
The fluttering-heart illusion: a new hypothesis

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Abstract. The fluttering-heart illusion is a perceived lagging behind of a colour target on a background of a different colour when the two are oscillated together. It has been proposed that the illusion is caused by a differential in the perceptual latencies of different colours (Helmholtz 1867/1962), a differential in rod–cone latencies (von Kries 1896) and rod–cone interactions (von Grünau 1975, 1976 *Vision Research* **15** 431–436, 437–440; **16** 397–401; see list of references there). The purpose of this experiment was to assess the hypothesis that the fluttering-heart illusion is caused by a differential in the perceived velocities of chromatic and achromatic motion. To evaluate this hypothesis, we tested observers possessing normal colour vision and deuteranopes. The perceived delay of a chromatic target relative to an achromatic target was measured as a function of background cone contrast and target colour. For observers with normal colour vision, the perceived delay of the chromatic target is greater in the L–S than the L–M testing conditions. The reverse is observed in deuteranope observers. We suggest that this is caused by the absence of an L–M opponent mechanism contributing to chromatic motion in deuteranopes. Greater background cone contrasts tended to yield smaller perceived delays in both normal and deuteranope observers, indicating that greater chromatic modulation decreases the perceived delay of the colour target. These results support the hypothesis that the fluttering-heart illusion can be explained by a differential in the perceived velocities of chromatic and achromatic motion.

1 Introduction

The classical visual phenomenon of the fluttering-heart illusion is a phenomenon occurring when a piece of coloured paper (target) is glued onto a larger one of a different colour (background) (Helmholtz 1867/1962). When the sheets are oscillated in front of an observer, the observer reports that the target seems to slide over the background. Helmholtz (1867/1962) reports that red and blue are the most effective colours to observe the illusion and that the colours must be very vivid and saturated for the effect to occur. It is also reported that the phenomenon is most apparent when observed in conditions of low illumination. Helmholtz argued that the phenomenon is caused by a differential in the perceptual latencies to the different colours of the target and background. A blue target would thus appear to lag behind a red background when the two are oscillated together because the perceptual latency for the colour blue is longer than that for red.

Von Kries (1896) suggested that the fluttering-heart illusion is caused by a differential in the response latencies of the rod and cone mechanisms. This explanation assumes that rods possess longer response latencies than the cone systems. He proposes that in the conditions of dim illumination, under which the effect is most apparent, a blue target would stimulate the rods more than a red background and red would excite mainly cones. According to von Kries (1896), a blue target would thus appear to lag behind a red background when the two are oscillated together because the rods possess longer response latencies than the cones. This theory can account for reports that the phenomenon is most apparent when observed under conditions of dim illumination in which both rods and cones are active (mesopic intensities). It can also explain why it is reported that the illusion is more readily perceived when the target lies in the near

periphery (~ 5 deg away from the fovea) because that area of the retina has both rods and cones. Finally, von Kries's theory can also account for the observation that blue and red are reported to be the optimal colours to observe the effect.

The most recent attempt at explaining the fluttering-heart illusion was made by von Grünau (1975a, 1975b, 1976). He suggested that lateral interactions between the rod and cone systems occurring at the chromatic border between the colour target and the background are the cause of the effect. In this account, the system stimulated by the background is hypothesised to inhibit temporally the system stimulated by the target at the border between the target and the background. This temporal inhibition would create a delay in the processing of the information at the border of the colour target and in the processing of the entire target as well, causing it to appear to lag behind the background when the two are moving together in the classic demonstration of the illusion. This explanation can account for the observation that the effect is optimal when viewed at mesopic intensities at which both rods and cones are active. It would also explain why the illusion is reported to be most apparent when blue and red are used because these two colours would result in the largest rod-cone interactions. Though rod-cone interactions have been demonstrated to affect colour vision in the mesopic range, no research has reported the type of interactions hypothesised by von Grünau to be the cause of the fluttering-heart illusion.

