

## **Why hearts flutter: distorted dim motions**

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### Abstract

When a display of red spots or hearts on a blue surround is moved around under dim light, the spots appear to wobble or flutter relative to the surround (the “fluttering hearts” effect). We explain this as follows: Rods and cones both respond to the hearts. Rods are more sluggish than cones, with a latency of ~50 ms, and they are also much more sensitive to blue than to red (the Purkinje shift). Thus a red spot oscillating on a blue ground produces a double image: a light spot seen by the cones, followed by a trailing dark spot seen by the rods. These interacting spots of *opposite luminance polarity* move like “reverse phi” (Anstis 1970) and this generates the fluttering hearts effect. We find that hearts flutter most markedly at or near *mesopic* equiluminance, when the red is lighter than the blue as seen by the cones, but darker than the blue as seen by the rods. These same red/blue luminance ratios give rise to two new illusions: the ghostly-twin illusion, and the reversal of red/blue grating movement.

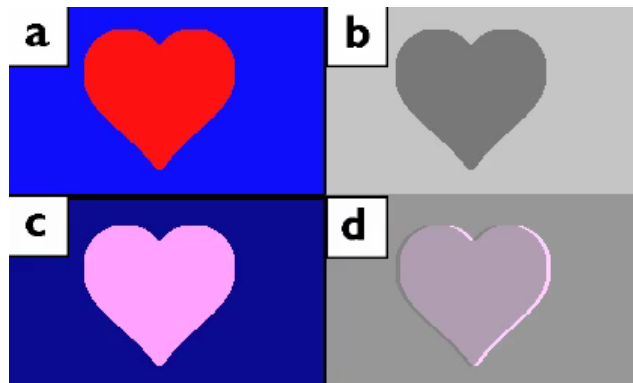
**Keywords** fluttering hearts cone vision rod vision mesopic vision color vision visual latency illusion

### Introduction

The “fluttering hearts” illusion is seen when a display containing red hearts or spots in an approximately equiluminous blue surround is jiggled in dim light. As a result, the hearts appear to flutter or float around on the blue surround. Baldwin (1901) writes: “a continuous to-and-fro motion gives rise to the appearance of a sudden springing of the Figures from side to side.” The illusion has been variously attributed to a slower response to blue than to red (Helmholtz 1867/1962), to retinal rods being more sluggish than cones (von Kries 1896), to lateral inhibition at red/blue borders (von Grunau 1975a, b, 1976), and to motion looking slower at equiluminance (Nguyen-Tri and Faubert 2003) or at low levels of luminance contrast (Arnold & Johnston 2003). The predominant account, however, has been the simple one due to von Kries and Helmholtz, in which a difference in latency between responses to the red heart and the blue surround makes the heart appear to move relative to its surround when both are jiggled together.

Our new analysis builds on the sluggish response of the rods as one element in the explanation, but adds two more crucial factors—the opposite contrast polarities seen by rods and cones (owing to the very different spectral sensitivities of rods and cones, Purkinje 1825), and a “reverse-phi” motion (Anstis 1970; Anstis & Rogers 1975, 1986) between the perceptually light and dark spots. Since we cannot readily present in a journal movie the exact mesopic moving stimuli we used, all of our movies are *simulations* of the separate rod and cone responses made to a single moving spot or heart.

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### Movie 1

**a.** the fluttering heart stimulus. **b.** the heart as seen by rods, colorless and dark. **c.** the heart as seen by cones. **d.** the superposition of rod and cone images, showing an exaggeration of motion amplitude and perceptual phase lag.

Movie 1 presents our theory in a nutshell. In this simulation, the stimulus (Movie 1a) is a dim red heart that moves back and forth across a dim blue surround. In Movie 1c, the cones see this as a light heart on a dark surround, because the cones are more sensitive to red than to blue. However, in Movie 1b the rods see the *same* stimulus as a dark heart on a light surround, because the rods are more sensitive to blue than to red (the Purkinje shift). In addition, the rods are more sluggish than the cones; note that the dark heart in Movie 1b lags slightly behind the red hearts in Movies 1a, c. Movie 1d shows the joint response of the rods and cones. The two hearts from Movie 1b, c are superimposed in Movie 1d to form a more complex profile with a light leading edge and a dark trailing edge. This double rod/cone image seems to *flutter* or wobble in a jelly-like way, and it also seems to move with greater amplitude than its two component hearts. This is particularly clear in peripheral vision. A model for the increased apparent amplitude is discussed later in connection with Movies 5 and 6.

