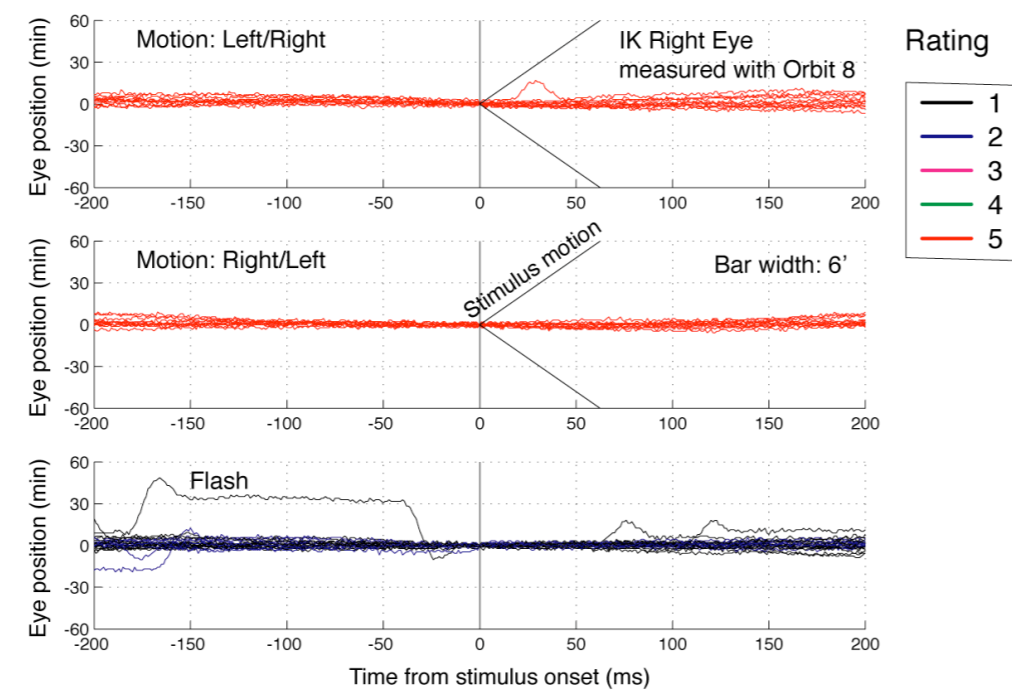
Procedure: In a session, patterns with various bar widths were randomly

shown with the physical colours corresponding to $M=1, 3$ or 5 . For each stimulus presentation, the observer chose the colour mixture value (1-5) closest to the impression of perceived colours.

Results

For a wide range of bar widths, the two colours were mixed more strongly for the motion pattern than for the flash pattern. Since the two stimuli were expected to paint similar patterns on the retina, the motion-induced colour mixture cannot be ascribed to the standard spatial colour integration. The pattern of the results remained the same when the stimulus was presented at 3° eccentricity, or when the two colours were made equiluminant.

Eye movement artefact: Rejected by eye movement recordings (see below) and by simultaneous perception of colour mixture for a moving stimulus with colour segregation for a stationary stimulus (Nishida *et al.* ACV'04).



