
Gaze stability of observers watching Op Art pictures

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Abstract. It has been the matter of some debate why we can experience vivid dynamic illusions when looking at static pictures composed from simple black and white patterns. The impression of illusory motion is particularly strong when viewing some of the works of ‘Op Artists’, such as Bridget Riley’s painting *Fall*. Explanations of the illusory motion have ranged from retinal to cortical mechanisms, and an important role has been attributed to eye movements. To assess the possible contribution of eye movements to the illusory-motion percept we studied the strength of the illusion under different viewing conditions, and analysed the gaze stability of observers viewing the Riley painting and control patterns that do not produce the illusion. Whereas the illusion was reduced, but not abolished, when watching the painting through a pinhole, which reduces the effects of accommodation, it was not perceived in flash afterimages, suggesting an important role for eye movements in generating the illusion for this image. Recordings of eye movements revealed an abundance of small involuntary saccades when looking at the Riley pattern, despite the fact that gaze was kept within the dedicated fixation region. The frequency and particular characteristics of these rapid eye movements can vary considerably between different observers, but, although there was a tendency for gaze stability to deteriorate while viewing a Riley painting, there was no significant difference in saccade frequency between the stimulus and control patterns. Theoretical considerations indicate that such small image displacements can generate patterns of motion signals in a motion-detector network, which may serve as a simple and sufficient, but not necessarily exclusive, explanation for the illusion. Why such image displacements lead to perceptual results with a group of Op Art and similar patterns, but remain invisible for other stimuli, is discussed.

1 Introduction

Breaking with a long tradition of developing a pictorial language to represent motion on the canvas, some artists, such as Bridget Riley, began to experiment with simple black and white patterns that go beyond mere representation by actually creating vivid dynamic illusions in static pictures (Riley 1999). The physiological and perceptual mechanisms that might underlie the illusory perception of motion have been a matter of debate since the early observations reviewed by von Helmholtz (1867/1962), who emphasised the effects of the optic system on the perceived image of a set of fine radiating lines and concentric black and white circles. MacKay (1957a, 1957b) suggested that dynamic aftereffects are elicited by exposure to a pattern of radiating lines. In combination with small eye movements, the interaction between the original pattern and afterimage could lead to dynamic, ‘moiré effects’ (Gregory 1993; MacKay 1958). Focusing on the potential effects of eye movements, without necessarily assuming aftereffects, a recent computational study (Zanker 2004) simulated a biologically motivated motion-detector network to assess the motion information resulting from image displacements produced by small saccades when viewing Bridget Riley’s painting *Fall* (1963 Tate Gallery London). The motion-signal maps (ie the information provided to the brain) resulting from shifting the *Fall* painting resemble the distribution of illusory motion perceived when looking at this painting. This suggests that small random eye movements—in combination with low-level processing algorithms—could indeed provide a simple explanation for the observed phenomenon.

A slightly different explanation that also focuses on the role of extra-cortical phenomena has been proposed to account for the shimmering and deformations that can be seen when viewing the radial line patterns of the *Enigma* painting (Leviat 1996): they have been attributed to a rather trivial consequence of naturally occurring fluctuations in eye accommodation ('hunting for accommodation'—Gregory 1994). This explanation follows from an initial suggestion by Campbell and Robson (1958) about the effects of changes in accommodation on the retinal images of ray patterns, which included the prediction that paralysis of ciliary muscle or looking through an artificial pupil (pinhole) should abolish the illusion. This view was immediately challenged by MacKay (1958), who claimed that complementary afterimages are still visible with paralysed eye muscles and flashed images, thus excluding such peripheral effects; but unfortunately his description is not unambiguous about what kind of effects are observed for the perceived spatial layout ('complementary images') and the perceived motion of the pattern, respectively.

By contrast, the circular-motion sensation observed within the uniformly coloured rings of *Enigma* has been attributed to some cortical brain mechanism that does not rely on image shifts (Zeki et al 1993). This view—which was based on functional brain-imaging studies demonstrating specific activation in motion-specific human brain regions related to the perceived illusion that differs from responses elicited by eye movements—was challenged by Gregory who reported an observation that the shimmer experienced in radiating line patterns was reduced or completely abolished when such patterns were viewed through a pinhole (Gregory 1993) and that the dynamic illusion disappeared in flash afterimages (Gregory 1994). In response, Zeki (1994) reported that the circular motion in the rings of *Enigma* was not abolished when looking through a pinhole, if intensity was adjusted appropriately and when the ciliary muscles were paralysed, both of which should have suppressed any effects resulting from accommodation. Furthermore, aphakic patients who are unable to accommodate still experience this illusion despite the fact that they have artificial lenses or none at all (Zeki 1995).

It seems obvious that this scientific discourse is burdened by the fact that different authors focus on different aspects of a particular stimulus, and that it appears difficult to define precisely the phenomenon to be considered. Also, the arguments regarding the possible reasons for the motion illusions have usually been stated as alternatives that exclude each other rather than accepting that a variety of causes could lead to the same or similar effects. For instance, even if there might be residual illusory effects when accommodation is not possible and retinal images are stabilised, the strong illusion experienced by 'normal' viewers under 'everyday' viewing conditions could result from quite different neural mechanisms dealing with the consequences of retinal image shifts. Furthermore, up to now remarkably little is known about the actual eye movements made by an observer when looking at Op Art paintings under natural viewing conditions. It is easy to demonstrate that eye movements can enhance the sensation of vivid pattern motion when looking at such patterns (Gregory 1994), but how stable is the gaze when an observer tries to fixate a specific point in the stimulus?