### Qualitative evidence

We note first some informal observations that fit a rod/cone theory. First, the best illusion comes from red and blue patterns viewed at 5° to 20° eccentricity in dim light, but not so dim that color vanishes. These conditions stimulate both rods and cones simultaneously. Second, bleaching out the rods with a strong adapting flash, as follows, reduced or abolished the fluttering hearts effect. Using a high-intensity BigMax back-projection system (MacLeod, Beer & Miller 2003) two observers (the authors) bleached out the rods in one half of the retina with a single brilliant flash of light (~108 trolands, 50 ms). They then viewed an array of red dots oscillating on a blue surround in dim light. The red dots appeared to flutter strikingly in the intact portion of the retina, but barely at all in the portion whose rods had been bleached out. Thus flutter requires the concurrent activity of both rods and cones.

## Quantitative evidence: Experiments 1, 2

Experiment 1 comprises three demonstrations that support our theory. Simulated stimuli are shown in Fig. 1 and Movie 2, and psychophysical results from our actual stimuli are shown later in Figs 2a, 2b.

1a. We report a new illusion called “light and dark twins”, which occurred near red/blue mesopic equiluminance: a dim red spot moving in a circular trajectory on a dim blue surround looks like two overlapping spots-- a leading, light red spot seen by the retinal cones, and a trailing, dark twin seen by the retinal rods, which are not only sluggish but also reverse the luminance polarity of the red spot, because rods are far more sensitive to blue than to red light (the “Purkinje shift”: Purkinje 1825: Anstis 2002). Conversely, a dim blue spot moving on a dim red surround appears as a dark blue spot seen by the cones, followed by a trailing, light twin seen by the rods.

1b. We measured the apparent displacement of the fluttering hearts with spots that jumped back and forth in *apparent movement* between two positions. In mesopic conditions the apparent motion can considerably overshoot the true motion, a new observation that we show is explained by our model.

1c. Another new illusion at red/blue equiluminance, consistent with our theory, is a perceptual reversal of a red/blue grating’s apparent motion, described below.

Note that all three effects –light or dark twins, fluttering hearts, and reversal of red/blue grating motion – were all best realized when the red and blue were close to mesopic isoluminance, namely when the red stimuli were lighter than the blue as seen by the cones, but darker than the blue as seen by the rods. This leads us to believe that all these illusions have a common underlying mechanism and require a common explanation, which our theory provides.

### Experiment 1

#### Methods

Three similar displays were set up to demonstrate and measure light and dark twins; fluttering hearts (not shown); and reversed motion of red/blue gratings (Fig. 1, Movie 2). All three effects were measured in similar luminance conditions, and results are plotted on common axes in Fig. 2. Chromaticities of the stimuli (CIE  $x,y$ ) were: (0.632, 0.330) for red and (.146, .070) for blue. Photopic and scotopic luminances were determined by measuring the output of the red and blue phosphors at every visible wavelength in 4 nm steps with the aid of a PSR650 spectroradiometer, and weighting this output by multiplying it by a standard cone-sensitivity curve, which peaks at 555 nm, or by a standard rod-sensitivity curve, which peaks at 505 nm (Wyszecki & Stiles 1982). We confirmed the physical photometric results by setting the red and blue phosphors to look equiluminous to the cones (same photopic luminance). When viewed through a  $-3.0$  log unit filter, the blue could be readjusted to give an exact match to the red, but for this scotopic match it had to be reduced twenty fold in intensity. Thus the scotopic isoluminance line in Fig. 2 is displaced up or to the left by 1.3 log units ( $= \log_{10} 20$ ).

### *Light and dark twins*

A circle of eight red spots, graded from light to dark over a hundredfold range, lay on a uniform blue surround. The set of spots rotated continuously clockwise, taking 3.27 s per revolution. Observers viewed the display, fixating its center, through neutral density filters placed near the eye, ranging in density from 0 to 3 log units. Across conditions, the blue surround varied from  $-3.16$  to  $+0.86$  log cd/m<sup>2</sup> and the red spots from  $-2.7$  to  $+1.3$  log cd/m<sup>2</sup>. The observer indicated which spots, if any, appeared to be trailed by a twin.

