
Reversed visual motion and self-sustaining eye oscillations

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Abstract. A random-dot field undergoing counterphase flicker paradoxically appears to move in the same direction as head and eye movements, ie opposite to the optic-flow field. The effect is robust and occurs over a wide range of flicker rates and pixel sizes. The phenomenon can be explained by reversed phi motion caused by apparent pixel movement between successive retinal images. The reversed motion provides a positive feedback control of the display, whereas under normal conditions retinal signals provide a negative feedback. This altered polarity invokes self-sustaining eye movements akin to involuntary optokinetic nystagmus.

1 A paradoxical motion effect

When looking at a random-dot field undergoing counterphase flicker (contrast reversal), we noticed a striking effect: the entire field of dots appeared to move with each eye and head movement. Paradoxically, the apparent motion of the dots was always in the *same* direction as the movement by which it was induced, ie opposite to the optic-flow field. The stimulus was a dense random-dot pattern, 50% black and 50% white, repetitively reversed in contrast so that every black dot became white and every white dot became black. In other words, the stimulus alternated rapidly between two patterns that were photographic negatives of each other. The contrast reversal gave the pattern a lustrous appearance not unlike that of binocular rivalry (Burr et al 1986). The contrast-reversing stimulus was displayed on the monitor of a Macintosh IIx computer.

Tracking a finger as it moves to the right across the display produces vivid coherent motion of the dots to the *right*. Similarly, tilting or rotating the head clockwise induces apparent clockwise rotation of the dots. Moving the head forward (or away from) the screen makes the field of dots appear to contract (or expand), with the fixation point as the centre of the flow field. Associated with these flow fields is a strong apparent depth movement zooming into or out from centre. The perceived motion is very robust except for a large central area which does not partake in the flow. It is most striking for frequencies ranging from about 10 Hz to 50 Hz and is seen over a wide range of pixel sizes, 0.65 to 65 min arc (46 to 0.46 cycles deg⁻¹). Furthermore, it occurs over a wide range of contrasts ($C = 0.86$ – 0.33 tested) and mean luminances, and is little affected by blur (+3 D glasses removed). Motion opposite to the direction of pattern displacement also occurs when the monitor is moved relative to the subject. Thus, when the monitor is moved to the right (simulating an eye movement to the left) with the head and eyes held steady, the random-dot pattern appears to move to the left. This observation rules out a contribution from the vestibular system, or from efference copy.

The paradoxical motion effect described here can be elicited by any smooth directional shift of the contrast-reversing random-dot field on the retina, as is brought about by head and eye movements. This statement is consistent with (i) the smooth movement perceived with translation of the eye (during tracking of the finger); (ii) the striking rotary effect when the head is tilted or rotated in the frontoparallel plane; and (iii) the strong contraction or expansion (and perspective depth effects) when the head moves towards or away from the screen. When the eyes are fixating a stationary target within the noise field, translation of the head is ineffective, because there is little displacement of the retinal image. On the other hand, the paradoxical effects caused by head rotation and to-and-fro motion are unimpaired.

All these observations may be confirmed in a large hemisphere where the dynamic random dots fill the entire visual field and where there is no frame of reference (eg the stationary window provided by the monitor). Under these conditions, the effect is quite pronounced: head and eye movements lead to an apparent motion of the dots all across the visual field. So does visual pursuit of a moving fixation point (courtesy of Dr M Lappe).

The finding that the paradoxical motion effect can be seen simultaneously in all directions ('inward or outward zooming') cannot be explained by an oculomotor process. The apparent shrinkage and expansion of the field as the head moves to and fro rules out an explanation based on eye movements for the same reason as the demonstration of a motion aftereffect with the use of a rotating spiral. To explain why the dots appear to move in the *same* direction as the observer (ie opposite to the optic-flow field), we invoke reversed phi movement. Anstis (1970), and Anstis and Rogers (1975) have shown that any black-and-white pattern moving slowly from left to right will appear to move in the opposite direction if the contrast of each pixel is periodically reversed. For an explanation they propose a backward shift of the peak of the superimposed luminance profiles combined with a smoothing of the edges (their figure 3). They call this 'reversed phi' motion. Eye movements in any one direction combined with contrast reversal of a random-dot pattern will produce the spatiotemporal sequence which elicited reversed phi in Anstis and Rogers's (1975) experiment, ie opposite to the flow field. To elicit the effect, the angular speed of the eye and head must be appropriate to the frequency of contrast reversal and dot density.

