

Looking at Op Art: Gaze stability and motion illusions

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Abstract. Various Op artists have used simple geometrical patterns to create the illusion of motion in their artwork. One explanation for the observed illusion involves retinal shifts caused by small involuntary eye movements that observers make while they try to maintain fixation. Earlier studies have suggested a prominent role of the most conspicuous of these eye movements, small rapid position shifts called microsaccades. Here, we present data that could expand this view with a different interpretation. In three experiments, we recorded participants' eye movements while they tried to maintain visual fixation when being presented with variants of Bridget Riley's *Fall*, which were manipulated such as to vary the strength of induced motion. In the first two experiments, we investigated the properties of microsaccades for a set of stimuli with known motion strengths. In agreement with earlier observations, microsaccade rates were unaffected by the stimulus pattern and, consequently, the strength of induced motion illusion. In the third experiment, we varied the stimulus pattern across a larger range of parameters and asked participants to rate the perceived motion illusion. The results revealed that motion illusions in patterns resembling Riley's *Fall* are perceived even in the absence of microsaccades, and that the reported strength of the illusion decreased with the number of microsaccades in the trial. Together, the three experiments suggest that other sources of retinal image instability than microsaccades, such as slow oculomotor drift, should be considered as possible factors contributing to the illusion.

Keywords: Op Art, visual illusions, eye movements, microsaccades, motion perception.

1 Introduction

Visual illusions have received considerable interest, one reason being that they may provide an important source of information about the working of the human visual system. One type of illusion that has been studied extensively is illusory motion, such as instances in which a static image results in a strong motion percept, although no physical motion is present. These illusions were used by artists as a way to convey motion in images composed of simple black and white patterns. One example, which will be the focus of the present study, is the painting *Fall* by the Op artist Bridget Riley, in which an ensemble of black and white undulating lines induces a strong motion percept, often reported as a 'shimmering' motion. Other motion illusions, with possibly different underlying mechanisms or combinations of underlying mechanisms, exist, such as the Enigma illusion, consisting of radial lines with superimposed rings (Leviant 1982; Troncoso et al 2008).

Works of arts like Riley's *Fall* and the Enigma illusion have received considerable interest from vision scientist debating the origin of the perceived motion illusions in static patterns. Three possible causes of the illusion have been discussed in the last half century (for a review, see Troncoso et al 2008). First, it was proposed that the illusions were caused by the accommodation movements of the eyes (eg, Campbell and Robson 1958), as, in some situations, the illusion was abolished when looking through a pinhole (Gregory 1993, 1994). Second, ruling out retinal causes when different patterns of brain activation were found for real and illusory motion, cortical mechanism have been proposed to underlie such illusions (Zeki et al 1993; Zeki 1994). Finally, it has been suggested that small eye movements during

visual fixation, known as fixational eye movements, play an important role in the illusion (Troncoso et al 2008; Zanker and Walker 2004).

We here focus on the role of fixational eye movements. These eye movements during visual fixation can be classified into three categories (eg, Martinez-Conde 2006; Martinez-Conde et al 2004, 2009; Rolfs 2009). First, there are microsaccades, which are movements of the eye during attempted fixation of a relatively large amplitude (but generally less than 1 deg of visual angle) and high velocity. Microsaccades tend to occur in both eyes simultaneously and appear to have properties similar to saccadic eye movements (Otero-Milan et al 2008). Second, there is slow oculomotor drift, which are also relatively large movements of the eye, but with velocities that are much smaller than those observed for microsaccades. Third, there is tremor, which are fast but small amplitude eye movements, which can occur in just one eye at a time. Microsaccades have been implicated in motion illusions (Troncoso et al 2008; Zanker and Walker 2004), but slow drift is also suspected to play a role (Zanker and Walker 2004). The contribution of microsaccades to the motion illusion in, for example, the painting *Fall* can be understood as follows. During microsaccadic displacements of the eyes, the projected image is shifted across the retina. Because of the particular pattern of alternating black and white curves in the painting, the human motion system interprets these shifts as motion, rather than changes in the direction of eye gaze (Zanker and Walker 2004). A second mechanism, however, could also play a role. Microsaccades are known to help prevent fading of the retinal image (eg, Martinez-Conde et al 2006). As a consequence, microsaccades could induce a transient spiking response of neural activity, which could add to the illusion of motion in the images.

Several lines of research provided evidence for the role of microsaccades in motion illusions. First, it has been shown that the motion illusion in patterns resembling Riley's *Fall* is weakened when the retinal image is stabilized, for example, by presenting the artwork as an after-image (Zanker et al 2003). Second, a direct relation was found between the strength of the streaming-like motion in the Enigma illusion and the occurrence of microsaccades (Troncoso et al 2008). Finally, computational modelling of motion perception in patterns resembling Riley's *Fall* suggested that the alternating patterns of black and white curves in this illusion induced a large range of motion directions for displacements of the retinal image, in agreement with the suggestion that the human motion system is confused by images inducing illusory motion. Control images, in contrast, induced only a single direction of motion, corresponding to the direction of the retinal shift (Zanker and Walker 2004).