### *Fluttering hearts*

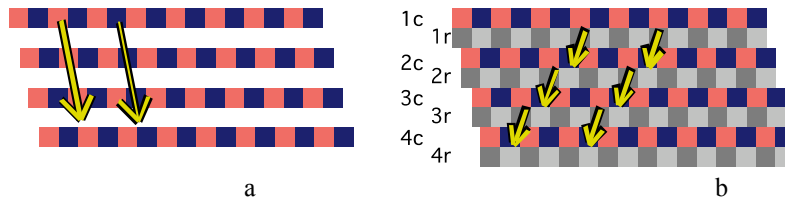
Instead of rotating continuously, the same spots now jumped through half a spot diameter clockwise and then back again repetitively at a rate of 3.67 Hz. This back and forth apparent movement could make some of the spots appear to flutter, and when this happened the fluttering spots were identified. In short, the spots that appeared to trail before now appeared to flutter.

### *Perceived reversal of apparent motion*

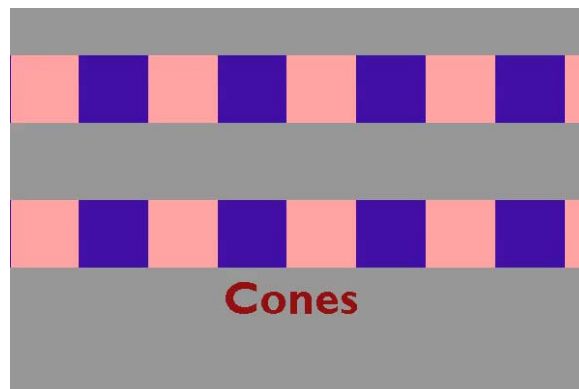
Instead of spots, the next stimulus was a square-wave red/blue grating comprising a horizontal row of twelve equi-spaced red and blue squares, positioned  $7^\circ$  above the fixation point, with each square subtending  $1.4^\circ$  (Fig. 1; Movie 2). This grating made four rapid quadrature (quarter-cycle) steps to the right, each step size being half a square's diameter, at a rate of 8 fps. This brief, 500 ms four-frame movie (Movie 2) normally appeared to move continuously to the right, because the stripes in successive frames corresponded in both color and luminance. However, luminance is far more important than color in establishing motion correspondences (Anstis 1970; Ramachandran & Gregory 1978; Anstis and Cavanagh 1983; Cavanagh, Anstis and Mather, 1984; Anstis, Cavanagh, Maurer, Lewis, MacLeod and Mather 1986; Anstis, Cavanagh, Maurer, and Lewis 1987; Cavanagh, MacLeod and Anstis 1987; Maurer, Lewis, Cavanagh and Anstis 1989). We predicted that under the red/blue luminance levels that gave flutter, each frame of a red/blue grating would be seen first by the cones, and then briefly afterwards by the rods *in reversed luminance*. Thus the cones would see light red and dark blue squares, but the rods would see dark red and light blue squares. The rod view would be achromatic, but it would be matched up according to luminance, not color, with the next frame to appear.

If so, the interplay of asynchronous and reversed-contrast rod and cone images would, and did, make the red/blue pattern appear to move in the *opposite* direction to its actual motion. Figure 1 explains why. Fig. 1a shows the four stimulus frames as static strips one below the other. Fig. 1b schematically illustrates the responses of cones and rods; each frame is seen first in color by the cones, then an instant later by the achromatic rods, with a contrast reversal (red looks darker to the rods). So frame #1 seen by the rods (labeled 1r) is seen as jumping to the *left* into frame #2 seen by the cones (labeled as 2c). Hence,

when we used the red and blue luminances that we had found to give fluttering hearts and light or dark twins, the movie seemed to move to the *left* (Fig. 1b).