To this day, the possible contribution of a differential in the perceived velocities of chromatic and achromatic motion to the fluttering-heart illusion still remains uninvestigated. It has been proposed that two distinct pathways carry the analyses of colour and motion (Ramachandran and Gregory 1978; Zeki 1978; Livingstone and Hubel 1987) and that the motion pathway responds only to luminance information (Ramachandran and Gregory 1978). Many studies have demonstrated the existence of a motion response to moving isoluminant colour stimuli (Moreland 1982; Cavanagh et al 1984; Cavanagh and Favreau 1985; Mullen and Baker 1985; Gorea and Pappathomas 1989; Bilodeau and Faubert 1997, 1999a; Faubert et al 2000). However, the perceived velocity of moving isoluminant chromatic stimuli has been consistently reported to be slower than that of achromatic stimuli of the same velocity (Cavanagh et al 1984; Cavanagh and Favreau 1985; Derrington and Badcock 1985; Troscianko and Fahle 1988; Cavanagh and Anstis 1991; Kooi and De Valois 1992; Mullen and Boulton 1992b). In some cases a phenomenon known as motion standstill, in which an observer cannot see the motion of a clearly visible chromatic stimulus, has been reported (Cavanagh et al 1984; Livingstone and Hubel 1987; Mullen and Boulton 1992a; Teller and Lindsey 1993; Lu et al 1999b). Thus, in this article, we propose to assess the hypothesis that the fluttering-heart illusion is caused by a differential in the perceived velocities of chromatic (isoluminant) and achromatic (isochromatic) motion.

2 Experiment 1

2.1 Methods

2.1.1 *Observers.* Five normal observers with normal colour vision, naïve to the purpose of the experiment, were tested. Normal subjects were undergraduate students from the School of Optometry. Two deuteranope observers, as determined with HRR colour plates and a Nagel anomaloscope, were also tested. These observers were selected because they do not possess a functional M-cone mechanism and could therefore serve as control subjects. One deuteranope was naïve to the experiment and the other is one of the authors (DN).

2.1.2 *Apparatus and stimuli.* Observers were tested with the use of a Power Macintosh G3 with an Apple Multiscan CRT monitor with CIE (x , y) coordinates (0.60, 0.36) for red, (0.28, 0.59) for green, and (0.14, 0.06) for blue with an 8 bit per gun video card.

The experiment was written in MATLAB and the extensions provided by the high-level Psychophysics Toolbox (Brainard 1997) and low-level Videotoolbox (Pelli 1997). Prior to each trial, only a near-equal-energy white adapting field [CIE (x, y) coordinates: (0.29, 0.30)] of an intensity of 33 cd m^{-2} and a fixation point were visible. During trials, a red background, 11 deg in height and 6.5 deg in width, was presented. The background differed from the white adapting field by 10%, 20%, or 30% in L-cone contrast [CIE (x, y, Y) coordinates of (0.323, 0.297, 35.13), (0.35, 0.294, 37.28), and (0.375, 0.291, 39.42), respectively] (Cole and Hine 1992; Bilodeau and Faubert 1999b). The display consisted of the stationary red background and two targets presented simultaneously on each trial; a colour target and a 'neutral' (luminance) target. The processing of the luminance target may also be delayed, however, and the variable of interest here is the relative delay between the chromatic motion of the colour target and the achromatic motion of the neutral one. Both targets were 1 deg in width by 3 deg in height. A fixation point 5 deg below the centre of the display was present at all times during testing. The display used in the experiment is illustrated in figure 1. The colour target was isoluminant with the background. The colour target was either blue (condition L–S), because blue on red has been reported to be the condition in which the effect is most apparent, or green (condition L–M) in order to assess the contribution of a chromatic motion mechanism to the effect. The neutral target possessed the same CIE coordinates as the background but differed by the same amount of cone excitation from the background as the colour target. The centre of the display was 5 deg above fixation. The two targets oscillated at an amplitude of 5 deg and a frequency of 0.94 Hz, which are the frequency and amplitude used by von Grünau. Velocity of the targets remained constant and direction of the motion changed abruptly. The two targets were separated by 0.75 deg in order to make judgments about delays easier for observers.