Whereas findings such as those described above provide compelling evidence that microsaccades can be sufficient to facilitate the perception of illusory motion, it needs to be kept in mind that microsaccades occur at a relatively rare rate. Most studies report frequencies in human observers under standard conditions in the order of one microsaccade per second (eg, Engbert and Kliegl 2003b). As a consequence, the duration of the interval between microsaccades can be relatively long, and it is rather possible that no microsaccades occur during brief stimulus presentations, while motion illusions have been found for stimuli presented as briefly as 250ms (Zanker et al 2010). Given the relatively low frequency of microsaccades, it therefore needs to be assumed that their effects on the motion system are reasonably long-lasting if they were the full explanation of the motion illusion.

1.1 The analysis of fixational eye movements

Several algorithms have been used to analyze eye movement recordings for microsaccades. However, in direct comparisons these have been reported to provide similar results (Otero-Millan et al 2008; Poletti and Rucci 2010; Troncoso et al 2008). In our study, we employ the often used algorithm developed by Engbert and Kliegl (2003b). In this algorithm, the overall noise in the velocity of the eye is estimated from the two-dimensional distribution

of instantaneous horizontal and vertical speed components (Figure 1; bottom panels). The velocity of the eye at each point in time is then compared to a threshold derived from the amount of noise. Signals that exceed the threshold for some amount of time, and that occur binocularly (ie, in both eyes simultaneously), are classified as microsaccades which can be easily verified in two-dimensional position diagrams (Figure 1; top panels, green segments of eye trajectory). Microsaccades detected with this algorithm follow the main sequence (Figure 1b), an approximately linear relation between the amplitude of the saccade and the peak velocity of the eye movement (Zuber et al 1965), suggesting that microsaccades are generated by a similar mechanism as are regular saccades (Hafed et al 2009).

1.2 The influence of Op Art on fixational eye movements

As indicated above, considerable evidence points towards the involvement of fixational eye movements in the occurrence of visual motion illusions (eg, Laubrock et al 2008; Troncoso et al 2008; Zanker et al 2003; Zanker and Walker 2004). An additional process, however, could also be at work. Because of the motion signals that motion illusions seem to induce in the visual system (Zanker 2004), it could also be possible that the additional fixational instability is induced by the illusion itself, increasing the number and/or amplitude of different types of fixational eye movements. If such increased fixational instability occurs, it is expected that when the strength of illusory motion of a stimulus increases, more fixational eye movements can be found. In a study comparing stimuli inducing weak and strong motion illusions, no increase in microsaccades was found (Zanker et al 2003; Zanker and Walker 2004), suggesting no link between the perceived motion illusion and fixational instability (see also Troncoso et al 2008). We here investigate this issue further by inspecting aspects of microsaccades going beyond their frequency, such as amplitudes and directions for patterns that elicit different illusion strengths (Experiments 1 and 2). Moreover, we will make a direct comparison of the perceived motion illusion and the occurrence of microsaccades, by asking participants to first fixate a stimulus for a fixed interval and then to rate the perceived motion strength (Experiment 3). By comparing trials with many and trials with few microsaccades, the relation between microsaccades and perceived illusory motion can be examined.

We conducted three experiments. In the first two experiments, we made use of stimuli introduced in a previous study, and of which the strength of the perceived illusion was therefore known beforehand (Zanker et al 2010). The study by Zanker and colleagues provided a new psychophysical method to measure the strength of illusory motion perceived when looking at synthetic versions of Riley's Fall (called 'Riloids'), which vary in the spatial layout of the undulating lines, as illustrated in Figure 2. A critical element of the psychophysical method was an independent manipulation of illusion strength by mixing Riloids with regular arrays of high-contrast squares that on their own are perceived as firmly static (illustrated in Figure 3b). The main finding of the study was that the strength of the motion illusion grows with the amplitude (A) and the spatial period (μ) of the wave-like undulations of the line gratings, but was unaffected by the spatial wavelength of the gratings (λ). In addition, we observed that the strength of the motion illusion was not influenced by the presence or absence of a fixation target (Zanker et al 2010). This latter finding provides an interesting opportunity to determine how the motion illusion relates to certain aspects of fixational eye movements. For example, if it were found that the presence of a fixation target increases the frequency of microsaccades, without affecting motion illusion strength, this would suggest that the exact frequency of microsaccades is not directly related to observing the illusion. These predictions were further tested in a third experiment, in which we used a broad range of Riloid patterns, varying several stimulus parameters. Because of this large range of randomly presented stimuli, we could ask participants to rate the strength of the illusion on each trial, without giving them an opportunity to base their responses mainly on their impression of