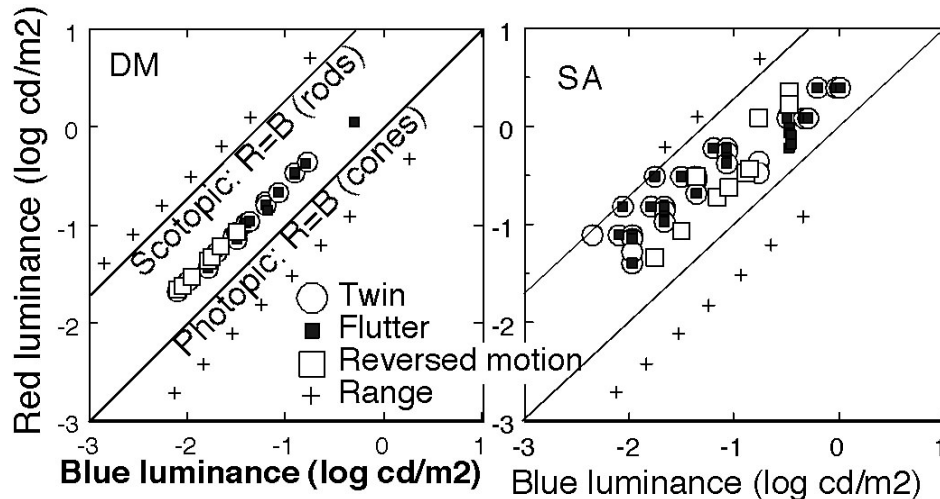
**Figure 1** **a**, in cone vision, dark blue bars are matched up in successive movie frames to give perceived motion to the *right*. **b**, in dim light that activates both rods and cones, movie frame #1 is seen first by the cones (1c); and then by the rods (1r), reversed in luminance because rods are more sensitive to blue than to red. Result: The dark (red) bars seen by the rods in frame 1r are matched up perceptually with the dark (blue) bars seen by the cones in frame 2c, giving perceptual motion to the *left*.



**Movie 2** Simulation of the movie. Top: the bars of Figure 1 appear in their 4 successive positions as seen by cones. Bottom: the “cone” images are interleaved in time with colorless and slightly delayed “rod” images in which the red bars appear dark instead of relatively light. The combined rod and cone images generate a motion reversal, an instance of reverse phi (Anstis, 1970).

## Results

Results for all three parts of this experiment are plotted in Figure 2. Each datum point shows a stimulus containing blue (x) and red (y) that gave rise to one of the three illusions – light or dark twin (circles), flutter (black squares), or reversed apparent movement (open squares).



**Figure 2a** Observer DM. Combinations of blue (x) and red (y) luminances that gave rise to red dark or blue light twins (circles), fluttering red or blue spots (filled squares), and perceptually reversed apparent motion (open squares). (Small crosses show total range of spot luminances investigated as a function of surround luminance). Note that the red/blue ratios were approximately the same for all three illusions, with the red exceeding the blue in photopic luminance ( $\text{cd}/\text{m}^2$ ), but less than the blue in scotopic luminance; scotopic (rod) equality (upper diagonal line) required a 20 fold (1.3 log units) greater photopic luminance of red than of blue. For all data points the red is dimmer than the blue for rods.

**Figure 2b** Same conventions as Fig. 2a. Observer SA

#### *Light and dark twins*

In mesopic conditions one or more of the red spots appeared to have an illusory "dark twin" following it. Figure 2 shows the luminances of the spots that were reported as twinned. The twin lags because the rods are sluggish, and it is dark because rods are insensitive to red. Conversely in many conditions certain of the blue spots had an illusory "light twin" following it. This twin is light because the rods are very sensitive to blue. Thus each spot, red or blue, was followed by its own trailing photographic negative, like a comet's tail. Red spots and blue spots had twins at the same red/blue ratios, namely when red was slightly lighter than blue in photopic (cone) vision, but darker in scotopic (rod) vision. These are just the conditions predicted by our Purkinje shift model.

#### *Rod delays*

In a follow-up experiment (not shown) we measured the physiological delay of the light or dark twin by rotating a single red spot on a blue surround, or vice versa. Two

observers adjusted the size of the spot until the spot and its twin were separated by one spot diameter, that is, they appeared just to touch. Converting this spatial lag into a temporal lag, we found that the rod response lagged the cone response by 53 ms for a red spot on a blue surround, and by 52 ms for a blue spot on a red surround. This is consistent with previous estimates of rod/cone relative latency, beginning with MacDougall (1904).

#### *Flutter*

Luminances that gave flutter are shown as filled square symbols in Figure 2a,b. Note that these occur at about the same luminances that gave light or dark twins; namely when the red spots were lighter than the blue in cone vision, but darker than the blue in rod vision. This gives the contrast reversal that we expect and observe.