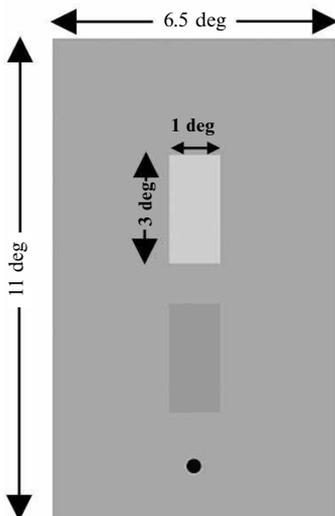


Figure 1. Representation of the display used to measure delay between a colour and a neutral target in the experiment. A fixation point was presented 5 deg below the centre of the display. The two targets were separated by 0.75 deg. Observers were instructed to remain fixated on a fixation point. The neutral and colour targets oscillated with a frequency of 0.94 Hz and at an amplitude of 5 deg. The neutral target differed by the same amount of cone excitation from the background as the colour target. A delay in phase could be created between the two targets. The observers' task was to indicate whether the colour target appeared in front of or behind the neutral target in terms of phase (2AFC).

2.1.3 Procedure. Observers viewed the monitor at a distance of 57 cm. Isoluminance between the colour target and the background had been determined prior to testing for each observer, in each condition, at the tested location by the method of heterochromatic flicker photometry. The perceived delay of the colour target (ie the delay in the phase of the neutral target relative to that of the colour target necessary for the two targets to appear to move in phase) was determined by the method of constant stimuli. Observers initiated each trial with a key-press, which was followed immediately by a presentation of the display for two cycles (2133 ms). Observers were instructed to remain fixated on the fixation point, which remained present during trial presentations.

The task of the observers was to determine whether the colour target appeared ahead of or behind the neutral target in terms of phase (2AFC). The minimal step size in delay of the neutral target was 8.33 ms. Five delay values around the expected perceptual delay of the colour target were presented in random order. The position (top or bottom) of the two targets was randomised to prevent possible effects of eccentricity on perceived delay. Each target appeared an equal number of times at each position.

3 Results

The amount of perceived delay of the colour target was estimated for each block of trials with a threshold estimation procedure (Foster and Bischof 1991) with a criterion of 0.75 for correctly answering that the colour target is ahead in phase. The data of normal and deuteranope observers are presented in figure 2. Perceived delays were comparable to the ones obtained by von Grünau (1975a) when he measured delays at low levels of illumination. Two trends can be observed in normal subjects. The first trend is that perceived delay decreases with increasing background cone contrast. The other trend is that blue–red yields greater lag values than green–red. This trend is reversed in deuteranope observers: greater delays were observed in condition L–M than in condition L–S. As in normal observers, lag values decreased with increasing background cone contrast for deuteranope observers.