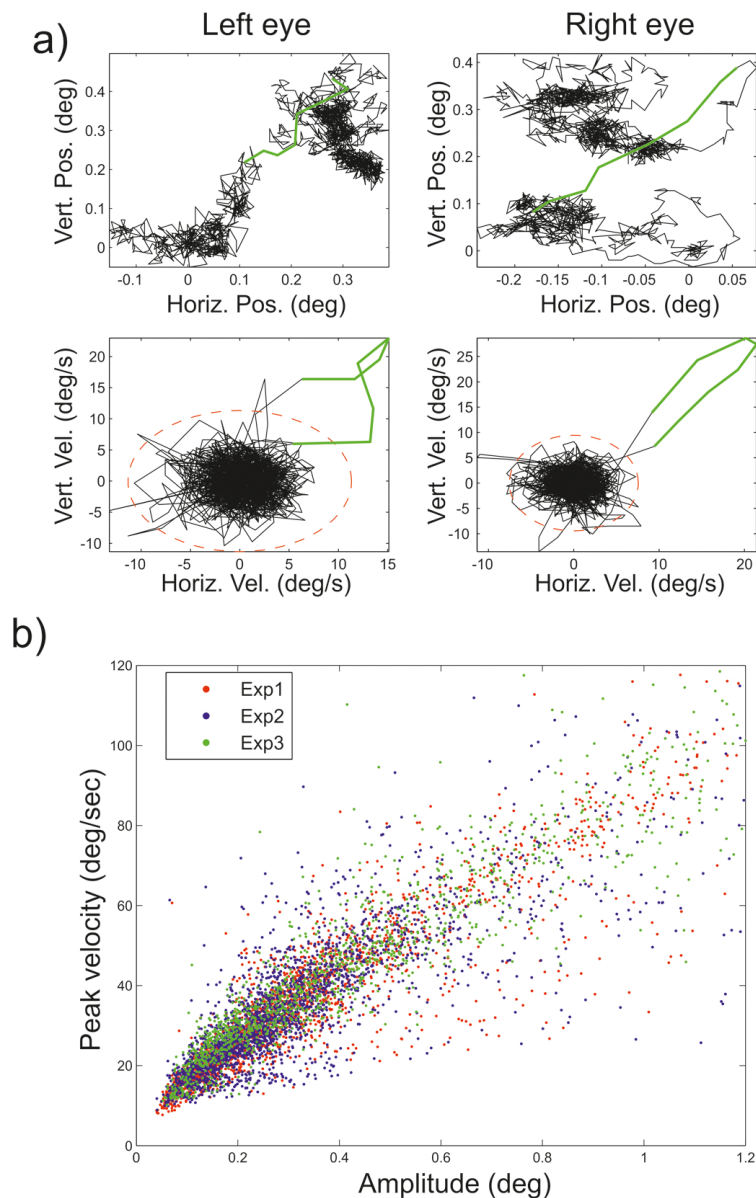


Figure 1. (a) Illustration of the algorithm used to detect microsaccades (Engbert and Kliegl 2003b). The red dashed lines in the velocity plots (bottom row of subplots) for both eyes (left and right subplots) indicate the (noise-dependent) thresholds for microsaccade detection. In green: The section of the trace belonging to the microsaccade, also shown in the position plots (top row). (b) Microsaccades have often been shown to follow the main sequence—an approximately linear relation between the amplitude of the eye movement and the peak velocity. This linear relation is also found for the present set of data (observations for Experiment 1, 2, and 3, shown in red, blue, and green, respectively).

the stimulus layout, by trying to respond as consistently as possible (as could, for example, occur for mixtures of Riloids and checker patterns, where observers might rate the strength of the checker pattern in the background rather than the perceived motion illusion per se). By obtaining ratings for the strength of the perceived motion and by recording eye movements on every single trial, a more stringent association could be obtained between the occurrence of microsaccades and the motion illusion.

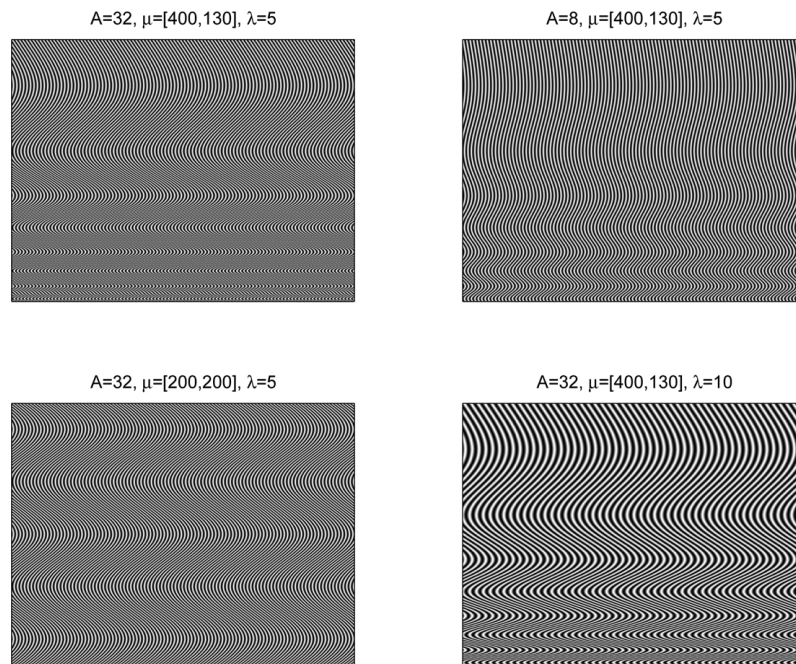


Figure 2. Examples of different 'Riloids' (parametric versions of the painting *Fall* by Bridget Riley), showing the influence of different parameters on the pattern: phase modulation amplitude A , phase modulation wavelength μ , and grating period λ . In psychophysical experiments (Zanker et al 2010), it was shown that variations of the amplitude (A) and the spatial period of phase modulation (μ) affected the strength of the illusion, whereas the spatial wavelength (λ) had little effect.