#### *Motion reversals*

We did find the predicted reversal of apparent motion, and as Fig. 2 shows, the conditions for observing it are the same as for flutter and twinning. This is expected if as we suggest, the rods are more sluggish than the cones and represent the spots with opposite spatial contrast. None of the other accounts of fluttering hearts can predict this finding. The motion reversal of Movie 2 is most clearly apparent at around 2 Hz for the four frame cycle shown in the Figure. The appearance of the reversal at this relatively low temporal frequency is consistent with our interpretation if the rod phase lag is 50-60 ms. At 2Hz the successive frames of the four stroke cycle are separated by 125 ms, and a rod lag of roughly half that interframe interval interpolates the 'rod' image neatly between the successively arriving cone images.

In addition to the motion reversal illustrated in Figure 1 and Movie 2, we have also noted a second, related motion reversal illusion at a higher temporal frequency. This occurs when a counterphasing blue/black grating alternates with a counterphasing red/black one in spatial and temporal quadrature, under parafoveal observation at the mesopic luminances of Figure 2. At frequencies around 8Hz, under steady fixation, the perceived direction of motion is unmistakably and consistently reversed. Here the phase lag of the rods relative to the cones is close to two frames, or half a cycle. Each red grating frame is thus perceptually followed not by the actually following blue grating, but by the previous one (with its opposite spatial phase) and the resulting direction of apparent motion is opposite to the actual one. Despite the large difference in temporal frequency, both our motion reversals are readily explainable by the same lag of the rod signal.

#### *General remarks:*

1. In Fig. 2, blue is plotted on the x axis, red on the y axis. Results for blue spots on a red surround were similar to those for red spots on a blue surround, so both data sets have been plotted together without distinction in Fig. 2.
2. There were clear differences between the two observers; for deuteranomalous observer DM (Fig. 2a) all the datum points lay close to a single straight line, whereas for normally sighted SA (Fig. 2b) they were diffused over a sausage-shaped area. However, for both observers and in all conditions, the data points fell within an elongated area whose long axis lay at 45° (unit slope). In deuteranomalous observers, the photopic isoluminance point is more well-defined than in normals, since the contributing L and M



cones share almost the same spectral sensitivity; this may account for the tighter luminance distribution for DM.

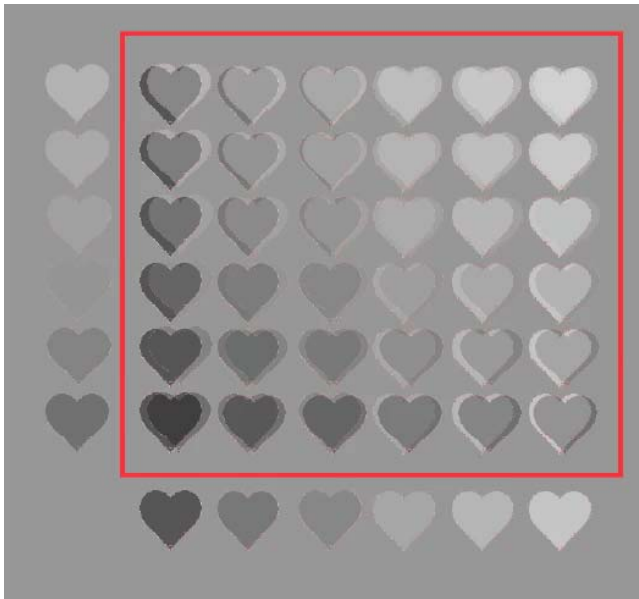
3. The data points were bounded by the two lines of unit slope shown on the graphs. The lower line (labeled ‘photopic’) shows the locus of points where blue (x) and red (y) had the same *photopic* luminance. It is simply the line of equality between the photopic luminances used for the vertical (red) and horizontal (blue) coordinates. The upper line (labeled ‘scotopic’) shows the locus of points where blue and red had the same *scotopic* luminance.

4. The fact that all the data points lay between the two unit-slope lines shows that for *all* our results the reds looked lighter than the blues to the retinal cones, but reds looked darker than the blues to the rods. This supports our theory in that the stimulus polarity looked opposite to the rods than to the cones on all trials for all three illusions.

