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A new look at Op art: towards a simple explanation of illusory motion

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Abstract Vivid motion illusions created by some Op art paintings are at the centre of a lively scientific debate about possible mechanisms that might underlie these phenomena. Here we review emerging evidence from a new approach that combines perceptual judgements of the illusion and observations of eye movements with simulations of the induced optic flow. This work suggests that the small involuntary saccades which participants make when viewing such Op art patterns would generate an incoherent distribution of motion signals that resemble the perceptual effects experienced by the observers. The combined experimental and computational evidence supports the view that the illusion is indeed caused by involuntary image displacements picked up by low-level motion detectors, and further suggests that coherent motion signals are crucial to perceive a stable world.

Motion illusions in arts and science

“Painting is a science and should be pursued as an inquiry into the laws of nature” (Thomas Gainsborough, as quoted in Zeki 1999). This notion is an obvious challenge for painters who attempt to capture a three-dimensional and dynamic world on a two-dimensional and static canvas. J.M.W. Turner, for instance, developed his own pictorial language for representing movement, advancing from the traditional approach of attaching motion to objects or gestures into an abstract representation of motion without form. Breaking with a long tradition of representing motion, some artists such as Bridget Riley began to experiment with simple black and white patterns that are able to create vivid dynamic illusions in static pictures (Riley 1999). Using perspective illusions or chromatic tension, sometimes leading to perception of flicker or

movement in stunningly simple geometrical patterns, a new form of visual art was developed in the 1960s which is now known as ‘Op art’. The phenomena that have been exploited by Op artists to such great effect seem to reflect Gainsborough’s challenge back to scientists who could use the experiences and products of their artistic companions as tools and data with which to learn about brain function, and thus question the view that the discourse between science and arts is of a rather superficial nature (see Lewis Wolpert in the *Sunday Observer* of 10/3/02).

The physiological and perceptual mechanisms responsible for motion illusions elicited by Op art paintings are a matter of ongoing scientific debate (see, for instance, Mon-Williams and Wann 1996), which can be traced back to the early descriptions of dynamic deformations observed in patterns that are composed of fine lines (Purkinje 1828, cited in von Helmholtz 1924; Wade and Brožek 2001). A recent example of such a dispute is the ‘Enigma’ painting (Leviant 1996), which consists of a pattern of radiating black and white lines (similar to the ray pattern used by MacKay 1957a) superimposed by concentric rings of uniform colour. The moiré pattern sensation elicited by ‘Enigma’ has been attributed to fading afterimages of the original image after saccadic eye movements (MacKay 1957a; Gregory 1993), whereas the shimmering and deformations that can be seen in the radial line patterns (which can be understood as dynamic moiré changes) have been interpreted as rather trivial consequences of accommodation fluctuations, ‘hunting for accommodation’ (Campbell and Robson 1958; Gregory 1994). On the other hand, the circular motion sensation within the uniformly coloured rings has been attributed to a cortical mechanism that does not rely upon image shifts (Zeki et al. 1993; Zeki 1994, 1995). Although explanations such as these are often put forward as alternatives that exclude each other, it could well be that the observed phenomena arise from a combination of causes and mechanisms, and that some of the discussed perceptual effects might be different issues.

The possible causes of such motion illusions can be seen as an exciting problem which could be a starting

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point to engage the arts and science communities in a productive debate. As a small contribution to such a discourse, here we review some recent developments in the field of neuroscience that may shed new light on this issue. Merging into a combined approach, three areas of enquiry are described in the following sections: (1) perceptual judgements under a range of conditions that affect the vividness of the illusion; (2) observations of eye movements of observers looking at Op art patterns; and (3) computer simulations of the motion information processing to be expected under such conditions.

An experimental analysis

A combined experimental and computational approach is advocated in order to shed new light on this issue. In a first step, one would like to characterise the perceived illusion in a more quantitative manner. Riley's 'Fall' (1963, Tate Britain, London) appears to be a good starting point, because it can be the basis of generating a family of stimuli with a small set of simple parameters (see Fig. 1). Usually, the experience of viewing this painting is described in terms of introspection, with labels like 'shimmer', 'flicker', or 'waves of movement'; or in a more specific way as a pattern of horizontal, not clearly