Figure 1 is an $x-t$ plot that illustrates how coherent apparent movement is produced by the interaction of a given dot with its nearest same-contrast neighbour each time the frame is changed. Space runs across the page (from left to right), time down the page, and each row represents a new time frame, shifted by one pixel to the right with respect to the previous row. This shift simulates an eye movement to the left. The top row of randomly chosen black and white dots is identical in figures 1a and 1b. In figure 1a the shift of each successive row to the right yields a percept of apparent motion to the right, visible here as random-width columns of black and white dots sloping down to the right. In figure 1b the dots reverse in contrast on every frame, being 'positive' in rows 1, 3, 5, 7, ... and 'negative' in rows 2, 4, 6, 8 As a result, apparent movement is seen to the *left*, opposite to the direction of physical displacement. This 'reversed phi' (Anstis 1970; Anstis and Rogers 1975) is visible in figure 1b as a series of irregular black and white zig-zagging lines sloping down to the left. The velocity of the reversed phi is a complex function of spatial and temporal frequency, as can be seen from the slopes of the zig-zag lines in figure 1b which vary irregularly over space and time.

By comparing two adjacent rows it can be seen that, on average, the nearest neighbour of the same polarity is found to the left. In some cases, the nearest neighbour in one row is found directly below a same-polarity pixel in the row above it. However, in no case is there a nearest neighbour of the same polarity to the right. Thus, on average one

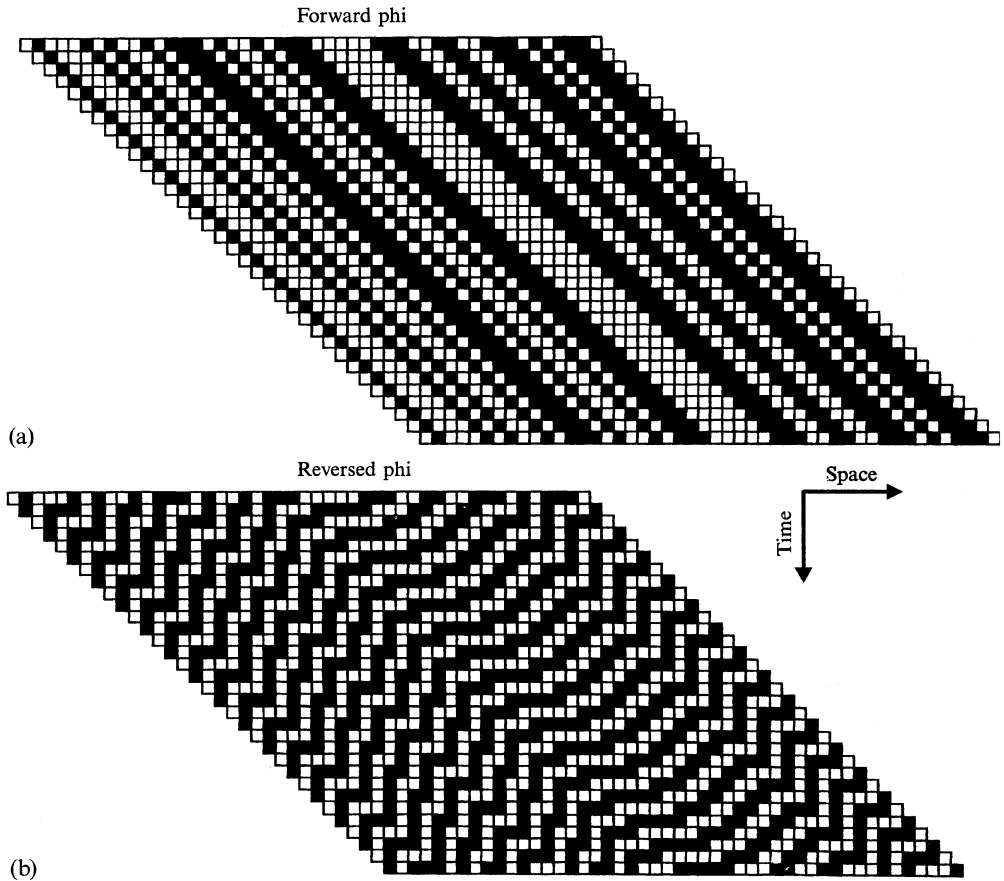


Figure 1. (a) Apparent motion to the right. (b) Reversed apparent motion is seen to the left.

would expect to see an apparent movement of the field of dots to the left, ie reversed phi. This explanation is consistent with Anstis (1970).