To address some of these issues, the work presented here had three main objectives: (a) Study the motion illusions elicited by static black and white patterns in a very simple configuration, which leads to a unitary and well-defined effect. To this end we chose Bridget Riley's *Fall* as an efficient example of motion-inducing Op Art painting. (b) Identify the conditions under which the illusion is perceived and under which it disappears, to assess the importance of eye movements for this particular illusion, which could shed some light on the conflicting results reported for earlier attempts.

To collect quantitative data, we used a scale to rate the strength of the illusion for a range of geometrical configurations and different viewing conditions—such as pinhole or flash afterimage, which exclude effects of accommodation and eye movements, respectively.

(c) Measure the actual eye movements that observers make when looking freely at Op Art paintings and control patterns that do not elicit motion illusions. This will help us to assess the potential consequences of retinal image shifts on the information provided for the visual cortex and thus can be related directly to brain mechanisms that may be responsible for the illusion.

Here we report some basic findings about gaze stability under natural operating conditions for a comparatively large sample of observers.

2 Methods

Four staff members from the Department of Psychology at Royal Holloway, who were experienced psychophysical observers but naïve to the purpose of this experiment, and two of the authors took part in the psychophysical experiments (ages ranging between 29 and 46 years, 36 years on average, all with normal or corrected-to-normal vision, without any known ophthalmic disorders). Nine naïve volunteers from the Department of Psychology student population at Royal Holloway, and two of the authors took part in the oculomotor experiments (ages ranging between 20 and 56 years, 30 years on average, all with normal or corrected-to-normal vision, without any known ophthalmic disorders). The experiments were approved by the College Ethics Committee.

For the first psychophysical experiments, line patterns similar to Bridget Riley's painting *Fall* were generated by a computer program (written in C under Windows 2000) to be presented for 5 s on the computer screen (Sony Trinitron 17sf II, image size 512 pixels \times 512 pixels, 16 cm \times 16 cm). Observers freely viewed the monitor with both eyes at normal reading distance (approximately 45 cm) and used the mouse to click on one of five buttons in a control window to enter their scores and trigger the next trial. The scores of 1, 2, 3, 4, and 5 reflect the perception of a static image, a weak, intermediate, strong, and very strong motion illusion, respectively. The stimulus patterns were generated by means of a simple algorithm modulating the intensity I of a basic sinusoidal grating along the horizontal axis x with a period λ , with grey levels varying between 0.0 (black) and 1.0 (white), according to the formula

$$I(x, y) = 0.5 \left\{ 1 + \sin \left[2\pi \frac{x - \phi(y)}{\lambda} \right] \right\}. \quad (1)$$

The phase of the sine-wave function ϕ , is modulated sinusoidally along the vertical axis y , as described by the function

$$\phi(y) = A \sin \left[2\pi \frac{y}{\mu(y)} \right], \quad (2)$$

with a phase modulation amplitude A , and a phase modulation period μ , decreasing linearly between a maximum at the top and a minimum at the bottom of the pattern according to the formula

$$\mu(y) = \mu_{\text{top}} + y \frac{\mu_{\text{top}} - \mu_{\text{bottom}}}{y_{\text{top}} - y_{\text{bottom}}}. \quad (3)$$

The crucial parameters that influence the appearance of such 'riloid' patterns are the fundamental grating period λ and the phase modulation period μ . With appropriate parameters ($\lambda = 5$ pixels, $A = 32$ pixels, μ varying between 400 pixels and 130 pixels), a pattern is generated that closely approaches the appearance of the original Riley painting.

In the second psychophysical experiment, observers viewed a poster of Riley's painting *Fall* (50 cm × 50 cm image size; ©2000 Tate Gallery Publishing Ltd) from a viewing distance of 100 cm (leading to an angular size of 27.0 deg × 27.0 deg). The strength of the illusion was compared, with the same rating scale, for three viewing conditions. First, the room light was switched on after a short period in the dark, to rate the illusion strength with free binocular viewing and similar dynamic conditions as in condition three. Second, observers were looking at the poster in full light, with their dominant eye, through a pinhole (1 mm diameter, drilled into a thin black carbon sheet), to minimise the effects of accommodation. Third, an afterimage of the painting was created by means of a photographic flashlight (Vivitar 283) after a 2 min period of dark adaptation, to rate the illusion strength with a stabilised image. For this experiment, ratings were recorded manually by the experimenter.