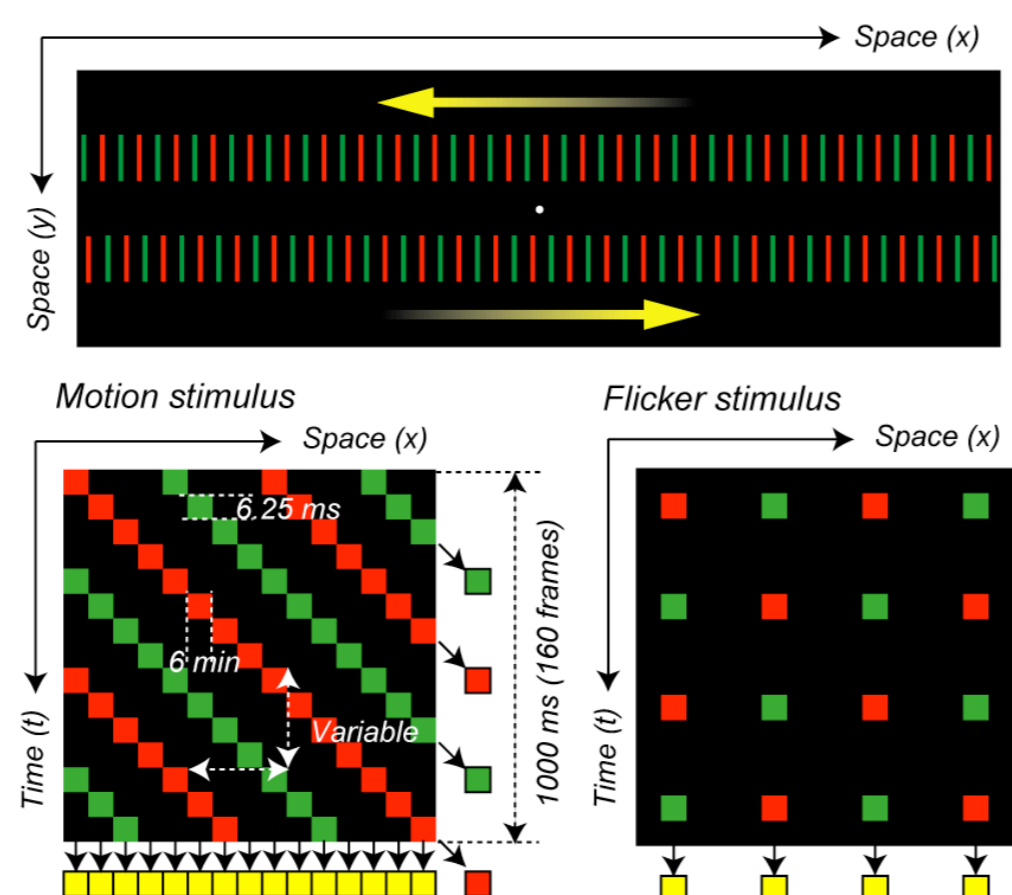
Discussion

The motion-induced colour mixture suggests that motion signals define a spatiotemporal path along which colour signals are integrated. Alternative possibility that motion signals simply lower the spatial resolution of the colour mechanisms can be excluded by the next new phenomenon — motion-induced colour segregation.

Motion-induced colour segregation

Phenomenon

Different colours presented at the same retinal location, but along separate motion trajectories, are veridically segregated more than expected from local flicker fusion.



Methods

Motion stimulus: Coloured bars continuously jumped with a step equal to the bar width ($6'$) with keeping their colours. As the inter-bar interval was decreased from 66 to 6 min, the colour alternation rate at each retinal location increased from 6.7 to 40 Hz.