The varying distance between neighbouring pixels of equal sign in figure 1 does not seem to be a hindrance, as there are always enough pixels to link up with to provide an overall impression of coherent motion. Newsome and Paré (1988) have shown, in the monkey, that only a small percentage of spatially distributed coherently moving dots in a dynamic random-dot field is needed for perceiving global motion. In our experiment, the group of motion detectors that is stimulated the most will dominate the percept. However, because of the different distances between neighbouring pixels the resulting movement is not perfectly smooth. Differences in the spatial correlation between dots show up as moving streaks ('schlieren') separated by regions where the effect is less compelling or absent.

During smooth pursuit movement, the apparent motion can assume different velocities relative to the stimulus movement by which it is induced. This can be seen best if one follows a finger moving across the random-dot screen: the dots typically seem to overtake the finger; however, given the right inducing speed, they also can stay in register or lag behind. We explain this as follows.

The random-dot pattern can, like any pattern, be regarded as the sum of a set of gratings which constitute its Fourier components. A subset of these components is shown in simplified form in figure 2a. (In practice, of course, these components would be sinusoidal, not square-wave as shown, and would include all orientations, not just vertical.)

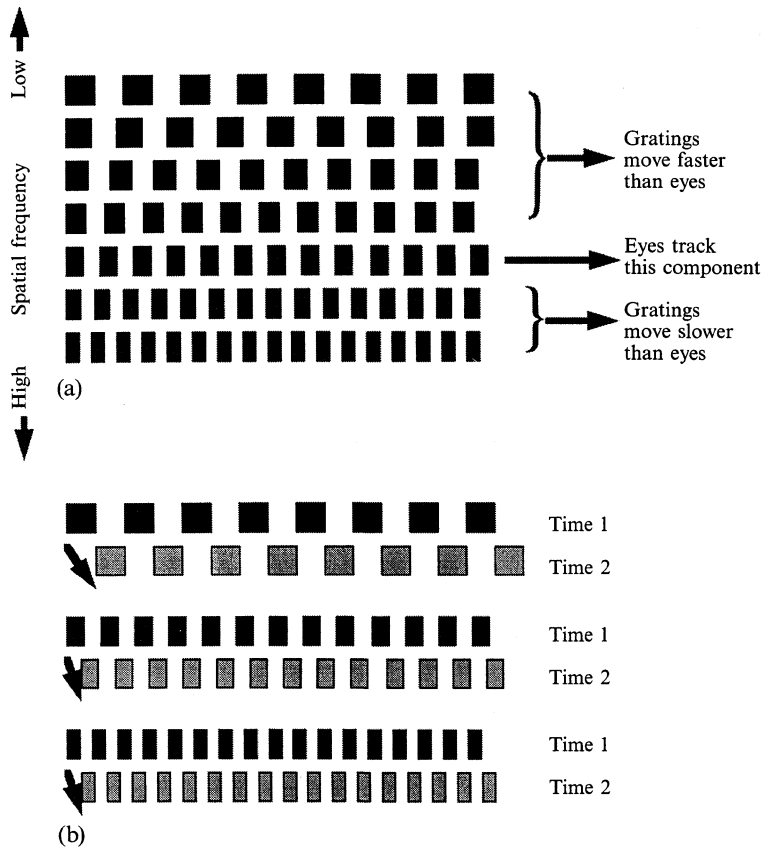


Figure 2. Fourier components of the contrast-reversing pattern.