For the oculomotor experiments, digitised versions (600 pixels × 600 pixels) of Riley's painting *Fall* (see figure 2a for a similar pattern) were presented on a computer screen (image size 24 cm × 24 cm, viewing distance 50 cm) spanning 27.0 deg × 27.0 deg (0.046 deg pixel⁻¹ in central regions). In comparison, at a viewing distance of 2 m a visitor of the Tate Gallery would see the painting spanning approximately 35 deg × 35 deg. In order to find out whether eye movements would critically depend on any of the most obvious geometric features of the display, the image was presented in four different orientations (vertical upright, vertical upside down, tilted left by 90°, and tilted right by 90°). Observers were instructed to fixate either the region in which the spatial phase of the lines is modulated with high spatial frequency [high-frequency modulation (HFM), left image region in figure 2a] or the region with low frequency of phase modulation [low-frequency modulation (LFM), right region in figure 2a]. Each of the eight images was viewed for 10 s. To guide the observers and help them fixate, a red spot (4 pixels × 4 pixels wide, eccentricity of 8.2°) was presented in the first 5 s within each block at the target location. Because we did not know whether the fixation target as such would interfere with the eye movements, the fixation target disappeared after 5 s and the observers were instructed to keep steady fixation for the remaining 5 s of the trial. At the end of each trial the stimulus pattern disappeared and a central fixation target appeared in front of a grey blank field, and after a short break (0.5 and 5 s) the next trial was initiated by the experimenter. All data analysis was restricted to the periods during which the stimulus pattern was presented. In the control trials, a blank grey field was presented for the first four trials and a black and white checkerboard pattern (16 fields × 16 fields) for the last four trials. These patterns were chosen because they obviously do not lead to any motion illusion, and represent two extremes, containing clearly visible and large contours that should strongly support gaze stabilisation, and no contours at all, offering the eye no support for stabilisation in the background pattern. The same set of fixation target locations (upper, lower, left, and right) was used as in the test condition, and identical timing and protocol were used.

Eye movements were recorded binocularly at a rate of 250 Hz with a head-mounted infrared video-based eye tracker (Eyelink SensoMotoric Instruments). Observer's head position was stabilised by means of a forehead–chin rest. For an initial data analysis the eye tracker software was used to detect saccades, with default criteria (amplitude > 0.3 deg; speed > 30 deg s⁻¹; acceleration > 8000 deg s⁻²), but smaller saccades were not detected (see figure 2). Therefore the first and second temporal derivative of the eye position were calculated directly from the horizontal and vertical components, with the use of a three-point difference algorithm, and a five-point sliding window with triangular weights to smooth the data. The instantaneous angular eye speed (movement vector length independent of direction) and acceleration were calculated, and the saccade displacement (amplitude and direction) was determined as 2-D-position difference

between the first and last point of the saccade, defined as acceleration growing beyond 500 deg s^{-2} and returning back to base fluctuations from decelerations larger than -500 deg s^{-2} , respectively. Initial fixation saccades and eye blinks were removed from the analysis by setting a maximum amplitude criterion of 5 deg, and very small saccades in the range of measurement noise were excluded by a minimum threshold of 0.2 deg displacement. This simple procedure picked up all clearly visible saccades, as was verified by individual inspection of the raw position traces, and the peak velocities and accelerations of all detected saccades clearly go beyond the noise levels of these respective variables.

3 Psychophysics

The first psychophysical experiment was designed to establish a perceptual scale for rating the strength of the motion illusion. A set of different ‘riloid’ patterns that should cover the full range of illusion strength was generated by varying the amplitude of phase modulation [parameter A in equation (2)] in the range between the values of 32 pixels and 0 pixels (straight sinusoidal gratings), in steps of 8 pixels, and setting the other parameters close to the configuration of Riley’s painting ($\lambda = 8$ pixels, μ varying between 400 and 130 pixels). After a 5 s inspection time, observers were asked to rate the strength of the perceived illusion in relative units between 1 (static) and 5 (very vivid movement). Five trials for each of the five configurations were presented in random order. The average scores for all six observers are plotted in figure 1a as function of modulation amplitude A , showing for all observers a very clear growth from values close to 1 at $A = 0$, ie an unmodulated grating perceived as static, to values between 4 and 5 at $A = 32$, strong illusory-motion effects associated with large modulation depth. Illusion strength appears to grow steadily with modulation amplitude, suggesting that observers are using the subjective scale appropriately to report a gradation of the perceptual phenomenon, and seems to level off at values above 20 pixels, which corresponds to the introspective reports that the motion illusion gets so vivid in some of these patterns that no differences can be detected any more.

Having established the validity of this rating scale, we used it to test whether the strength of the illusion depends on the orientation of the painting, ie whether the HFM of grating needs to be at the bottom, as originally intended by the painter. ‘Riloids’ ($\lambda = 6$ pixels, $A = 24$ pixels, μ varying between 400 and 130 pixels) were generated in four orientations: 0° —HFM down; 90° —HFM right; 180° —HFM up; and 270° —HFM left. The scores (average of five trials for each condition) are plotted for all six observers in figure 1b as a function of pattern orientation, which suggests no consistent pattern of preference for any of the configurations—you can hang your Riley in whatever orientation you like!