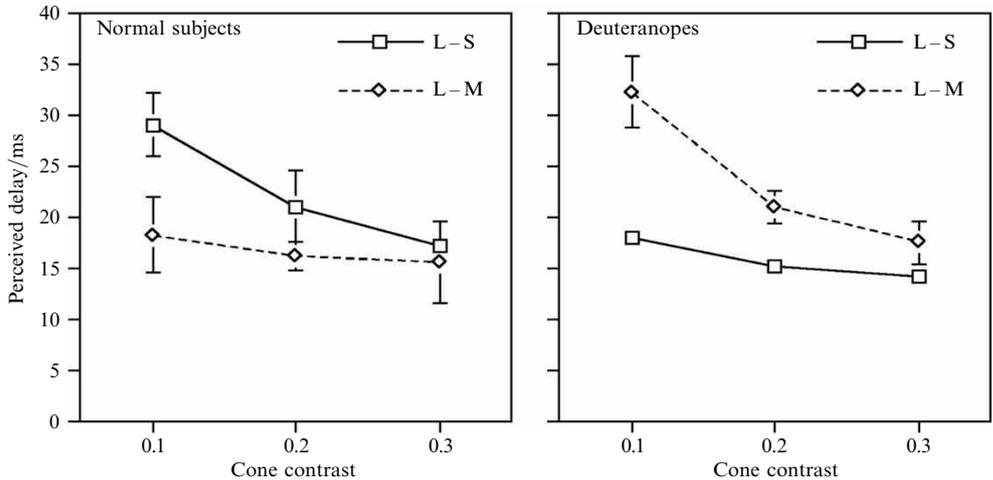


Figure 2. Perceived delay of colour target relative to the neutral target for normal observers and deuteranope observers as a function of background cone contrast and test conditions. Vertical lines represent standard error of the mean.

4 Discussion

Helmholtz's explanation that the fluttering-heart illusion is caused by a differential in the perceptual latencies of different colours cannot account for the dependence of the effect on background cone contrast because it simply assumes that perceptual latency is a function of stimulus wavelength. It also cannot account for the greater perceived delays in condition L–M than in condition L–S in deuteranope observers, the reverse of normal observers, because deuteranopes possess only functional S-cone and L-cone mechanisms. The hypothesis that the illusion is caused by a differential in the latencies of the rod and cone mechanisms also cannot account for the current results because it predicts that the effect should be strongest in L–S regardless of whether an observer is a deuteranope or possesses normal colour vision. We thus conclude that neither a differential in the perceptual latencies of different colours nor a differential in the response latencies of rods and cones can explain our results.

Von Grünau's data (1975a, 1975b) are in concordance with our hypothesis that the fluttering-heart illusion is caused by a differential in the perceived velocities of chromatic and achromatic motion. When an oscillating colour target and a neutral (black) target were presented on a stationary background, von Grünau found that the colour target always seemed ahead of a neutral target in terms of phase, regardless of the display arrangement (red target on a blue background, or blue target on a red background). Both earlier accounts of the phenomenon predict that a red target on a blue background should be perceived as ahead in phase relative to a neutral target. Therefore von Grünau concluded that neither of the earlier attempts at explaining the phenomenon was adequate. However, a contribution to the effect of a differential in the perceptual latencies of different colours or a differential in the response latencies of rod and cone mechanisms cannot be ruled out completely because measured delays were twice as long in the blue-on-red condition than in the red-on-blue condition.

The hypothesis that the illusion is caused by lateral rod-cone interactions at the border between the colour target and the background cannot explain the results obtained in this article. Like the account that the illusion is caused by a differential between rod and cone latencies, it predicts the effect should be strongest in condition L-S, regardless of whether an observer is deuteranope or has normal colour vision. Also, these two hypotheses can best account for the phenomenon when it is observed at mesopic intensities, in which both rods and cones are active. However, the conditions at which this experiment was conducted were clearly photopic because of the intensity of the adapting field (33 cd m^{-2}). Although rod-cone interactions may still occur at these luminance levels, they should be minimised (Aguilar and Stiles 1954; He and Macleod 2000). Furthermore, the use of isoluminant stimuli should also minimise rod-cone interactions. The fact that perceived delays in our experiment were comparable to those obtained by von Grünau (1975a), when he measured delays under mesopic conditions, strongly suggests that increased luminance could not account for our results.