When the random-dot pattern reverses in contrast, say on every TV frame, each Fourier component does the same. That is, every component shifts by 180° of spatial phase on every TV frame. If the array of gratings shown in figure 2a were displayed and reversed in contrast on every TV frame, an observer could arbitrarily pick any grating and track it to the left or right by moving his/her eyes at a speed of one bar width of the grating per TV frame. The coarser the grating selected, the faster the eyes would have to move. Figure 2b shows three of these components on successive frames, flashed up at Time 1 (black in figure 2b), then phase reversed, that is, shifted through one bar width, and flashed again at Time 2 (grey in figure 2b). It can readily be seen from figure 2b that whichever phase-reversing component is tracked, all the phase-reversing components that are finer than the tracked one will effectively move in the same direction as the eyes relative to the head, but more slowly; and all those that are coarser than the tracked one will also move with the eyes, but faster (see arrows). This is why the whole field of contrast-reversing dots appears to move with the eyes. However, the pattern does not appear to move uniformly as a sheet, but looks more like blowing sand or rippling water with different components moving at different speeds (eg streaks). This is to be expected from the different Fourier components.

The observer can do exactly the same with the contrast-reversing random dots. The component gratings, which are arrayed in an orderly fashion in figure 2a, are jumbled up together in the random-dot pattern. But the observer can track any frequency component in the pattern by moving his/her eyes at the appropriate velocity; the higher the spatial frequency selected, the lower the required eye velocity. We found that the

tracked target could be placed well outside the noise field, so that all the dots fell onto the peripheral retina. Yet, we still perceived the paradoxical motion.

When the amplitude of the stimulus displacement on the retina is small, contrast reversal leads to luminance averaging without apparent movement. Presumably this is the reason for the large central 'scotoma' perceived when the head is moved towards and away from the screen (zooming). Apparent motion for the central region is absent because the phase-reversed random-dot pattern is effectively superimposed onto itself, whereas in the peripheral retina consecutive images of the same pattern are displaced relative to each other, hence reversed ϕ .

Reversed motion direction continues to be seen and may actually be more vivid when a gray uniform field with a variable interstimulus interval ($ISI = 0 - 67$ ms) is interspersed before each contrast reversal, ruling out afterimages as a cause for the effect (Shioiri and Cavanagh 1990). No movement can be elicited from counter-phasing equiluminant red and green pixels, which suggests that the percept of coherent motion due to reversed ϕ requires luminance changes and perhaps activates the magnocellular pathway. Anstis (1970), Ramachandran and Gregory (1978), and Cavanagh and Anstis (1991) have shown that the motion system is relatively colour-blind and the opponent-colour system makes only a very small contribution to motion sensitivity.

The flow of movement perceived when tracking a moving target is reminiscent of the coherent motion observed with uncorrelated dynamic random-dot patterns. MacKay (1961, 1965) showed that if you track a moving finger across a TV screen filled with twinkling dynamic noise, the noise immediately surrounding the finger appears to adhere to it and move exactly in step with the finger. He also demonstrated that the noise could be perceptually captured with a wire loop, the frame-adhesion effect (1961). Here, the whole assembly of 'Brownian particles' within the loop are seen to move with it. Ramachandran and Inada (1985) extended this observation to a moving low-frequency grating, and Ward and Morgan (1978) showed that one can track a foveal region of the noise even without a helping finger. However, uncorrelated noise always appears to move at the same speed as the moving eye, as an afterimage does, whereas our contrast-reversing pattern usually appears to overtake the moving eye. The observation that the apparent motion is seen over the *entire* field, whereas in MacKay's and Ward and Morgan's experiments, it is seen only at the fovea or in areas enclosed by the moving guide, as well as the difference in perceived speed of the random-dot field, are further proof that reversed ϕ is the cause of our effect.

2 Self-sustaining eye movements

If the moving finger that elicited paradoxical motion was suddenly removed something unexpected happened: the phase-reversing pattern often appeared to continue moving, first in the same direction as the finger did and then snapping back in a repetitive sawtooth waveform. Sometimes the pattern oscillated back and forth in a pendular fashion, usually horizontally, but often vertically or obliquely, and sometimes moving along a circular or elliptical path. The reason is that the eyes were set into nystagmic oscillations by positive retinal feedback from the contrast-reversing pattern, and the pattern was perceived as moving in the same direction as the eye movements. Eye movements occasionally began spontaneously, but generally needed to be started by tracking a finger that moved across the surface of the stimulus screen. Once begun, the eye movements were self-sustaining for a short period (3–5 s), then damped down and died out. Hereafter, pursuit could not be self-initiated but had to be restarted as before with a moving finger. But on most trials the eyes moved with a sawtooth nystagmic waveform, with the slow phase generally to the right in our two observers. These sawtooth eye movements were more robust and often lasted for a minute or more.