With the second psychophysical experiment we intended to establish if eye movements are required in order to experience the motion illusion when watching the *Fall*, and what kind of eye movements might be relevant. The critical condition involved the inspection of the afterimage (which is stabilised in retinal coordinates) of a poster showing Riley’s painting, created by a strong photographic flash after dark adaptation. Because it is difficult to suppress attempts to fixate particular regions in the afterimage, these afterimages lasted only a few seconds—but during this period all observers saw the lines crisp and clear, without any indication of shimmer, swaying, or jazzing. This is reflected by the consistently low scores, very close to 1, shown in the right set of columns in figure 1c. In comparison, shortly after switching on the light in the experimental room, which initially should create a similar transient stimulation as the flash afterimage, but does not prevent eye movements from generating retinal shifts, the illusion is experienced with full strength, as indicated by the high scores close to 5 in the left set of columns in figure 1c.

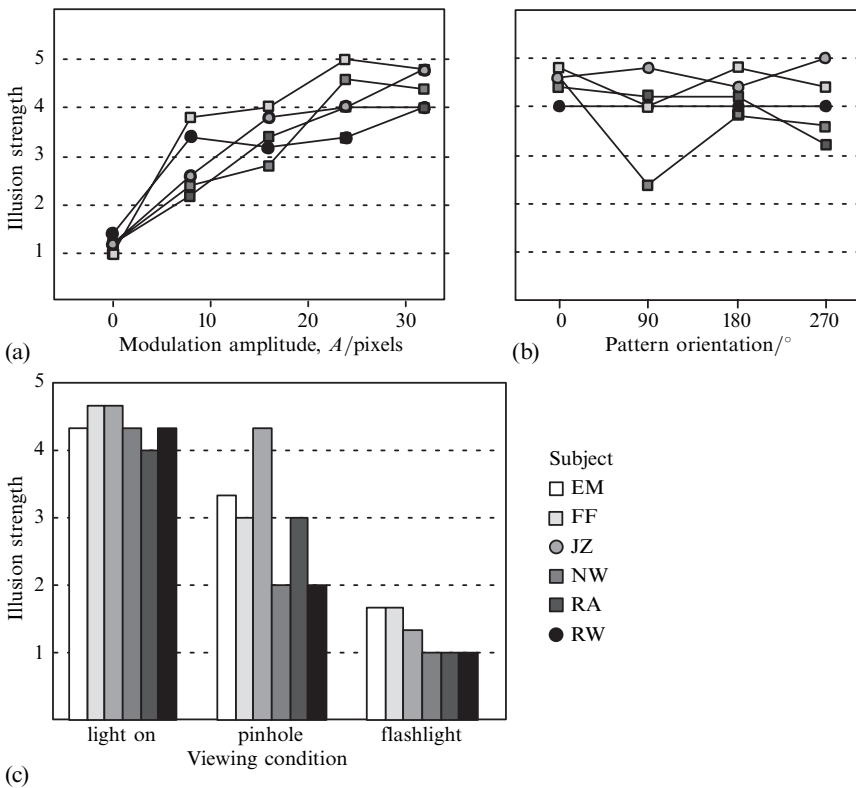


Figure 1. Results of psychophysical experiments in which observers ranked the strength of the perceived motion illusion on a scale between 1 (static) and 5 (very strong motion). (a) Illusion strength as a function of phase modulation amplitude A . Averages from five trials for each condition are shown for six observers (indicated by different grey-level symbols, see legend). (b) Illusion strength for four different orientations of the pattern. Averages from five trials for each condition are shown for six observers. (c) Illusion strength for normal viewing conditions, for looking at the pattern through a pinhole, and or inspection of a brief stabilised image (flash afterimage). Averages from three trials for each condition are shown for six observers.

Finally, the scores in the range between 2 and 4 in the middle set of columns in figure 1c quantify the intermediate percept when looking at the well-illuminated poster through a pinhole; this should minimise the consequences of accommodation fluctuations, because the artificial pupil effectively sets the depth of focus to infinity. Introspective reports from the observers indicate that the quality of the illusion seen through the pinhole differs from that seen without such restrictions, being slightly smoother and having less shimmer, but the lines are clearly perceived not as static, but as moving back and forth, perhaps in more of a swinging fashion. The fact that the image is not perceived as completely static suggests that 'hunting for accommodation' cannot be the full explanation for the illusion, but the fact that it is less strong than in free viewing indicates some contribution of accommodation. It is important to note that the remaining small eye movements, which are possible when looking through the pinhole, and thus would lead to retinal image shifts, are the most likely candidates to account for the illusion perceived under such restricted viewing conditions.

4 Eye movements

The main focus of the present study was to analyse the eye movements made by observers under natural operating conditions when viewing Riley's *Fall* for an extended period of time. On stimulus onset, observers moved their eyes from central fixation to the location of the small fixation target by making one or two large saccades. Fixation was maintained in this region for the rest of the trial and after the disappearance of the fixation target. From the overlaid scan paths from four trials with different target locations (shown in figure 2a) it can be seen that this typical observer (JMZ) maintained a somewhat unsteady eye position within a region of approximately 1–2 deg diameter. As a rough quantitative measure of gaze stability, we show in figure 2b the average distance of the positions of both eyes from the fixation target for the last three 2.5 s intervals within each trial (the first interval was excluded from the analysis as it contains the large initial fixation saccades). There is a small increase of this error over time, but no significant difference between the four stimulus conditions (grey field, checkerboard, LFM, HFM). It is worth noting that this drift away from the fixation target is not accompanied by a dynamic instability (larger excursions around the average position) as indicated by the small standard deviations of the error angle (figure 2c) and there is no prominent change for the last two intervals (5–10 s) during which time there was no fixation target.