delineated bands in which gratings seem to move in one coherent but random and often changing direction, and different directions within each band. To assess the conditions for seeing the dynamic illusions (Zanker et al. 2003), observers were asked to rate the strength of the illusion perceived in a number of stimuli on a scale between 1 (completely static) and 5 (moving vividly). In an initial experiment the expectation was confirmed that the strength of the illusion varies with the modulation amplitude of the riloid (i.e. similar to those in the works of Riley) gratings (parameter A , see Fig. 1, the inverse of the straightness of the gratings), thus also validating the measurement technique itself. This provided a basis to assess quantitatively the effects of stabilising the retinal image, by inducing retinal afterimages from illumination of the 'Fall' with a strong photographic flash that restricts the retinal exposure to a very brief time interval, or those of excluding ocular accommodation by looking at the image through a small pin-hole that reduces the effective aperture of the lens (Gregory 1994). The results of this experiment are shown in Fig. 2b, together with a control: the same perceptual judgement made the moment immediately after stimulus onset, under normal viewing conditions. It is clear from these data that the illusion virtually disappeared when the retinal image of the pattern was stabilised, while ratings close to maximum

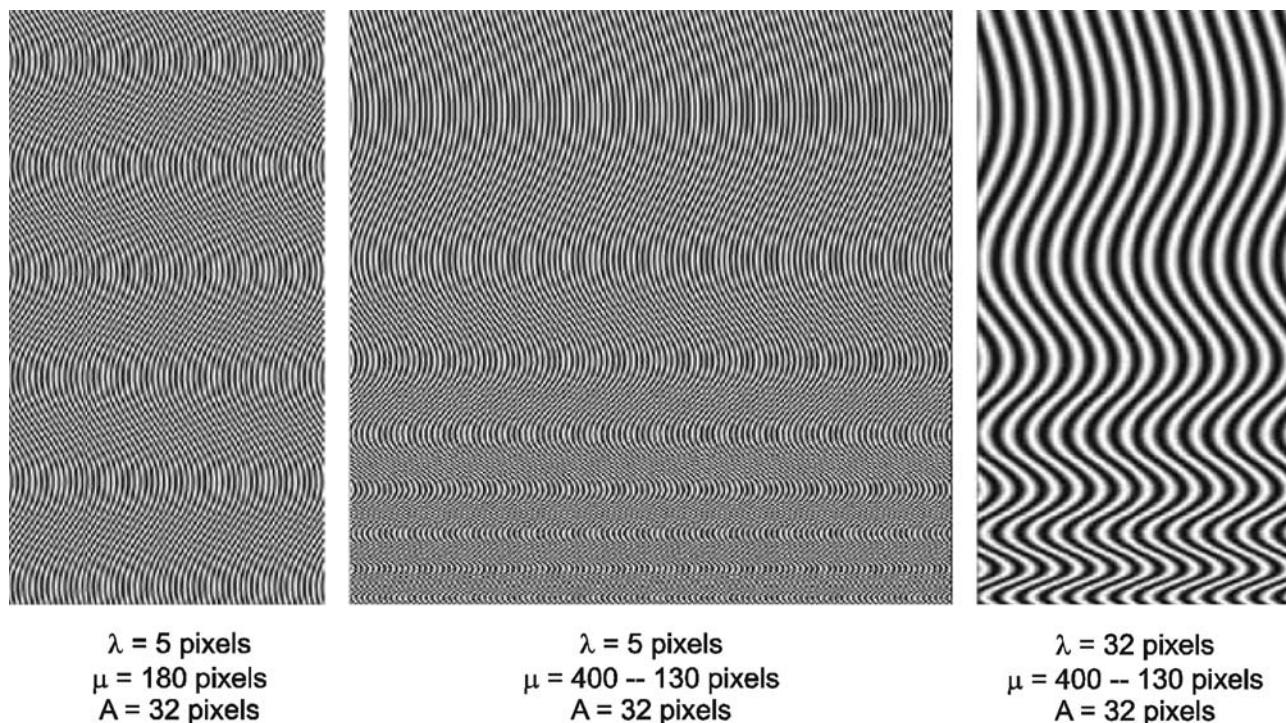


Fig. 1 Riloids – synthetic Op art patterns – can be generated according to a simple mathematical expression (see Zanker et al. 2003; Zanker 2004) by sinusoidal modulation of intensity with a grating period, λ , and a phase modulation of amplitude A and modulation period μ that can vary along the vertical dimension. Resulting grey-level bitmaps of wiggly line patterns resemble Riley's 'Fall' (Riley 1999), and were therefore dubbed 'riloids'.