2 Experiment 1

In Experiment 1, we investigated whether characteristics of microsaccades are related to the strength of the motion illusion. To vary the strength of the illusion, different contrast ratios were used for a mixture of a regular array of squares with a Riloid pattern (see Figure 3; for details, see Zanker et al 2010). Participants were asked to maintain fixation while looking at an image, first presented together with a fixation target, which was later removed.

2.1 Methods

2.1.1 Participants

Seven participants took part in Experiment 1. Four participants were naive with respect to the purpose of the experiment, whereas the others (three lab members) had heard about the aim of the experiment before taking part in it. All participants had normal or corrected-to-normal vision and gave their informed consent before taking part in the study, which was approved by the local ethics committee.

2.1.2 Apparatus

Stimuli were presented on a 21 inch CRT screen (refresh rate of 100Hz) controlled by an AMD Athlon 2400+ PC using the Experimental Builder software package (SR Research Osgood, ON, Canada). Binocular eye movements were recorded with an Eyelink II system (SR Research Osgood, ON, Canada) at a rate of 500Hz (pupil only mode) by means of a second, Pentium 4, PC. The Eyelink II system allows for eye movements to be recorded at a spatial resolution of less than 0.01 degrees and an accuracy of at least 0.5 degrees. A standard 9-point calibration route was performed before each 12th trial. An additional drift correction preceded each trial, in which participants were asked to fixate a centrally presented fixation target and press

the spacebar of a computer keyboard, to correct for drift in the recorded eye position due to possible slippage of the head-band to which the cameras of the system were mounted. Participants viewed the computer screen from a distance of 57cm, which was maintained by means of a chin rest.

2.1.3 Stimuli

Figure 3a illustrates the stimulus sequence. Each trial started with a bullseye fixation target of 1.2 deg, consisting of two rings partitioned in four patches alternating in colour from red to white, presented at the centre of a white screen. After 3s, a stimulus pattern measuring 23 deg by 23 deg was presented behind the fixation symbol. Another 3s later, the fixation symbol was removed.

A basic Riloid pattern was constructed using the equations reported earlier (Zanker and Walker 2004), with a modulation amplitude (A) of 32 pixels and modulation wavelengths (μ) equal to 400 and 130 pixels (top and the bottom, respectively). The grating period (λ) was set to 8 pixels.

This basic Riloid pattern was mixed with a regular pattern consisting of 16 evenly distributed squares each measuring 3 deg. The space between the checkers equalled 3 deg and the distance to the edge was 1.5 deg. Three different weights were used for mixing the two components, resulting in relative contrasts of 10% to 90%, 50% to 50%, and 90% to 10% of Riloids and square pattern, respectively, as illustrated in Figure 3b (indicated by the Riloid contrast in the mixture, c). From an earlier study (Zanker et al 2010), these three combined patterns were known to induce weak, medium, and strong motion illusions, respectively.

2.1.4 Design

Participants completed a total of 36 trials, which were presented in three different experimental blocks of 12 trials each. In these blocks four trials of each of the three combined Riloid and square patterns were presented in a random order.

2.1.5 Procedure

Participants started each trial by looking at the central fixation target of the drift correction procedure and pressing the spacebar on the keyboard in front of them. After releasing the spacebar, the stimulus sequence shown in Figure 3a was presented. Participants were instructed to fixate the fixation target and to maintain fixation on this location during the entire sequence, after which they were free to move their eyes. In addition to maintaining fixation, participants were asked to avoid blinking until the end of the stimulus presentation. After the presentation of the sequence, participants could take as much time as they wanted until starting the next trial. Typically, participants took about 4 to 10s before moving on to the next trial.

2.1.6 Data analysis

The measured horizontal and vertical gaze positions were analysed for microsaccades using the algorithm by Engbert and Kliegl (2003b). Microsaccades were defined as movements of the eye for which the horizontal and vertical velocity exceeded a set criterion, based on the overall noise in the signal (6 standard deviations of velocity fluctuations), for at least 6ms in both eyes. An additional amplitude criterion of less than 30 pixels (1.13 degrees) was used, removing the data from accidental saccades to different areas of the screen.