An examination of the eye-movement record in figure 2b (observer JMZ) reveals characteristics found in steady fixation with pairs of small saccades (< 0.5 deg), predominantly in the horizontal direction, along with a high-frequency tremor and a

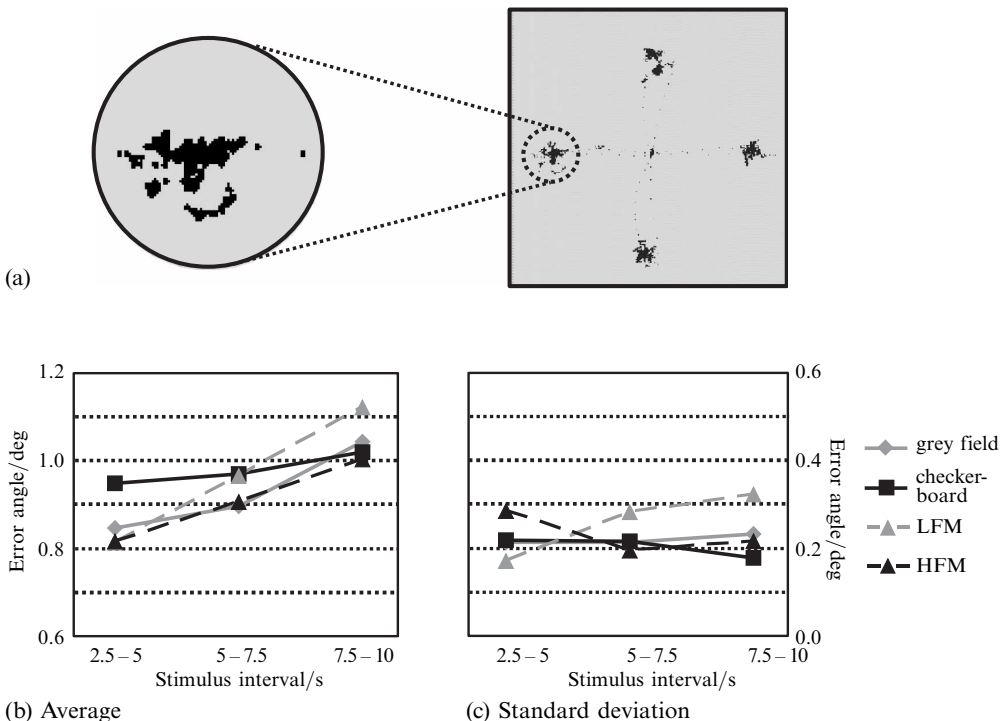


Figure 2. Distribution of eye positions when viewing Riley's *Fall*. (a) Scan paths for four different fixation target locations, superimposed on a contrast-reduced stimulus pattern (observer JMZ: one region blown up on the left side—radius of the circle about 2 deg). (b) Average distances of eye position from target location (average error angles) for three stimulus intervals (interval for initial fixation saccade excluded) and four different stimulus conditions (indicated by different symbols). (c) Standard deviations of error angles for the same conditions.

slow drift (see Carpenter 1988). The pairs of small saccades in opposite directions in many aspects resemble square-wave jerks that are observed in connection with neuropathology but also in normal subjects at a low frequency, somewhat depending on test conditions (Shallo-Hoffmann et al 1989). Some of these rapid displacements (indicated by black arrows) are classified as conventional saccades which are picked up by standard saccade-detection criteria (larger than 0.3 deg, see section 2) while other rapid eye movements, that fall outside the conventional saccade criteria (grey arrows), apparently correspond to the class of micro-saccades described in the literature (Carpenter 1988; Kowler 1990). Since the classification of different types of saccades is not relevant in the present context, we refer to all these small saccades (displacements ranging between 0.2 and 2 deg) as ‘miniature saccades’.

The amplitudes of the horizontal and vertical displacement for two observers are illustrated in figures 3b and 3c as endpoints of all miniature-saccade trajectories relative to their origin. It can be seen that these data points scatter around the horizontal axis for one observer (figure 3b, same observer as figure 3a), and that, in particular, the upper sector of vertical displacements larger than horizontal displacements