5. The overall intensity range spanned as the intensities of red and blue are varied together is the range of mesopic vision where both rod and cone signals are important. Within that range we probed a wide range of red/blue ratios, but our data do not fill the whole area between the lines of scotopic and photopic isoluminance. Instead the illusions are most apparent under a narrowly constrained condition of mesopic isoluminance, that occurs when the luminance profile seen by rods is opposite to that seen by cones; although not easily diagnosed by flicker photometry, we could recognize the point of mesopic isoluminance under the conditions of Figure 2 by a characteristic loss of border distinctness (Boynton and Kaiser 1972) and an increased tendency to fading (Frome, Buck and Boynton, 1981) when the adjacent red and blue fields were in a critical intensity ratio. Raphael and MacLeod (2011) have documented the validity of this minimally distinct border criterion a measure of isoluminance under mesopic conditions, and they find that as in earlier work using flicker (MacLeod, 1972), the mesopic luminance signal can be modeled as a sum of rod and cone contributions. Accordingly the condition of mesopic isoluminance, as recognized by minimal border distinctness, occurred at a blue/red intensity ratio intermediate between the scotopic and photopic lines of Fig. 2, and it was at just that ratio that the phenomena of Figure 2 were most apparent.

## Experiment 2: A photopic analog

Experiment 2 *simulates* our hypothetical account of fluttering hearts. We suggest that each moving red spot on a blue surround provides a double retinal image, namely a light spot (seen by the cones) followed by a trailing but overlapping dark spot (seen by the rods). Movie 3 illustrates the principle of this experiment by *simulating* the mesopic rod and cone signals under photopic conditions in an array of hearts, each consisting of a light gray heart followed by a trailing but overlapping dark heart. These stimuli clearly show the apparent wobbles and speed variations that are characteristic of fluttering hearts.



**Movie 3** Simulation of positive and negative hearts sliding over one another. The hearts in the x-axis array form six columns, ranging from dark on the left to light on the right. The y-axis array forms six rows, ranging from dark at the bottom to light at the top. The x array and the y array move back and forth horizontally across each other. Result: Hearts seem to flutter every which way.

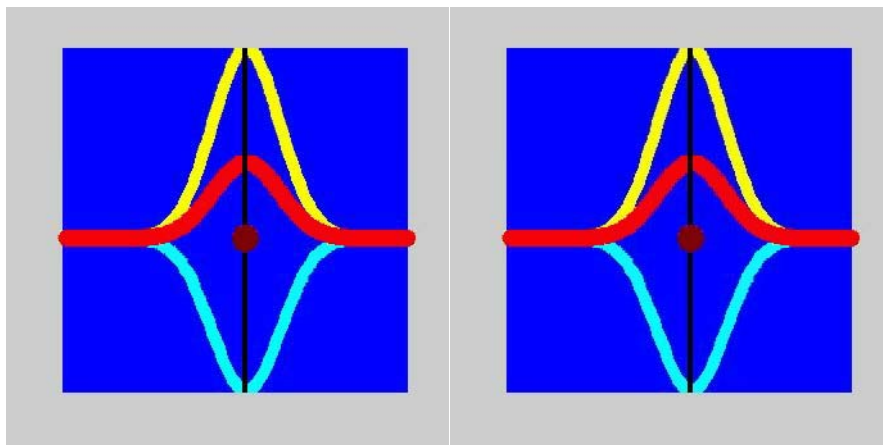
In Movie 3, superimposed positive and negative hearts are sliding over one another. The two square arrays of 6 x 6 hearts, as shown on the x axis and y axis respectively, slide horizontally back and forth across one another in counterphase. The movements are rigid, so if geometry were the only factor then the pattern should be seen to move all of a piece. In fact, however, the hearts seem to “flutter” and move every which way. The positive diagonal runs through the top-right and bottom-left quadrants. In these two quadrants, hearts of the same polarity move back and forth across each other, and look like hearts that expand and contract slightly (“beating hearts”?) while staying more or less in place. The top-left and bottom-right quadrants, on the other hand, which are bisected by the negative diagonal, are filled with overlapping pairs of hearts of opposite polarities. These correspond in our model to the rod and cone images of red hearts moving on a blue surround. The motion of these opposite-polarity pairs is akin to “reverse phi” (Anstis 1970: Anstis & Rogers 1975, 1986: Edwards & Nishida 2004: Bours, Kroes & Lankheet 2009), often running in the opposite direction to the same-polarity pairs, or to one another, depending on whether the light or dark heart has greater contrast (compare, for instance, the heart in column 3, row 2 with the diagonally reflected one in column 2, row 3, or compare the heart at the bottom right corner of the matrix with the one immediately above it). Such reversals in direction (or phase) are characteristic of fluttering hearts. The component hearts in the margins of Movie 3, along the x and y axes, move rigidly with the overlapping hearts, yet the latter often appear to move with a greater amplitude

than their components: matching experiments showed that it can be almost doubled.