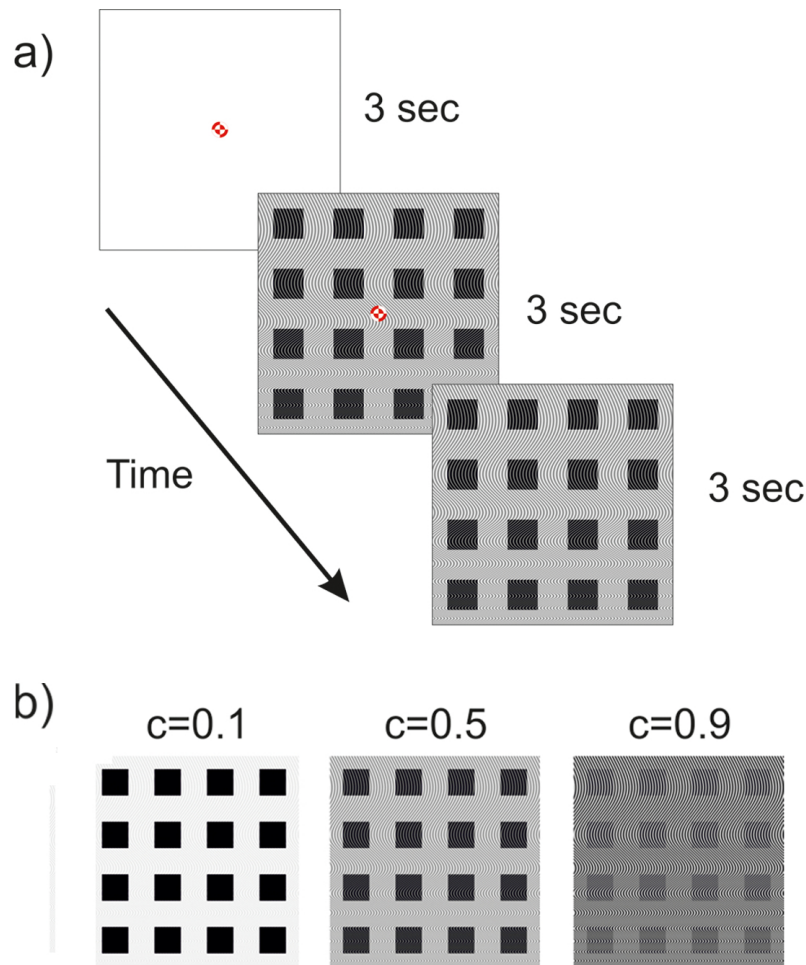


Figure 3. (a) Stimulus sequence in Experiment 1. Participants were asked to maintain visual fixation for 9s, at a location that was first indicated by a fixation target that was presented on a white background for 3s, followed by the Riloid pattern (and fixation target) for 3s, after which the fixation symbol was removed for another three s. (b) Riloid patterns used in Experiment 1, with contrast mixtures between the Riloid and the square pattern indicated by the contrast of the Riloid component in the mixture, with $c = 0.1, 0.5, 0.9$ referring to a 10%, 50%, and 90% component of the Riloid component, respectively.

2.2 Results

Participants made on average 0.91 microsaccades per second, with microsaccade rates varying from 0.39 to 1.37 per second between participants. Microsaccade rates also varied substantially within trials, with the highest rate found early after the onset of the fixation point and the lowest rate at the end of the trial (see Figure 4a), showing an overall decay of the rate with prolonged fixation (see also, Zanker et al 2003).

Figure 4b illustrates the effect of the fixation condition (fixation symbol only, fixation and stimulus pattern, stimulus pattern only) and the contrast-ratio in the mixed pattern on the rate of occurrence of microsaccades across participants. Whereas the fixation condition, or time in the trial, had a huge effect on the number of microsaccades, no such an effect was found of the relative contrast of the two components. These observations were confirmed by a repeated measures analysis of variance, testing these two factors and their interaction, demonstrating a significant main effect of the fixation condition ($F_{2,12} = 25.8, p < 0.001$), in the absence of a main effect of contrast ratio ($F_{2,12} = 0.59, p = 0.57$) or an interaction between these factors ($F_{4,24} = 0.54, p = 0.95$).

Important for understanding the role of microsaccades in the motion illusion might not only be the rate but also the amplitude of the microsaccades, because this determines how far the retinal image shifts during each microsaccade. In [Figure 4c](#) a histogram of the microsaccade amplitudes is plotted as an average across stimulus conditions, trial intervals, and participants, showing that the majority of the detected microsaccades had amplitudes in the 0.1 to 0.5 deg range and that few (micro)saccades occurred with amplitudes larger than the cut-off value of 1.13 deg (or 30 pixels). In [Figure 4d](#) the role of the fixation interval and relative contrast of the two components (Riloid and squares) on the amplitude saccades is investigated, revealing no effect of either factor, which was confirmed in a repeated measures analysis of variance (fixation interval: $F_{2,12} = 0.31$, $p = 0.74$; relative contrast: $F_{2,12} = 0.89$, $p = 0.44$; interaction: $F_{4,24} = 0.26$, $p = 0.90$).

A second important variable of gaze stability is the direction of the microsaccades, which for the illusion determines the direction of the shift of the retinal image. In [Figure 4e](#) the microsaccade rates are shown for the four cardinal directions (rightward, upward, leftward, downward) for the three stimulus intervals and three different relative contrast of the two stimulus components. The following observations can be made. First, microsaccade rates decrease across the three intervals, in agreement with [Figures 4a and 4b](#). Second, more microsaccades are found in horizontal (leftward, rightward) than in vertical directions (upward, downward). Third, no systematic differences in the direction of microsaccades are found for the different contrast conditions. The statistical significance of these observations was tested using a three-way repeated measures analysis of variance, testing differences in microsaccade direction (horizontal versus vertical), differences due to the fixation interval (fixation, stimulus plus fixation and stimulus only), and the relative contrast ($c = 0.1$, $c = 0.5$, $c = 0.9$). A main effect of the interval was found ($F_{2,12} = 26.12$, $p < 0.001$), as well as a main effect of the direction of the microsaccade (horizontal versus vertical; $F_{1,6} = 9.67$, $p = 0.021$). The interaction between the interval and the direction was also significant ($F_{2,12} = 4.23$, $p = 0.041$). The remaining interactions and main effects did not reach significance.