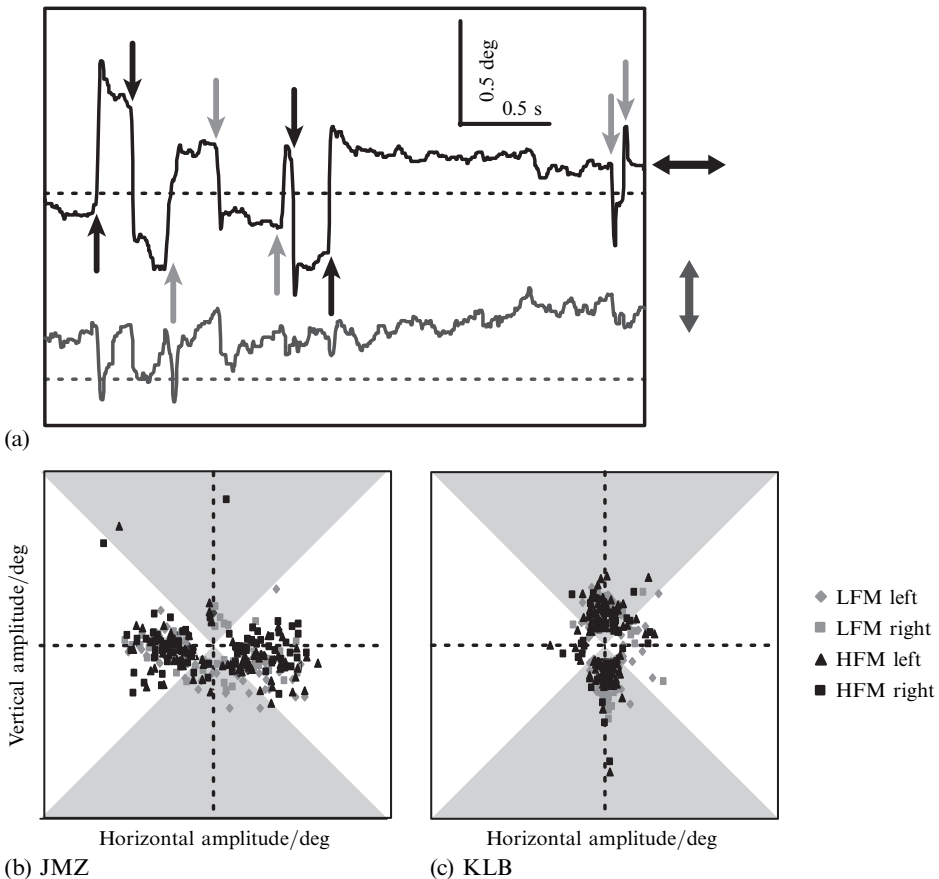


Figure 3. (a) Horizontal (top trace) and vertical (bottom trace) eye position shown as function of time for a 3 s interval. Conventional (amplitudes larger than 0.5 deg) and miniature (smaller than 0.5 deg) saccades are marked by black and grey arrows, respectively (for observer JMZ). (b) and (c) Horizontal and vertical amplitudes of all saccades carried out by two observers when looking at the Riley stimulus (different target locations—LFM and HFM—and eyes indicated by different symbols) plotted on a grid of ± 2 deg horizontal and vertical; grey triangles indicate saccade endpoint regions where vertical displacement is larger than horizontal displacement.

(light-grey triangle) is virtually empty. For this observer (JMZ) saccades are predominantly horizontal for both eyes: for vertical and horizontal orientation of the stimulus pattern (data not shown), for both fixation target locations in the Riley pattern (HFM and LFM), and for both control patterns (grey field and checkerboard, data not shown). The pattern of saccade amplitudes for the other observer (KLB) (figure 3c) shows very similar characteristics, with one crucial difference—the excursions of this individual are predominantly vertical. On average for the eleven observers tested here, the proportion of saccades ending in the horizontal sectors is 39%, ranging between 10% and 72%. The overall saccade amplitude varies considerably, showing no obvious relation to the spatial period of the lines (0.26 deg) and the phase modulation period of the Riley pattern at the target location (always larger than 3 deg). Introspective reports of our observers indicate that stimulus orientation and location of the fixation target did not affect the subjective quality of the perceived illusion. These reports are confirmed by the results of our psychophysical experiments, which found no difference in the illusion strength reported for different pattern orientations (see figure 1b). Interestingly, the energy and structure of the motion-signal maps resulting from step-like displacements of ‘riloids’ are not systematically affected by the direction of such displacements, because the variation of line orientation in the ‘riloids’ leads to grating displacements of a quarter cycle in some regions for almost any sizeable pattern displacement (Zanker 2004).

To identify the possible factors contributing to gaze instability, we analysed the occurrence of saccades in more detail. The overall frequency of miniature saccades can vary considerably between observers (ranging from 38 to 236 saccades min^{-1} , 122 on average) and can also differ between the two eyes of an observer (correlation between left and right eye, across all conditions and observers: 0.64). The number of miniature saccades could be influenced by different noise levels in the measurements from the two eyes, or differ between observers, or when approaching the resolution limits of the eye tracker. However, we observed a consistent pattern of clearly visible miniature saccades when the experiment was repeated with one observer after several months, and the number of saccades executed by any particular observer during a given stimulus interval tends to have little variation, suggesting that the variability between observers could be a result of individual differences. The scatter diagram (figure 4a) in which the saccade frequency when looking at HFM Riley patterns is plotted against saccade frequency for the grey-field stimulus, for each of the eleven observers, demonstrates a high degree of correlation of saccade frequencies between conditions (0.86 in this example). The same basic result is found for all other combinations of stimulus conditions, confirming the qualitative observation that the scan paths and the time courses of eye position from all subjects show no immediately obvious differences in fixation stability at the eight different target locations on the Riley pattern (four orientations, fixation targets in the LFM or HFM region). Some observers generated more saccades during the Riley stimulation than during the control conditions, while other observers showed the opposite pattern. The overall average frequency of miniature saccades for all observers (figure 4b) does not significantly differ for the four basic stimulus conditions (Riley *Fall* LFM and HFM, control grey field, and checkerboard).