The *three panels* illustrate how the three parameters influence the appearance of riloids. A pattern that is close to the original painting is shown in the large (*central panel*), and compared to a pattern with larger grating period λ (*right panel*) and a pattern with a constant modulation period (*left panel*) (adapted from figure 2 in Zanker 2004)

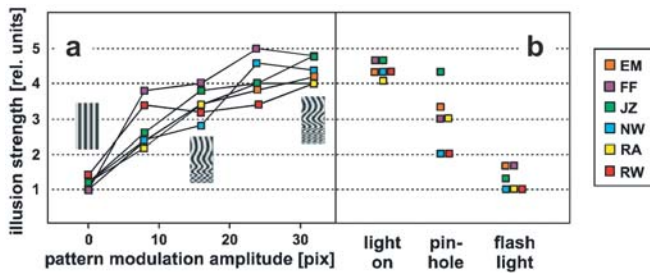


Fig. 2a, b Psychophysical estimates of motion illusion strength (data from six observers, indicated by *different colours*); observers had to rate the sensation created by a particular stimulus on a scale between 1 (completely static) and 5 (vivid movement) for a variety of stimulus conditions and several repetitions. **a** Illusion strength as function of modulation depth of the riloid pattern (see *inset sketches*, cf. Fig. 1) of riloid patterns. **b** Illusion strength for short inspection time ('light on'), exclusion of accommodation ('pin-hole'), and stabilised retinal images ('flash light') (adapted from figure 1 in Zanker et al. 2003)

illusion strength were obtained with normal viewing even for the shortest inspection times, suggesting that eye movements are crucial for experiencing the illusion. Furthermore, reducing the influence of accommodation did diminish but did not completely abolish the illusion, indicating that 'hunting for accommodation' has a modulatory effect but is not a necessary condition for the phenomenon to be explained (Zanker et al. 2003).

Voluntary saccadic eye movements have been suggested earlier to enhance the sensation of vivid pattern motion in radiating line and similar patterns (Gregory 1994) and may be involved in a recently discovered motion after-effect (Murakami and Cavanagh 1998; Bruno 1999), but little is known about the actual characteristics of eye movements carried out when viewing Op art paintings. Therefore we review in the following a recent oculomotor experiment (Zanker et al. 2003), which was designed to 'look through the eyes of the observer' at Op art. Bridget Riley's painting 'Fall' was used as an exemplar because (1) its fine lines restrict the range of early visual mechanisms involved, (2) it allows for a simple mathematical description, and (3) it is not composed of distinct image regions with qualitatively different image properties (such as in 'Enigma'). Combining the well-defined stimulus conditions and the recordings of gaze shifts, a computational model of visual processing can then be employed to assess what kind of sensory information the brain has to deal with.

How stable is gaze when looking at simple patterns?

A digitised version of Riley's 'Fall' was presented on a computer screen, approximating the angular size of the original painting in the Tate Gallery for a viewing distance of 2 m. The orientation of the image was varied in a counterbalanced fashion (showing the image upright, inverted, tilted 90° to the right and left, respectively), and a small fixation target was presented halfway between the

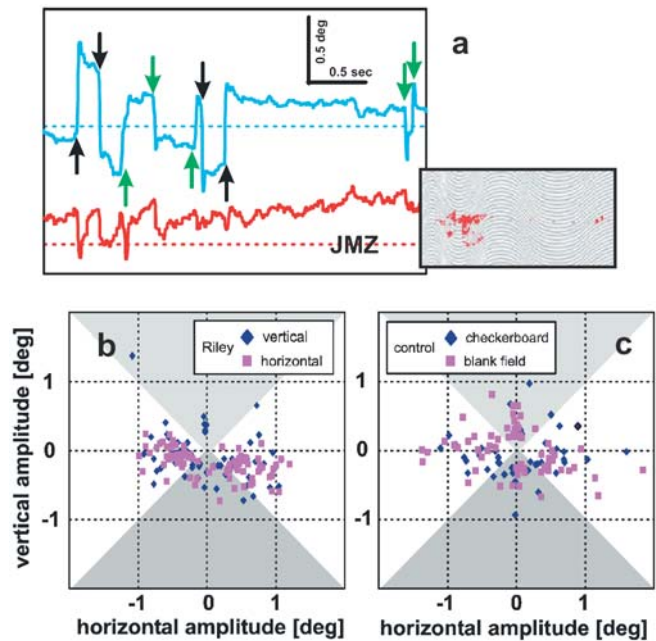


Fig. 3 a Example of a typical scan-path (*inset*: gaze positions superimposed on a low-contrast version of the stimulus) and time-course (horizontal: *blue trace*, and vertical eye position: *red trace*, plotted as a function of time for an interval of 3 s) of one observer's eye position when viewing Riley's 'Fall'. Conventional (amplitudes $>0.5^\circ$) and miniature saccades ($<0.5^\circ$) are marked by *black* and *green arrows*, respectively. **b** Horizontal and vertical displacement amplitudes of saccades for Riley patterns (vertical pattern orientation: *blue diamonds*; horizontal: *cyan squares*) and **c** for control patterns (checkerboards: *blue diamonds*; blank fields: *cyan squares*), plotted on a $\pm 2^\circ$ horizontal and vertical grid; *grey triangles* indicate saccade endpoint regions where vertical displacement is larger than horizontal displacement (adapted from figure 3 in Zanker et al. 2003)