When fluttering hearts are seen under mesopic conditions, we find that multiple hearts side by side may appear to move relative to one another just as the photopic simulated hearts do in Movie 3; this phenomenon contributes to the impression of flutter.

The relative motion of the hearts in Movie 3 is due to their variation in physical luminance. If, as we propose, the relative mesopic luminance of heart and surround is critical for the heart's perceived motion, the relative movement in an array of mesopic hearts may originate, analogously, from the retinal variation in relative *effective* luminance of the hearts relative to the surround. For an array of red hearts on a blue surround, whichever heart is directly fixated looks pale pink, whilst more peripherally viewed hearts look much darker relative to the blue surround; the brightness of the blue surround is greater in the periphery because the periphery is not only rod-rich but is devoid of the blue-absorbing macular pigment. In Movie 3, the opposite contrast components of the image oscillate in opposite phase, whereas with fluttering hearts, substantial common motion is combined with the relative motion arising from latency differences. The relative motion of different hearts helps make the relative motion salient, but the exaggerated motion of a single heart near mesopic isoluminance can also be noticed in relation to the relatively stable framework provided by high contrast contours in the image.

Why is contrast polarity critical for flutter? After all, even if rods and cones see the same contrast with different latency we might expect the latency difference to create a certain amount of relative apparent motion of red and blue. A key point, in our view, is that under conditions where the rod intensity profile and the cone luminance profile are opposite in polarity, both the effective latency difference and the spatial displacements of a moving spot can be considerably magnified through the reinforcement or partial cancellation of rod and cone signals.



**Movies 4a and 4b.** This movie simulates the mesopic rod and cone responses to a bright red spot (4a) and a dark red spot (4b) on a dim blue surround. In Movie 4a, the yellow and cyan curves represent the

excitation profiles of cones (in yellow) and rods (in cyan), drawn as Gaussians to reflect optical and neural blur. See text.

In Movies 4a and 4b, the red spot is an increment for cones and a decrement for rods. Hence the yellow curve indicates a spatial increment, the cyan one a decrement. The resultant mesopic luminance profile (red curve) is the sum of the rod and cone profiles, and in this case, is represented as a spatial increment: the incremental cone signal is only incompletely cancelled by the decremental rod signal. As the stimulus spot moves between the positions shown by the vertical lines, the cone and rod excitation profiles respond with different latencies. Critically, the peak of the resultant red curve springs across more rapidly than the cone signal alone, and overshoots its final destination. The center of gravity of the mesopic luminance contrast profile undergoes a similar but still greater overshoot. Movie 4b shows the same three curves, but adds a fourth, dim red curve to represent the decremental mesopic luminance profile expected if the red spot has a mesopic luminance dimmer than the surround (because now the decremental rod signal outweighs the incremental cone signal). In this case the mesopic luminance profile is a spatial decrement, shown by the dim red curve. The bright red curve for a mesopic increment is copied from Movie 4a to facilitate comparison of the two cases. The dim red spot behaves quite differently than the bright one: it moves initially in the wrong direction, and lags behind even the rods in reaching its eventual destination. The spatial profiles associated with the rod and cone systems were obtained by convolving the stimulus disc with a spatial Gaussian. The stimulus time courses were convolved with temporal weighting functions of the form  $t \cdot \exp(-t/\tau)$  for both rods and cones, with  $\tau$  set to delay the temporal centroid by 10 frames for rods and 20 frames for cones; the corresponding real world delays are 50 ms and 100 ms respectively if we assume 5 ms per frame. On that basis, the movie is a slow motion depiction of a stimulus oscillation at about 1 Hz.