Finally, we analysed how the probability of making a saccade changes during the course of a given stimulus presentation, by averaging number of miniature saccades for each of four consecutive intervals of 2.5 s duration of a stimulus trial. The mean values of all eleven observers and both eyes are shown in figure 4c. Whereas no clear pattern of differences can be seen between the different stimulus conditions (LFM, HFM, grey field, and checkerboard), less saccades were produced during the second half of the stimulus block (5–10 s), when no fixation target was presented.

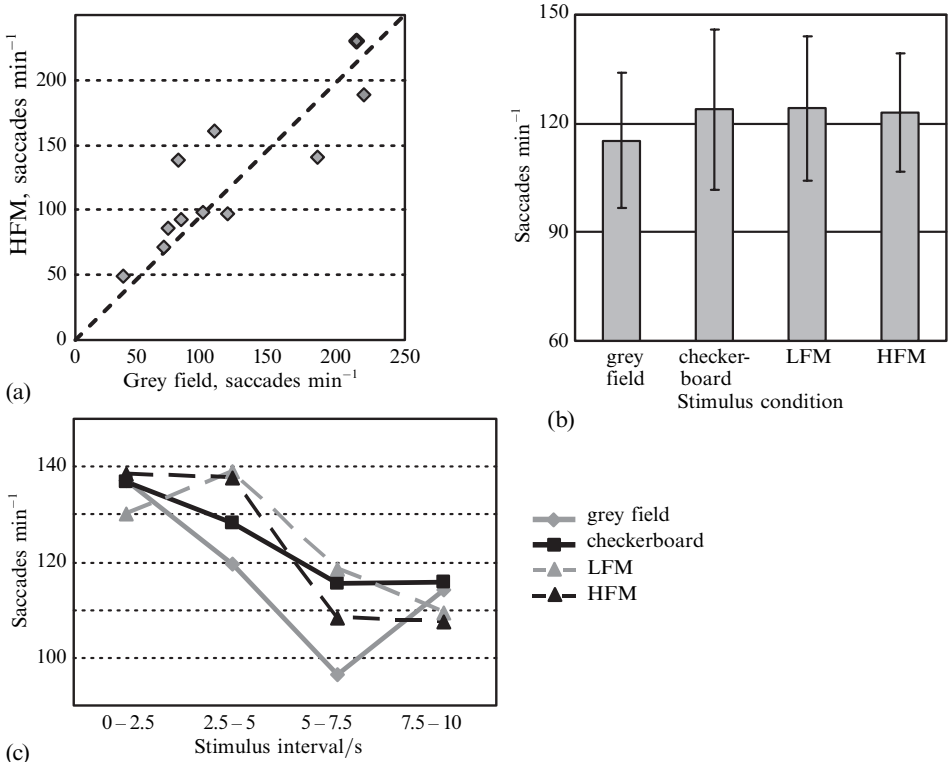


Figure 4. (a) Scatter diagram of the frequency of miniature saccades carried out by eleven observers when fixating the HFM region of Riley's *Fall* and a grey field, respectively. (b) Average saccade frequencies (and SEMs plotted as error bars) for four stimulus conditions: grey field, checkerboard, Riley *Fall* LFM, and HFM. (c) Average saccade frequencies during each of four consecutive 2.5 s intervals within each stimulus block, plotted for four stimulus conditions.

5 Discussion

The results of our psychophysical experiments with afterimage and pinhole viewing techniques can be interpreted as evidence that eye movements are required to see the shimmer and jазzing movement in Riley's *Fall*. A similar suggestion was made by Gregory (1993, 1994) to explain the shimmer in the radiating line patterns. The observation that the stabilised image looks completely static (see figure 1c) clearly suggests that retinal image motion is a prerequisite for the dynamic illusion. One should keep in mind that the afterimages last only for a few seconds, and it cannot be excluded that after some longer time the illusion might build up slowly. However, the illusion develops fast in the control condition after switching on the room light, and achieves full strength by around 5 s—the presentation time used in our computer-controlled psychophysical experiments (see figures 1a and 1b). The intermediate results when looking at the painting through the pinhole (see figure 1c) suggest, on the one hand, that the fluctuations in accommodation discussed by Campbell and Robson (1958) may contribute partially to the effect, because a manipulation that is generally believed to neutralise the optical apparatus indeed reduces the illusion. On the other hand, the fact that the illusion remains visible under these conditions indicates that accommodation cannot exclusively account for the perceived motion, and therefore leads us to conclude that eye movements are essential for the full strength of the stunning illusion perceived under free viewing conditions. In conclusion, the previously inconsistent results for stabilised images and pinhole viewing, as reviewed in the introduction,

may be reconsidered and reconciled in the light of multiple possible explanations. Furthermore, because retinal displacements resulting from eye movements have been identified in our experiments as a crucial factor, it is of interest to analyse the gaze stability of observers looking at such patterns under natural operating conditions.