centre and the stimulus edge in the high- or low-frequency region of phase modulation (HFM or LFM) of the line pattern. Eye movements were recorded with a video-based eye tracker (see Zanker et al. 2003 for technical details) to find out how eye movements and motion sensations are influenced by the geometric features of the stimulus. In a control experiment, eye movements were recorded while observers viewed a checkerboard pattern or a blank grey field which generated no motion illusion. Observers moved their eyes towards the fixation target with one or two large saccades and then stayed within a region of approximately one degree diameter (see exemplary scan-path in inset of Fig. 3a). There were no systematic differences between the eye positions of the two eyes, such as they would be expected for the occurrence of vergence eye movements or independent eye drifts. The time-course of eye position plotted in Fig. 3a reveals irregular slow fluctuations which are superimposed by small saccadic eye movements. Saccades sometimes appear in conspicuous pairs – jumping back and forth to almost the same location – which resemble the square-wave jerks that have been observed in 'normal' observers and at increased rates with

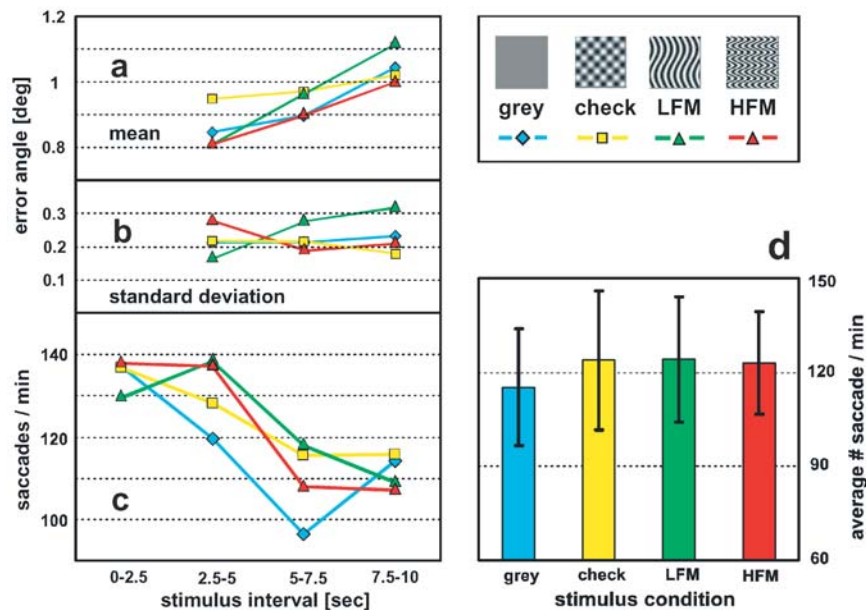


Fig. 4a–d Quantitative measures of gaze stability for 11 observers looking at grey and checkerboard control patterns (*blue and yellow symbols*) and LFM and HFM regions of Riley’s ‘Fall’ (*green and red symbols*). **a, b** Mean and standard deviation of angular distance between eye position and the location of the fixation target on the Riley stimulus are shown for the three stimulus intervals (of 2.5 s)

after the initial fixation. **c** Mean number of saccades is shown for all four consecutive stimulus intervals of 2.5 s. **d** Average number of saccades carried out throughout the complete stimulus period, for each of the four stimulus conditions (adapted from figure 4 in Zanker et al. 2003)

certain neuropathologies (Shallo-Hoffmann et al. 1989, 1990). Some of these rapid eye movements had much smaller amplitudes than ‘conventional’ saccades (displacements $<0.5^\circ$, indicated by green rather than black arrows in Fig. 3a). Although these miniature saccades within the limits of measurement accuracy fall on the same function describing the relation between saccade magnitude and peak velocity (called the ‘main sequence; see Carpenter 1988; Abadi et al. 2000), there are functional reasons why saccades might be rather different because they would keep a fixated target within the fovea, whereas ‘conventional’ saccades are usually made to correct for substantial displacements and bring a target into the fovea. Reports that there are clear latency differences (Kalesnykas and Hallett 2002) support this view that different mechanisms are involved in the generation of very small and large saccades, respectively.