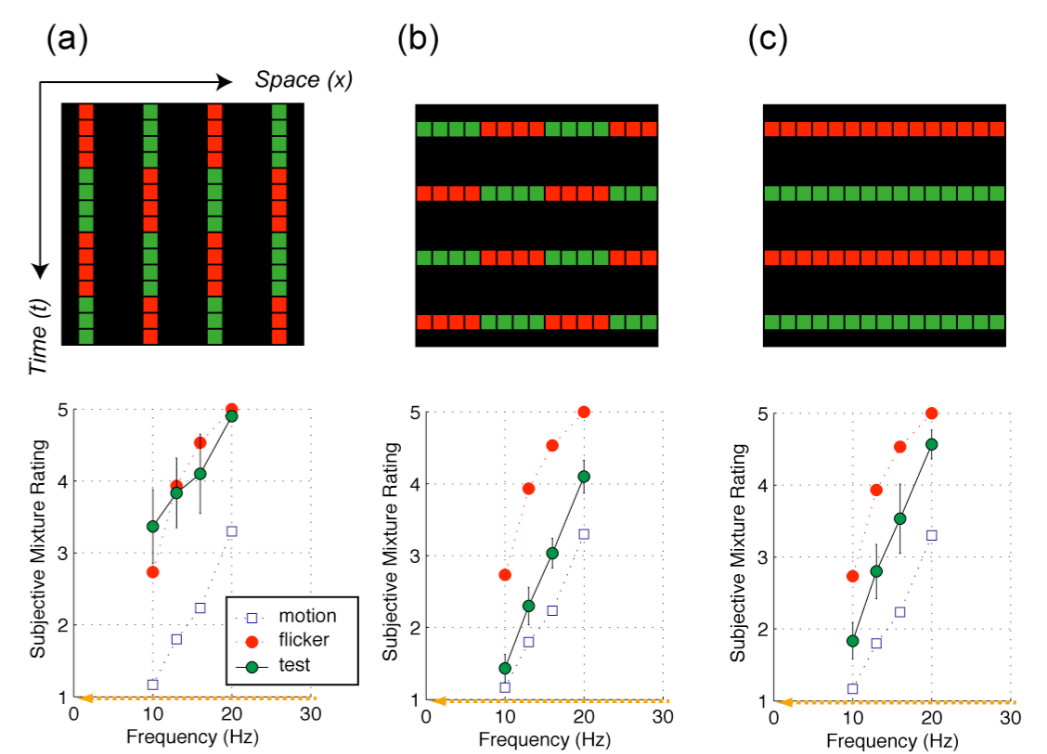
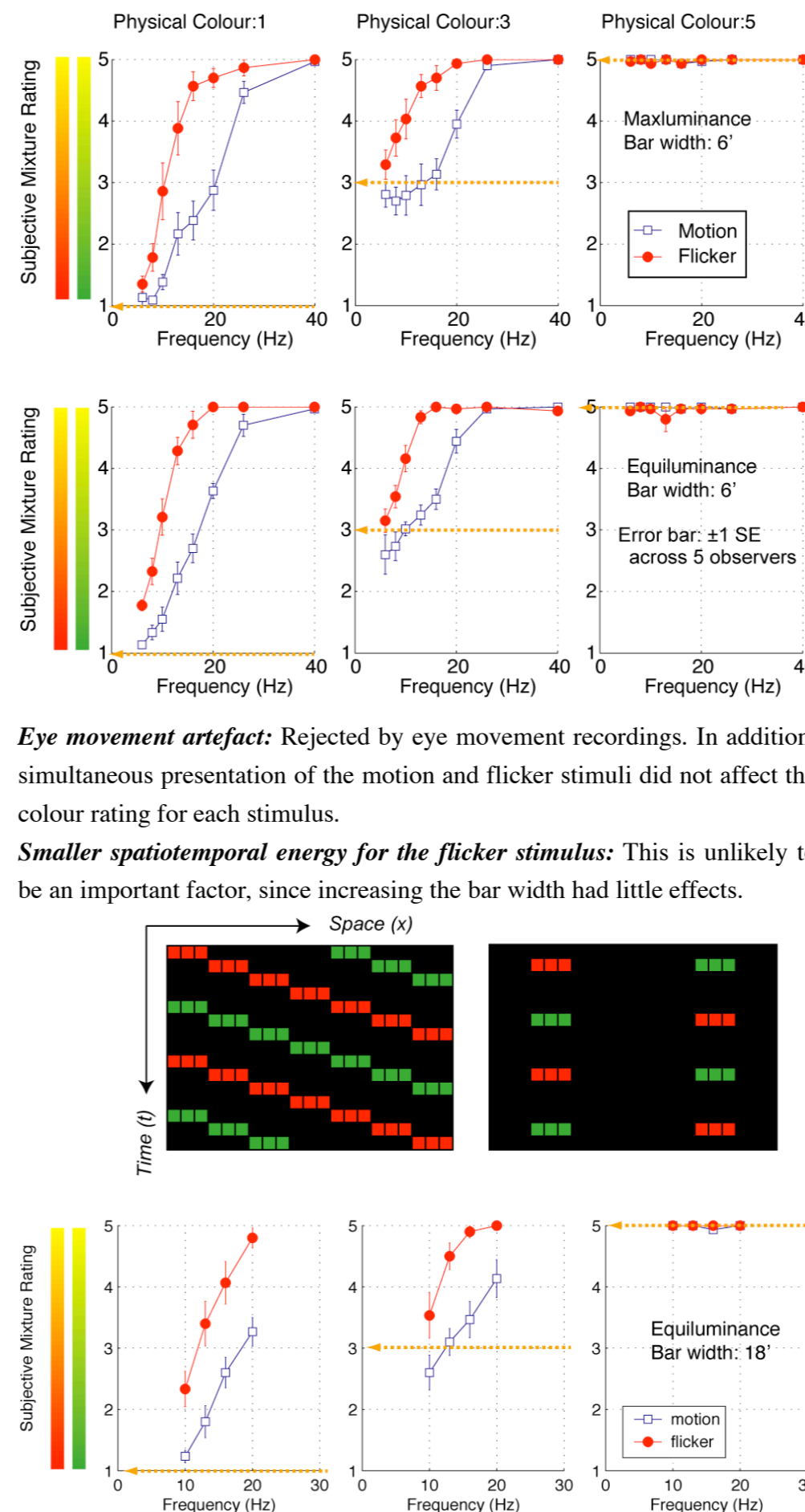
Flicker stimulus (control): The local colour change of the motion pattern was viewed through stationary apertures.