In our oculomotor experiments we found that large numbers of small involuntary saccadic eye movements were made when observers fixated simple black and white patterns such as the painting *Fall*, which in all of our participants elicited a vivid motion illusion. The properties of these miniature saccades can differ between individuals, for instance in showing a predominant direction, and often come in pairs of opposite direction similar to square-wave jerks. It is known that the frequency of involuntary saccades can be affected by neuropathology and depends on stimulus conditions (Shallo-Hoffmann et al 1990), but the frequencies usually reported for this phenomenon (for instance, 6 square-wave jerks and 5 additional isolated saccades per minutes for a typical case of central fixation, and a few more in the dark or with closed eyes) are much smaller than those found here (more than 100 per minute for the example shown in figure 3a). The reason for this difference is unlikely to be related to the stimulus patterns as such, because they are similar for the blank field control, but may be mainly due to the highly sensitive and 2-D measurement technique employed here, and the low-threshold criteria for detecting saccades in a clinical context (Shallo-Hoffmann et al 1989). Frequencies reported for miniature saccades, on the other hand, can also vary a lot between individuals and experimental conditions, and can reach a few hundred per minute (reviewed by Kowler 1990), so our results are in accordance with earlier observations. There were large variations between individual observers in terms of the overall number of miniature saccades made, but apart from a 10%–20% reduction in the second half of each stimulus presentation (in which no fixation target was present), we could not find any pattern with respect to stimuli presented. In particular, saccade frequency did not differ between the Riley and the two control conditions. Thus the motion-detection systems of the brain will be confronted with a large number of small ($< 1^\circ$) retinal image shifts, irrespective of the actual stimulus pattern viewed.

The significance and consequences of natural gaze instability as such have been discussed in various studies (see, for instance, Carpenter 1988; Findlay and Walker 1999; Land 1999; MacKay 1973). What neural mechanism could be involved in generating motion illusions from such small involuntary saccades when viewing the picture *Fall*? First, one may be led to believe that the saccades themselves would generate motion signals, because the optical image is shifted across the retina. There is, however, considerable evidence that motion vision is impaired during saccades, and it is disputed whether this is achieved by active suppression (Bair and O'Keefe 1998; Burr et al 1994) or by the dynamic limitations of the visual system (Castet and Masson 2000). However, insensitivity to motion during the saccade still leaves the brain with an image displacement (from the fixation position before to the fixation position after the saccade), which the visual system might pick up as a motion signal. For the Riley picture, random saccadic displacements in the range of a degree of visual angle will shift the retinal image of the line patterns in any phase of the spatial period of the grating (which is about a quarter of a degree). Because there is a variation of local grating orientation, there always would be (spatially contiguous) regions that experience a 90° phase shift of the periodic patterns during the saccade—which naturally would create a strong motion signal in motion detectors receiving their input from those regions. This expected distribution of motion signals can easily be demonstrated by simulating a motion-detector network (cf Zanker 2001; Zanker and Zeil 2002). One recent computational study demonstrates that displacements of Riley patterns lead to characteristic motion-signal maps—horizontal streaks of motion signals in various directions—which strongly resemble the perceived motion illusion (Zanker 2004).

In contrast, the same image displacements for the checkerboard pattern would lead to small phase shifts and a rather regular pattern of motion signals perpendicular to the horizontal and vertical edges which directly correspond to the actual image shift. In consequence, small random saccadic image displacements of the control patterns would generate simple patterns of motion signals, which contain unambiguous information about the retinal shift, whereas Riley patterns would lead to intricate horizontally banded patterns of strong motion signals, which make it difficult to recover the original image shift. This seems to suggest that the motion illusion is a result of a breakdown of perceptual mechanisms compensating for eye movement, which rely on retinal motion information (eg Carpenter 1992; Wurtz 1996).

Combining the experimental observations and the theoretical considerations, we feel inclined to put forward a minimalistic interpretation of the observed illusion. Our explanation is rooted in the fact that the highly repetitive pattern structure of Riley's *Fall* does not contain prominent visual landmarks that could be used to correct perceptually for natural gaze instability. By contrast, the same patterns of involuntary eye movements generate the information necessary to compensate the perceptual effects of retinal image shifts for our control stimuli, which are much closer to natural operating conditions in this respect. It should be noted that we do not claim that this is an exclusive explanation of the motion illusion, and do not deny the importance of other types of image instability, such as those resulting from fluctuations in accommodation (see, for instance, Gregory 1994) or some more elaborate cortical information processing strategies of so far unknown character (Zeki 1994; Zeki et al 1993). Instead, we intend to offer no more than a straightforward explanation of the illusion experienced under natural viewing conditions by simply combining experimental data on miniature saccades that are carried out despite the attempt to stabilise gaze, with considerations of processing mechanisms that are almost trivially involved in human motion vision. In its basic approach, this proposal resembles an earlier attempt to understand motion illusions in a computational framework (Fermüller et al 1997, 2000), but the emphasis here is on biologically inspired mechanisms in the early visual system. Future experiments will have to show whether this low-level explanation can hold for a wider range of conditions (eg Zeki 1995), and whether critical predictions, for instance about pattern dependence of the illusory percept, can be confirmed or rejected by more detailed psychophysical experimentation.

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