The distribution of error angle (eye position relative to the fixation target) was used to quantify gaze stability under various stimulus conditions and time intervals, revealing that the mean error angle increased with time (Fig. 4a) after the disappearance of the fixation target (stimulus interval 2.5–10 s) for all test and control stimulus conditions, whereas the error angle variance remained rather constant. This observation suggests that eye position was subject to a slow drift but exhibited the same pattern of local excursions throughout the complete stimulation period. Figure 4b shows that the eye stays within a region of less than 0.3° radius (about ten times the visual system’s spatial resolution limit) around its target location for about 67% of the time. These data give

no indication of any difference between the different stimulus conditions, suggesting that net gaze stability is excellent (less than $0.05^\circ/\text{s}$) and comparable for the Riley stimulus and the control patterns.

To assess the role of miniature saccades in gaze stability, saccades were selected which were smaller than 5° to exclude the initial fixation and larger than 0.2° to stay well above the eye tracker resolution. The horizontal and vertical saccade displacements are shown in Fig. 3b for the Riley stimulus as trajectory endpoints relative to their origin. For this observer the data points were scattered around the horizontal axis, irrespective of the stimulus orientation and fixation target location in HFM or LFM regions (neither of which were found to affect the subjective quality of the perceived illusion). The overall saccade direction and amplitude showed no obvious relation to the spatial period of the lines (0.26°) and the phase modulation period at the target location (always greater than 3°). The distribution of saccade endpoints for the checkerboard and blank field control patterns (Fig. 3c) showed a similar range of amplitudes and a less pronounced preference for horizontal displacements. Such a tendency of a preferred saccade direction was found in many observers, but it could be vertical as well as horizontal. Data collected from 11 observers did not show any clear trend for a general preference towards any particular direction (Zanker et al. 2003).

Counting the number of saccades carried out during the four consecutive 2.5-s intervals of a stimulation period indicated a slight decrease during the second half of the stimulation (Fig. 4c), supporting the view that the

growing error angle is indeed a result of a slow eye position drift rather than being caused by a growing tendency to make saccades. Once again, there was little convincing evidence for any influence of stimulus condition or systematic differences between the two eyes. Looking at the overall number of saccades (Fig. 4d), it appeared that slightly fewer saccades are carried out when watching the blank field than for LFM and HFM fixation and for checkerboard control patterns, but this difference was small and, due to the large, but not significant inter-individual variations. Despite the variability between individuals in overall number and specific saccade patterns, it was concluded that observers always produce a considerable amount of small involuntary saccades, which do not strongly depend on the particular stimulus pattern (Zanker et al. 2003). Most crucially, this indicates that even when an observer attempts fixation and indeed is able to keep net drifts rather small, the brain always has to deal with small and rapid shifts of the retinal image. So why do we perceive motion illusions with some patterns, but not with others?

Motion signal distributions resulting from small saccades

The answer to this question can be revealed from a computational analysis. Superimposing the retinal representation of riloids (see Fig. 1) before and after a saccadic displacement (Spillmann 1993; Gregory 1994) leads to characteristic moiré patterns which would indicate regions of image blur and dynamic change, but does not account for any sensation of (directed) motion. In order to look at this aspect of perceived motion, we need a more thorough analysis which precisely describes the information provided to the visual system and the mechanisms that process the available input signals. A first attempt along these lines can be found for the ‘Enigma’ motion illusion (Leviant 1996), which has been explained in terms of high-level mechanisms of analysing optic flow (Fermüller et al. 1997). Small displacements of this image would lead to weak motion signal patterns that could be interpreted as typical motion fields by such mechanisms extracting flow components. The same approach of looking at motion patterns in noisy signal distributions has been extended (Fermüller et al. 2000) to the famous Ouchi illusion, where relative motion is perceived between differently textured regions (Ouchi 1977). The importance of eye movements for eliciting this illusion has indeed been demonstrated (Hine et al. 1997), and the illusion has been independently interpreted in the context of motion integration (Mather 2000). So far these considerations are, however, largely based on general notions of image displacements, and confined to high-level mechanisms analysing hypothetical distributions of local motion signals. The recent work on Riley’s ‘Fall’ reviewed above offers an opportunity to directly combine perceptual effects with oculomotor observations in a computational framework, taking a close look at actual

motion distributions that are available to high-level mechanisms that may be responsible for analysis of optic flow or segmentation.