Under normal conditions, retinal signals provide negative feedback from eye movements. When the eyes move upwards, the visual field moves downwards. Our display provided positive feedback gain. When the eyes moved upwards, the complementing display was seen as moving upwards also, in the same direction as the eye movements but faster, owing to reversed phi movement. As a result, any small corrective movement of the eyes made the error larger instead of smaller (Fender and Nye 1961). Thus, the eyes would start to oscillate at the frequency for which the phase lag around the control loop is 180° . It is not clear why the oscillations damped out. It may be that after a few cycles of oscillation the system parameters adjust themselves to correspond with the predictability of the stimulus: the phase lag is then reduced, and consequently the stability of the system increases (Robinson 1965; Carpenter 1977).

We recorded the eye movements of two subjects with an infrared movement monitor. Results are shown in figures 3 and 4 as a function of the alternation rate of the random-dot pattern and as a function of dot size.

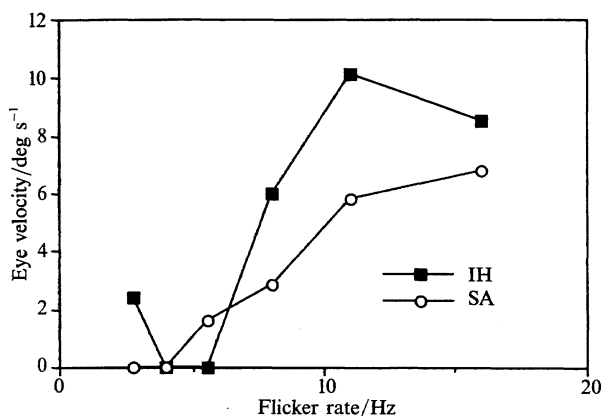


Figure 3. Effects of temporal alternation rate upon eye velocity.

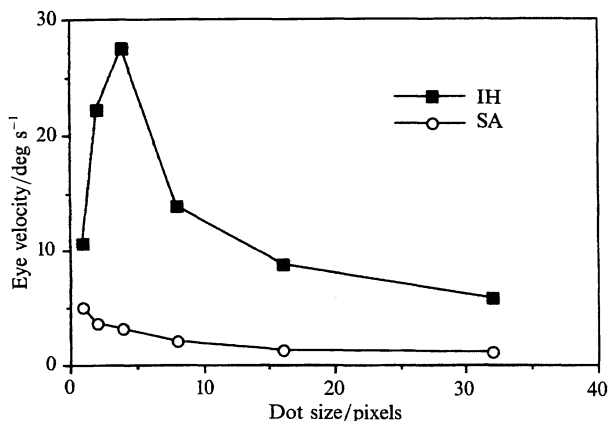


Figure 4. Effects of dot size upon eye velocity.

2.1 Temporal frequency

Mean eye velocity increased with flicker rate (figure 3), reaching a maximum at the highest alternation rate used (12–16 Hz). However, eye velocity increased more slowly than the alternation rate—it was not that the eyes moved through a constant distance on each temporal cycle regardless of velocity.

2.2 Dot size

The size of the dots was set to 1, 2, 4, 8, 16, or 32 pixels (12.6 min to 6.7 deg). Results were different for the two observers (figure 4). For subject SA, mean eye velocity was greatest for the smallest dot size, 12.6 min, and decreased gradually for larger dots. For subject IH, mean eye velocity rose steeply as dot size increased from 12.6 to 50 min, then fell with increasing dot size. In short, eye velocity for both observers was highest for rather small dot sizes. Note that the mean spatial frequency in the stimulus (x -axis) increased as the dot size became smaller (dot size = $1/\text{spatial frequency}$), and the mean spatial frequency tracked by the observer (y -axis) increased as eye velocities became smaller (the finer the grain of the tracked component, the more slowly the eyes moved).