Rationale: The two stimuli should be seen in the same colours, if the apparent colour mixture is solely determined by the retinal temporal integration. However, if the colour signals are integrated also along a motion trajectory, colours should be more veridically segregated for the motion case (where the colour does not change along the trajectory of moving bars, i.e., diagonal direction in the space-time plot) than for the flicker case (where the colour alternates along the trajectory of stationary bars, i.e., vertical direction in the space-time plot).

Procedure: Similar rating experiment as the first experiment.

Results

The colour mixture rating was lower (colour segregation was stronger) for the motion pattern than for the flicker pattern. Similar results were obtained regardless of luminance condition.



Subsidiary experiment: Comparison with the stimuli that have the same total spatiotemporal energy as the motion stimulus. (a) Flicker stimulus in which each colour flash held on until the next flash. (b) Counterphase grating. (c) Uniform field flicker. The colour mixture magnitude for these control stimuli should be the same as the motion stimuli, if total stimulus energy is the critical factor. The result however indicates: “motion” < (b) < (c) < (a) = “flicker”. These results are consistent with the notion of motion-based colour integration, since the pattern (a) has a strong motion energy in the vertical (stationary) direction that supports integration of different colour signals, while the pattern (b) is an ambiguous motion stimulus, having substantial motion energy in diagonal directions that supports segregation of different colour signals. (Additionally, the pattern (b) contained colour edges.)

Discussion

Functional role: Integration of colour signals along motion trajectory is a useful mechanism to see veridical colours in dynamic scene, as in the case of motion-based pattern integration (Burr *et al.*, 1986; Nishida, 2004). This mechanism can suppress motion-induced colour blur, segregate colour signals of a moving object from signals of the background, and improve the signal-to-noise ratio by excluding fluctuations of colour signals over motion trajectory.

Cross attribute interaction: A number of anatomical and physiological studies suggest that colour and motion are processed through separate retinal-geniculo-cortical pathways. However, our findings, together with other lines of evidence of colour-motion interactions, indicate functional inseparability between colour processing and motion processing. In comparison with the previous reports (Cicerone *et al.*, 1995; Nijhawan, 1997; Moller & Hurlburt, 1997), the present findings reveal a more direct and functionally significant influence of motion signals on colour perception.

Neural mechanism: Involvement of motion processing indicates significant contribution of cortical processing to colour mixture/segregation. Physiologically, colour-selective neural mechanisms in early visual processing can carry chromatic temporal modulations well above the perceptual fusion limit (Lee *et al.*, 1989; Gur & Snodderly, 1997). Our findings suggest that the temporal limit of chromatic perception depends on the way the cortical processing integrates colour signals. A possible neural mechanism of motion-based colour processing is local spatiotemporal integration of colour information by neurons sensitive both to motion direction and colour. Another possibility is that feedback signals from motion analysis in the dorsal pathway may globally modulate the pattern of spatiotemporal integration of neurones in the ventral pathway.