An attempt to close the gap between observed eye movement patterns and mechanisms of early visual processing was made in a recent study of the distribution of low-level motion signals (Zanker 2004), which used a simplified version of the two-dimensional array of biologically motivated motion detectors that has been used previously – the ‘2DMD model’ (Zanker et al. 1997; Patzwahl and Zanker 2000). This computational model was used to generate response maps that represent the spatial distribution of motion signals resulting from saccadic displacements, which are the most conspicuous oculomotor events observed. Such maps show the motion signal distributions expected for single-step displacements of simple black-and-white patterns, as they might be produced from small eye movements (Zanker 2004). This approach provides valuable cues about what kind of integration mechanisms are necessary to disambiguate the non-veridical local motion signals. The basic building blocks of this model are elementary motion detectors (EMDs) of the correlation type, which have been shown in many psychophysical, behavioural and physiological studies to be the most likely candidate for biologically implemented motion detectors (for reviews, see Reichardt 1987; Borst and Egelhaaf 1989). This specific kind of local motion detector was used to represent a variety of possible models that would produce the same pattern of results, such as motion energy detectors (Adelson and Bergen 1985; Van Santen and Sperling 1985). The 2DMD model, consisting of a two-dimensional network of pairs of such local EMDs, detects horizontal and vertical motion components, and has been used to simulate a variety of psychophysical phenomena (Zanker et al. 1997; Patzwahl and Zanker 2000; Zanker 2001). Because the narrow spatial frequency band of the riloid patterns would only elicit motion responses in a small population of motion detectors tuned to this frequency, the spatial scale of the 2DMD model in the present context was adjusted to the stimulus, thus focusing on the largest motion signals available (Zanker 2004). Exemplary signal maps for saccadic displacements of riloids are plotted in Fig. 5 in 2D-pseudo-colour, in which signal direction and strength is coded by hue and intensity, respectively (right–green; up–yellow; left–red; down–blue, see right inset).

For a two-frame riloid displacement sequence, such a motion detector network produces motion maps which contain horizontal streaks of strong motion signals in various, seemingly random and clearly very different, directions (see Fig. 5). The simulated displacement step of 8 pixels rightwards and 8 pixels downwards corresponds to a quarter of the riloid grating period for the example shown here, which corresponds to the amplitude of a small saccade in the oculomotor experiments. Most importantly, for almost any displacement of the riloid, we find large amounts of motion energy in a limited range of spatiotemporal frequencies, but in virtually all possible directions which are arranged in irregular sequences as