2.3 Equivalent spatial frequency

We took the eye velocity data from the temporal frequency experiment (figure 3) and calculated the equivalent spatial frequencies for each condition. This averaged approximately 2.5 cycles deg^{-1} for SA and 1.5 cycles deg^{-1} for IH. We made the same calculations for the different dot sizes used in our experiment (figure 4), and found that IH tracked a dominant spatial frequency of 4 cycles deg^{-1} and SA tracked a frequency of 0.5 to 1 cycle deg^{-1} .

2.4 OKN or voluntary pursuit movements?

We found that eye velocity was not affected by occluding about 10 deg of the central field with a horizontal occluder. This is similar to reports for regular optokinetic nystagmus (OKN) (van Die and Collewijn 1982; Howard and Ohmi 1984; Murasugi et al 1986) and for sigma-OKN (Behrens and Grüsser 1979). On the other hand, when the upper and lower peripheral visual fields were occluded, eye velocity increased gradually with increasing height of the central horizontal field but, as reported for regular OKN (van Die and Collewijn 1982; Murasugi et al 1989), a horizontal strip of moving dots less than 10 deg high is enough to elicit eye movement. Eye velocity decreased substantially for a tall narrow field that was less than about 30 deg wide from left to right. This is also similar to reports for regular OKN (Schor and Narayan 1981; Murasugi et al 1989). The similarity between our results and those reported for regular OKN suggests that the eye movements we measured were akin not to voluntary pursuit movements controlled by the observers, but more to involuntary nystagmic movements evoked by the contrast-reversing pattern.

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References

- Anstis S M, 1970 "Phi movement as a subtraction process" *Vision Research* **10** 1411–1430
Anstis S M, Rogers B J, 1975 "Illusory reversal of depth and movement during changes of contrast" *Vision Research* **15** 957–961
Behrens F, Grüsser O-J, 1979 "Smooth pursuit eye movements and optokinetic nystagmus elicited by intermittently illuminated stationary patterns" *Experimental Brain Research* **37** 317–336
Burr D C, Ross J, Morrone C, 1986 "A spatial illusion from motion rivalry" *Perception* **15** 59–66
Carpenter R H S, 1977 *Movements of the Eyes* (London: Pion)
Cavanagh P, Anstis S M, 1991 "The contribution of color to motion in normal and color-deficient observers" *Vision Research* **31** 2109–2148
Die G van, Collewijn H, 1982 "Optokinetic nystagmus in man" *Human Neurobiology* **1** 111–119
Fender D H, Nye P W, 1961 "An investigation of the mechanism of eye movement control" *Kybernetik* **1** 81–88

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- Howard I P, Ohmi M, 1984 "The efficiency of the central and peripheral retina in driving human optokinetic nystagmus" *Vision Research* **24** 969–976
- MacKay D M, 1961 "The visual effects of non-redundant stimulation" *Nature (London)* **192** 739–740
- MacKay D M, 1965 "Visual noise as a tool of research" *Journal of General Psychology* **72** 181–197
- Murasugi C M, Howard I P, Ohmi M, 1986 "Optokinetic nystagmus: The effects of stationary edges, alone and in combination with central occlusion" *Vision Research* **26** 1155–1162
- Murasugi C M, Howard I P, Ohmi M, 1989 "Human optokinetic nystagmus: Competition between stationary and moving displays" *Perception & Psychophysics* **45** 137–144
- Newsome W B, Paré E B, 1988 "A selective impairment of motion perception following lesions of the middle temporal visual area (MT)" *Journal of Neuroscience* **8** 2201–2211
- Ramachandran V S, Gregory R L, 1978 "Does colour provide an input to human motion perception?" *Nature New Biology* **275** 55–57
- Ramachandran V S, Inada V, 1985 "Spatial phase and frequency in motion capture of random-dot patterns" *Spatial Vision* **1** 57–67
- Robinson D A, 1965 "The mechanics of human smooth pursuit movements" *Journal of Physiology (London)* **180** 569–591
- Schor C, Narayan V, 1981 "The influence of field size upon the spatial frequency response of optokinetic nystagmus" *Vision Research* **21** 985–994
- Shioriri S, Cavanagh P, 1990 "ISI produces reverse apparent motion" *Vision Research* **30** 757–768
- Ward R, Morgan M J, 1978 "Perceptual effect of pursuit eye movements in the absence of a target" *Nature (London)* **274** 158–159