This can be seen in Movie 4a, where the yellow and cyan curves respectively represent the luminance profiles of the red spot against its blue background as seen by the cones and the rods respectively. The spot appears as an increment to the cones and a (slightly weaker) decrement to the rods, and each profile is broadened into a smooth curve by optical and neural blur. The sum of the rod and cone responses gives the mesopic luminance profile, a net increment shown by the red curve. When the stimulus spot moves between the positions indicated by the vertical black line, the cones respond quickly and the rods more slowly. The mesopic profile behaves in a more complex manner than either of those. It leaps ahead of the cone response, and its peak clearly overshoots the new position before relaxing back to an accurate steady state location. This nonrigid motion of the mesopic luminance profile (also evident in our photopic analog, Movie 3) may underlie the ‘springing’ quality of flutter described by Baldwin (1901). The overshoot arises because a submaximal cone response momentarily yields the peak net response when the delayed rod response is subtracted from it. If the red heart is made slightly dimmer, the decremental response of the rods (cyan) becomes greater than the incremental response of the cones (yellow) (Movie 4b). Now the behavior is very different. Rather than leaping ahead of the cone response, the predominantly rod-driven net response (dark red curve) is further slowed through

cancellation by the quick but opposite response of the cones. Indeed, it initially moves in the wrong direction, and takes a much longer time to reach its destination than even a pure rod response would do.

Although the addition of rod and cone excitation profiles in space and time is a simple theoretical postulate, the resulting profiles are complex enough to complicate quantitative predictions. When the targets are small, as is typical for fluttering hearts, the range of spatial integration in the motion-sensing system may be comparable with the size of the target. This was the assumption employed in making Movie 4. On that assumption the movement of the spatial peak of the mesopic luminance profile can exceed the actual stimulus excursion by an amount comparable with the receptive field radius with which the target's image is convolved, and the spatial centroid of the luminance profile can undergo larger excursions even than that. If, on the other hand, optical and neural blur are slight enough that the edges of the heart are localized independently—for instance using the inflection points of the excitation profile—the theoretically expected exaggerations of motion are relatively modest. In all cases, however, the temporal phase of the resultant motion can differ greatly from the stimulus phase. The simulated perceptual latency can vary by several times the rod-cone latency as target luminance varies across the point of mesopic isoluminance, much as illustrated in Movie 4. This exaggerated temporal phase shift, which was confirmed in separate experiments to be reported separately, must also contribute to the fluttering hearts phenomenon..

## **Discussion**

A simple model involving only static neural blurring can readily explain the perceptual phenomenon of enhanced or reversed displacement (Movies 3 and 4). These experiments do not involve the latency difference that is essential to the fluttering hearts phenomenon, but the simulations of Movie 4 show how the moment-by-moment addition of differently delayed signals from a moving stimulus can in principle generate similarly exaggerated or reversed perceptual displacements. A single red heart, moving in mesopic conditions, generates superimposed positive and negative pictures of the kind we have just simulated. Since a jiggling display of numerous red hearts will lie on different and non-uniform retinal areas, with more peripheral rod-rich regions responding more strongly to blue, we can suppose that the effective mesopic luminance contrast will differ for different hearts, so that different individual hearts will appear to move with different amplitudes, and some in opposite directions. In short, they will exhibit the complex motions that we call flutter.

The three illusions we report – light and dark twins, fluttering hearts, and reversing gratings – occurred for identical luminance ranges of red and blue (see Fig. 2). We conclude that they all have the same underlying causes. The spatial lag of the twins behind their spots shows that the rod response lagged the cone response by ~52 ms. The luminance reversal in the lagging twins – dark for a moving red spot, light for a moving blue spot – shows that the Purkinje shift in the rods reversed the perceived luminance polarities of the twins. Flutter was seen when a spot moved back and forth over its

overlapping photographic negative. The same lag and shift in the rods also explains the perceived reversal of the red/blue moving grating.

The fluttering hearts stimulus can exhibit a relatively subtle perceptual instability at luminances exceeding those of Figure 2 where full-fledged flutter is evident. If this happens under conditions where rods make no contribution (a question that we have not endeavored to examine), the relatively slight difference in latency between the L and M cones that contribute to photopic luminance might account for it on the same principles that apply in the mesopic situation.

In conclusion, von Kries (1896) came close to the truth just over a century ago, but it is the fact that the retinal cones and rods register the red/blue stimuli in opposite and partially cancelling luminance polarities that fully accounts for the fluttering hearts illusion.

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