The results of this experiment support the hypothesis that the fluttering-heart illusion is caused by a differential in the perceived velocities of chromatic and achromatic motion. The perceived delays decreased with increasing contrast between target and background, in agreement with findings of a contrast dependence of perceived velocity of chromatic gratings (Gegenfurtner and Hawken 1996) and in the reaction times to motion onset of chromatic gratings (Burr et al 1998) at low velocities. The conclusion that the effect is caused by a differential in the perceived velocities of chromatic and achromatic motion is in agreement with Burr et al (1998), who concluded that the reaction times to the motion onset of chromatic and achromatic gratings are determined by the perceived velocity of the gratings. The greater perceived delays of the colour target in condition L-M than in condition L-S in deuteranope observers is consistent with the hypothesis that the fluttering-heart illusion is caused by a differential in the perceived velocities of chromatic and achromatic motion. We suggest that these greater perceived delays in condition L-M than in condition L-S occur because deuteranopes do not possess an adequate L-M opponent mechanism, which has been suggested to contribute to the processing of chromatic motion of red-green stimuli (Cavanagh and Anstis 1991).

In the classic demonstration of the illusion, the colours of the background and target are very vivid and saturated. When viewed in conditions of dim illumination, the background would be defined by luminance differences. However, the target would differ from the background in terms of chromaticity. The target and the background need not be isoluminant, as adding chromatic modulation to a drifting grating with a constant low luminance contrast has been demonstrated to cause a decrease in its perceived velocity (Cavanagh et al 1984). When the display used in the classic demonstration of

the illusion is oscillated laterally, the motion of the background would be achromatic, whereas that of the colour target would have a chromatic component. This could create a differential in the perceived velocities of the target and the background. This perceived velocity differential could result in a delay in the perceived onset and offset of the motion of the colour target relative to that of the background. This would also result in a delay in the perceived change of direction of the colour target relative to that of the background, and hence the percept of the colour target lagging behind the background.

In von Grünau's (1975a, 1975b) experiments on the fluttering-heart illusion, the neutral target was always black and thus a luminance difference existed between it and the background. The colour target had a different colour than the background and thus there was a chromatic difference between the two. We suggest the measured delays of the colour target relative to the neutral target result from a differential between the perceived velocities of the neutral and the colour targets. The motion of the colour target thus had a chromatic component, whereas the motion of the neutral target was achromatic. The measured delays between the two targets could therefore be explained by a differential in the perceived velocities of the two targets causing a difference in their perceived motion onset and offset.

It has been reported that the fluttering-heart illusion is best observed at mesopic intensities (Helmholtz 1867/1962). We suggest that a reduction in cone responses during dark adaptation causes a decrease in the responses of 'opponent-colour' mechanisms, resulting in a greater loss in the perceived velocity of chromatic motion. This would be in agreement with findings supporting the involvement of 'opponent-color' mechanisms in the processing of chromatic motion (Cavanagh and Anstis 1991). We also propose that the effect is most apparent in peripheral vision because of a greater decrease in the perceived velocity of chromatic motion with increasing eccentricity. This would be in agreement with findings of a greater decrease in sensitivity to chromatic motion than to achromatic motion with increasing eccentricity (Bilodeau and Faubert 1997). We suggest that the phenomenon is reported to be most apparent with blue on red because the processing of this type of chromatic motion would involve the S-(L + M) system whose contribution to the motion has been demonstrated to be much weaker than that of the L-M opponent mechanism (Cavanagh and Anstis 1991). One of the most interesting predictions of this hypothesis is concerned with the perceived speed of stimuli modulating the different chromatic mechanisms: this hypothesis predicts that the apparent slowing of chromatic motion should be greater for gratings that stimulate the S-(L + M) chromatic system in isolation than for isoluminant chromatic gratings that excite the L-M chromatic mechanism. Research comparing the perceived speed of isoluminant chromatic stimuli for gratings that stimulated the different mechanisms has supported this prediction (Dougherty et al 1999; Nguyen-Tri and Faubert 2002).

In conclusion, we reject the previous hypotheses that the fluttering-heart illusion is caused by a differential in the perceptual latencies of different colours (Helmholtz 1867/1962), a differential in rod and cone response latencies (von Kries 1896), or by rod-cone interactions (von Grünau 1976). A difference in perceived velocity between chromatic and achromatic motion mechanisms appears adequate and sufficient to account for the effects related to the fluttering-heart illusion.

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