2.3 Discussion

In Experiment 1 we investigated the properties of the small saccadic eye movements during visual fixation of stimuli that induce illusory motion with varying strength. Our results suggest that microsaccade properties (rates, amplitudes, directions) are not related to the strength of the motion illusion. Whereas the particular stimulus pattern did not affect microsaccades, the rate at which they occurred, varied with the stimulus interval and therefore possibly with the type visual stimulation (fixation symbol or Riloid). Higher rates were found when the screen contained just a fixation symbol, whereas lower rates were found when the Riloid pattern was presented. Microsaccade amplitudes, in contrast, were not significantly different for the different intervals of visual stimulation.

Our findings agree with earlier observations (Zanker et al 2003; Zanker and Walker 2004), who found that microsaccade rates were not influenced by the type of visual stimulus (either a pattern inducing illusory motion, or uniform grey field or checkerboard control patterns which were perceived as static). Zanker and colleagues (Zanker et al 2003; Zanker and Walker 2004) also observed that during the course of visual fixation the rate of microsaccades decreased. It is therefore possible that the difference that we observed of the presence of the fixation symbol could be the consequence of prolonged fixation rather than being related to the fixation stimulus. This possibility is investigated in a second experiment, in which the presence or absence is varied across rather than within trials.

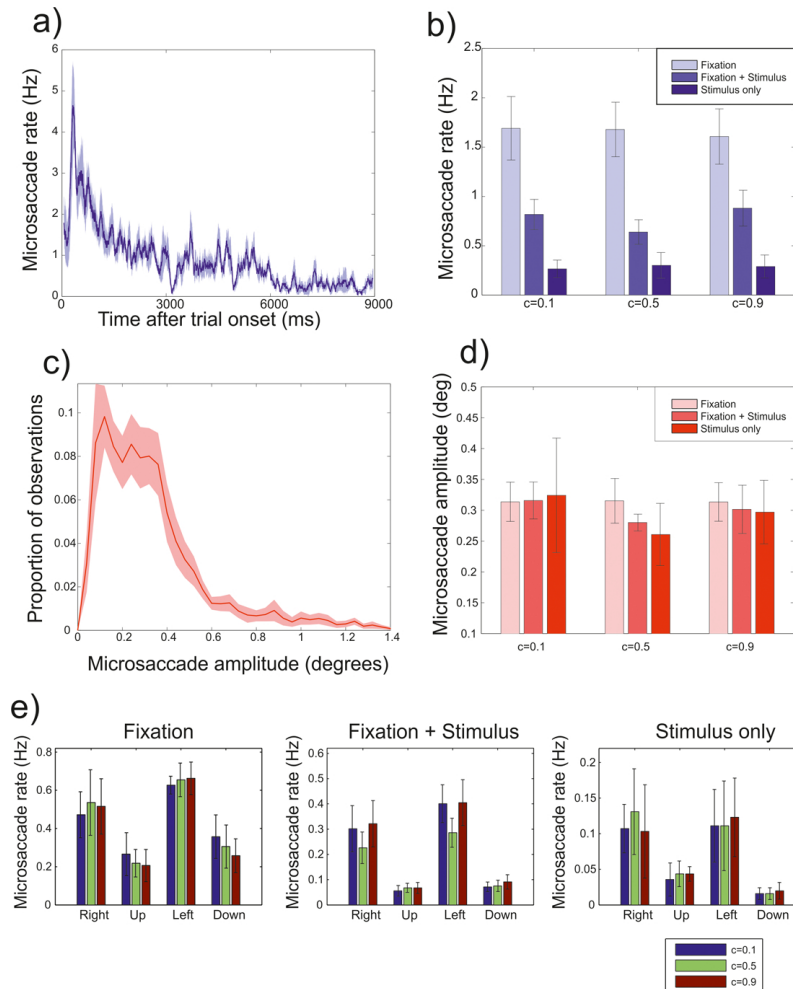


Figure 4. Microsaccade properties. (a) Microsaccade rate as a function of the time from trial onset across all conditions. (b) Microsaccade rate for each contrast condition and stimulus interval. (c) Histogram of observed microsaccade amplitudes. (d) Microsaccade amplitudes for each contrast condition and stimulus interval. (e) Microsaccade rates for the four cardinal directions (rightward, upward, leftward, downward) for the three stimulus intervals (fixation, fixation+stimulus pattern, stimulus pattern only) and stimulus conditions (relative contrast of 0.1, 0.5, and 0.9). Averages are based on data of all seven participants. Error bars and shaded intervals in time-course plots show the standard error of the mean.

3 Experiment 2

In Experiment 2, we investigated whether the effects of the fixation symbol found in Experiment 1 were due to prolonged fixation by varying the presence or absence of the fixation symbol across trials.

3.1 Methods

Eight new participants took part in the experiment. Except for author FH, participants were students at Royal Holloway University, taking part in return for course credit.

The stimulus sequence in Experiment 2 is illustrated in [Figure 5a](#). Trials started with the presentation of a fixation target, after which the composite stimulus pattern appeared. With the presentation of the stimulus pattern, the fixation symbol either remained ([Figure 5a](#), left) or was removed from the display ([Figure 5a](#), right).