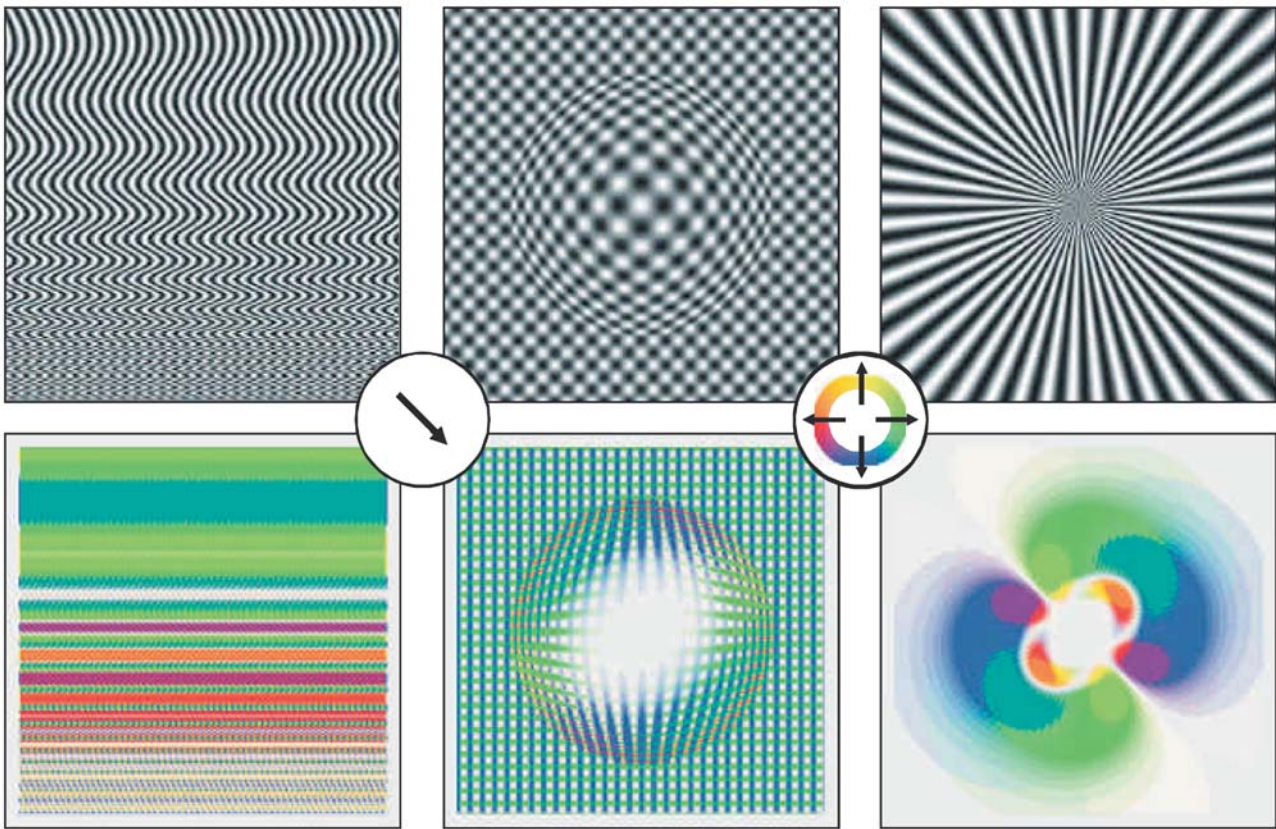


Fig. 5 Pattern displacements and motion signals. Three different stimulus patterns with smooth intensity gradients ranging between black and white are shown together with the motion signal maps (256×256 pixels, pseudo-colour code for direction of motion signals) generated by the 2DMD model for a single-step diagonal displacement (8 pixels to the right and 8 downwards, indicated in *left inset* by *arrow* – magnified four times). *Left*: The signal map resulting from a displacement of a typical riloid pattern shows horizontal stripes of rather different colour (i.e. a variety of motion directions) without any overall direction bias. *Middle*: The displacement of an artistic modification of checkerboards (dubbed

‘vasareloids’ because of their similarity to patterns designed by Victor Vasarely: ‘Vega’, 1957), leads to a regular pattern of colours with an overall bias towards blue-green (corresponding to the diagonal direction of displacement). *Right*: Shifting a radial grating with the same structure as the ‘ray pattern’ studied by MacKay 1957a, 1957b) generates motion signal maps dominated by blue and green colour, predominantly in the regions where contours are perpendicular to the direction of displacement. Inconsistent motion signals are found in the central regions of the pattern, which nicely reflect the ‘shimmering effect’ perceived when looking at these patterns

horizontal bands similar to those shown in the left panel of Fig. 5. Consequently, this stimulus does not lead to any substantial coherent average motion signal that reflects the actual image displacement (Zanker 2004). This structure resembles the sensations described by some observers when viewing Riley’s ‘Fall’, in which a number of fuzzily outlined, and dynamically changing, horizontal pattern sections seem to move in rather incoherent directions. Without being able to segment different directions into separate regions, the observer detects several directions simultaneously, in a manner similar to the phenomenon of motion transparency (Van Doorn and Koenderink 1982; Zanker 2001). In contrast, the same image displacement of the checkerboard control pattern leads 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. Two such control stimuli, together with motion

signal maps resulting from a saccade-like displacement, are depicted in Fig. 5 in direct comparison to the results for the riloid, demonstrating coherent and systematic patterns of motion signals for the control stimuli, whereas small random saccadic image displacements would be expected to produce horizontal bands of rather strong motion signals in various directions for riloids.

The similarity between the simulation results and the perceived illusion suggests that our combined experimental and computational approach can indeed provide a fairly simple explanation of this impressive phenomenon in terms of eye movements and low-level motion processing which generate distributions of local motion signals that are available to the perceptual system. This explanation is similar to some accounts of the motion illusions elicited by radial gratings (MacKay 1957b) and related patterns in that it relates to retinal image displacements of various kinds (Campbell and Robson 1958;

Gregory 1994; Leviant 1996; Mon-Williams and Wann 1996), but it goes beyond these suggestions in demonstrating by means of both computational simulation and experimental measurement, that normally occurring gaze instability would be sufficient to elicit the illusions. Keeping in mind that alternative explanations do not necessarily exclude each other, the persistence of the illusion under experimental conditions that were employed specifically to minimise (or to eliminate) image shifts (MacKay 1958; Zeki 1994), apart from being an empirical issue about the size of any perceptual effect, does not contradict the proposition that image shifts are responsible for the illusion when they are present.