The basic Riloid pattern was changed with respect to Experiment 1, by setting the modulation amplitude (A) to 24 (instead of 32) pixels, and the modulation wavelength

(μ) to a constant of 200 pixels across the entire pattern (instead of changing from 400 to 130 pixels from top to bottom) to better match the stimuli used by Zanker et al (2010). In addition to using a set of stimuli with the same three contrast mixtures as in Experiment 1, a second set was created in which the overall contrast of the pattern was strongly reduced (see Figure 5b) to test for the effects of the contrast of the pattern, which has been shown to strongly affect the motion illusion (Zanker et al 2010). By adding these low-contrast stimuli, the number of trials doubled to 72 (12 repetition of each of 6 contrast conditions).

Except for the above changes to the design (using two trial intervals), to the basic Riloid pattern, and the inclusion of the low-contrast stimuli, all methods used in Experiment 2 were identical to those used in Experiment 1.

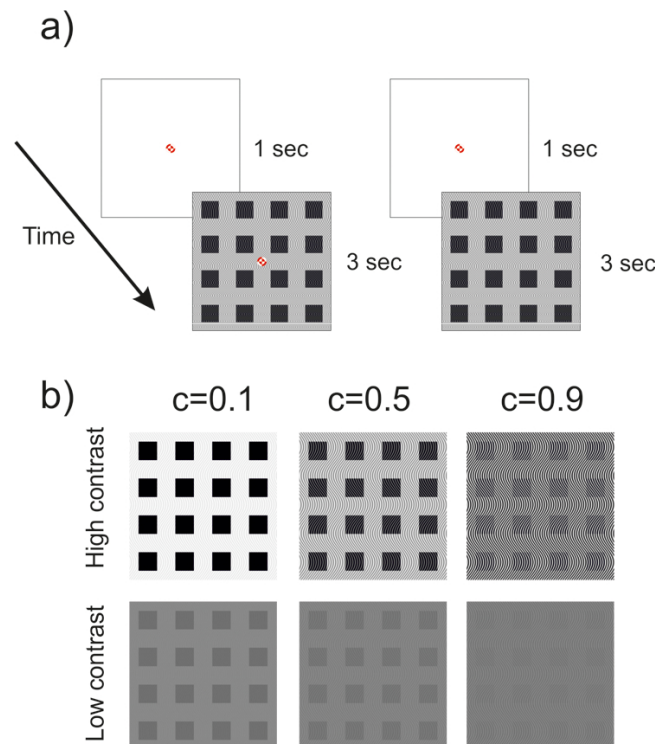


Figure 5. (a) Stimulus sequence of Experiment 2. Trials all started with the presentation of a fixation target for 1s. After presentation of the fixation symbol, the stimulus pattern appeared for 3s, whilst the fixation target was still present on the screen (left panel, in 50% of the trials) or disappeared (right panel, in the other 50% of trials). (b) Composite stimulus patterns used in Experiment 2. The high-contrast patterns (top row) had the same contrast mixtures of Riloids and square patterns as those used in Experiment 1. Low-contrast stimuli were added, in which the overall contrast of the stimulus was strongly reduced (bottom row).

3.2 Results

As for Experiment 1, microsaccade rates were found to vary considerably between participants. The lowest rate observed was 0.52 per second, whereas the largest rate was 1.82 per second. On average, participants generated 1.08 microsaccades per second. Figure 6 presents an overview of different microsaccade properties, with the average plots (b, d, e) showing the data for the high-contrast stimuli. Those for the low-contrast stimuli are shown in Figure 7.

Figure 6a shows the microsaccade rate as a function of the time after the onset of the trial, based on the data across all conditions, displaying a pattern quite similar to that observed for Experiment 1. Just after the onset of the fixation point, the microsaccade rate shows a

short dip, followed by a marked increase. After the onset of the stimulus pattern, a distinct dip in the rate is found, followed by a shallow rebound and slow drop-off.

Figure 6b plots the microsaccade rate for the different stimulus conditions for the high-contrast stimuli. The microsaccade rate during the presentation of the fixation target and white background was remarkably larger than during the presentation of the composite stimulus (with or without the fixation symbol), in agreement with the data of Experiment 1. This higher rate is likely to be the consequence of the huge rise in the microsaccade after fixation onset. Interestingly, the rates are also higher during the presentation of the composite stimulus with the fixation target than without the fixation symbol, demonstrating that the difference observed in Experiment 1 was not solely due to prolonged fixation. A repeated measures analysis of variance was used to investigate the statistical significance of the differences between conditions. A significant main effect of the trial interval (fixation versus stimulus pattern with or with and fixation symbol) was found ($F_{2,14} = 4.52, p = 0.031$), which did not interact with the relative contrast of Riloid and square pattern ($F_{4,28} = 0.532, p = 0.71$). The relative contrast did not influence the microsaccade rate ($F_{2,14} = 0.82, p = 0.46$). When the two stimulus trial sequences are compared, a significant main effect of the presence of the fixation target is found ($F_{1,7} = 15.1, p = 0.06$), in the absence of a main effect of relative contrast ($F_{2,6} = 1.07, p = 0.40$) and an interaction with the relative contrast ($F_{2,6} = 0.32, p = 0.74$).