Conclusion: How to live with involuntary eye movements

The minimalistic explanation of the motion illusion perceived in Riley's 'Fall' put forward here is rooted in the fact that there are no prominent visual features, such as low spatial frequency components, in the highly repetitive pattern, which on the other hand is not homogeneous enough to provide a single dominating motion detector response when the image is displaced. Therefore no coherent signal is available that could be used to correct for retinal image shifts from small involuntary saccades. Instead, almost any such image displacement would end up with (spatially contiguous) regions that experience a 90° phase shift of the periodic patterns, which creates strong signals in motion detectors receiving their input from those regions. It should be noted that cause and effect are difficult to separate because small involuntary or corrective eye movements that could be caused by image instability would lead to further image displacements that may trigger further saccades. However, it is important to appreciate that the strong, irregular and highly characteristic patterns of motion signals conceal the actual image displacement, and thus cannot be exploited to stabilise gaze! Since saccades may come in a wide range of directions and amplitudes, there will always be distinct and meaningful variations of the speed and direction of local motion signals, and the observer will see neither a static pattern nor a coherently moving one, but experiences an intriguing mix of motions in incoherent directions. This 'motion without displacement' somewhat resembles motion after-effects in that we have a vivid impression of movement that is not accompanied by a corresponding change of position (Nishida and Johnston 1999). An oculomotor explanation of the motion illusion is certainly not exclusive, and various types of image instability, such as those resulting from saccades and from fluctuations in accommodation (see Gregory 1994) or from vergence eye movements, could produce similar effects, as well as more elaborate cortical information processing strategies of so far unknown character (Zeki et al. 1993; Zeki 1994). We intend here to offer a straightforward explanation of the illusion that requires minimal assumptions because it is consistent with our

knowledge of early vision and incorporates the tiny eye movements actually observed. Future experiments will have to show whether such a simple explanation can hold for a wider range of conditions (e.g. Zeki 1995), and whether critical predictions, for instance about pattern dependence of the illusory percept, can be confirmed or rejected by more systematic psychophysical experimentation.

Perhaps the most surprising consequence of this view arises from the question of why small involuntary eye movements do not lead to similar illusions with other patterns, starting from straight gratings (see Fig. 2) or checkerboards, through displays containing simple objects, and extending to complex natural scenes. As can be seen from the simulation of control pattern displacements (see Fig. 5), motion signal maps in these cases are dominated by direction components which on average correspond to the actual displacements, and thus enable the visual system to recover the direction of image shift, which could then be used to compensate for the image displacement elicited by small involuntary saccades. This is not possible for the rilloids. Could that be a key to understanding why we usually perceive a perfectly stable world, although every eye movement leads to retinal image shifts that should be perceived as movement of the environment? The classical answer to this puzzle is based on the suggestion that extra-retinal signals, such as the motor commands themselves, could be used to compensate for the image shifts elicited by eye movements (von Helmholtz 1924; von Holst and Mittelstaedt 1950). However, extra-retinal signals for fast and tiny saccades might not be accurate enough to compensate for small image displacements. Alternatively, the information contained in the image displacement itself could be used for compensation (MacKay 1973). It has been suggested that motion perception is actively suppressed during saccades in the human visual system (e.g. Burr et al. 1994), but on the other hand it has been shown that primate MT neurons respond to image displacements that are elicited by saccades (Bair and O'Keefe 1998). Other authors argue that displacements are invisible due to the dynamic limitations of motion perception (Castet and Masson 2000). There is also evidence that the retinotopic space is remapped with respect to external space when saccades are performed (Ross et al. 1997; Lappe et al. 2000). Basically, each of these possible compensation mechanisms should always work for a wide variety of stimulus patterns – so why are they not successful for rilloids? A simple solution to this problem lies in the fact that for rilloids we observe a considerable amount of motion energy in a narrow frequency band without a clearly dominating motion direction, which does not allow for the reliable estimation of the direction of displacement. This is not the case for the control patterns where the veridical displacement can be recovered by means of spatial integration of local motion signals (see Fig. 5). Therefore, the only source of information available in this case for compensation of image displacement would be extra-retinal. However, it is questionable whether the precision

of this information source would be sufficient to signal small eye movements with the necessary accuracy, and a default mechanism of that nature could leave the visual system with net displacements that are still substantial, compared with the spatial features of the stimulus gratings. The simple fact that we perceive 'illusory' motion when looking at the Riley painting but not for the control patterns, for which the simulations reveal consistent motion directions, suggests that in this limiting case it is indeed the retinal image shift itself which – if available – is used to make the outside world appear stable.

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