Figure 6c shows a histogram of observed microsaccade amplitudes, showing a similar pattern to that observed in Experiment 1, with most microsaccades of amplitudes of 0.4 deg or less. Figure 6d plots the microsaccade amplitude for the different conditions with overall high-contrast. As in Experiment 1, no clear effects of the interval or trial sequence or relative contrast on microsaccade amplitude can be detected. This observation was confirmed with a repeated measures analysis of variance (ANOVA), showing non-significant main effects of the interval—fixation target on white background versus composite stimulus with or without fixation target ($F_{2,14} = 0.93, p = 0.42$), relative contrast ($F_{2,14} = 0.75, p = 0.49$), and no interaction between the two factors ($F_{4,28} = 1.23, p = 0.32$). Also, when the two composite stimulus intervals were compared directly, no significant main effects—with and without fixation target ($F_{1,7} = 1.09, p = 0.33$), relative contrast ($F_{2,14} = 0.93, p = 0.42$), or interaction ($F_{2,14} = 1.17, p = 0.34$) were found.

In Figure 6e the microsaccade rates in the different directions (right, down, left, up) are displayed. Interestingly, no clear bias towards horizontal directions was observed during the presentation of the fixation target on a white background (left panel). During the presentation of the composite stimulus (with or without a fixation target; middle and right panels, respectively), the bias towards the horizontal directions was restored. During the presentation of the composite stimulus together with the fixation symbol, there appears to be stronger bias towards the horizontal for the stimuli with low relative contrast. Using a three-way repeated measures ANOVA, the statistical significance of the differences between the rates for horizontal and vertical microsaccades as well as the effects of the interval and the relative contrast were tested. A significant main effect of the interval was found ($F_{2,14} = 5.84, p = 0.014$). The main effect of microsaccade direction (horizontal versus vertical), however, failed to reach significance ($F_{1,7} = 5.25, p = 0.056$). The interactions and the main effect of relative contrast were not statistically significant either.

In Figure 7 we investigate whether the pattern of results changes by changing the overall contrast of the stimuli. Whereas the microsaccade rates are very similar to those observed for the high overall contrast stimuli, the microsaccade amplitudes show an increase during the presentation of the Riloid without a fixation point. As for the high-contrast stimuli, the only factor that significantly affected microsaccades rates for the low-contrast stimuli was

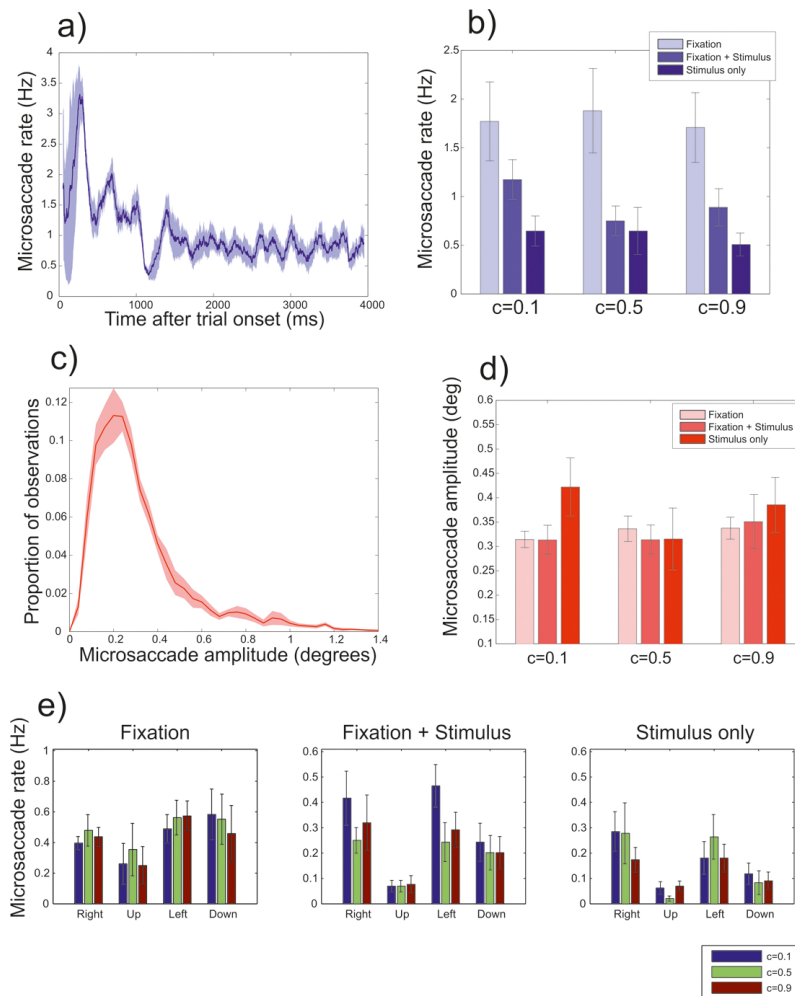


Figure 6. Properties of microsaccades observed in Experiment 2. (a) Microsaccade rate as a function of the time from trial onset across all conditions and stimuli. (b) Microsaccade rate for different relative contrasts ($c = 0.1, 0.5,$ and 0.9) and trial interval (fixation, stimulus pattern) or stimulus sequence (composite stimulus with or without fixation symbol), for the high-contrast stimuli. (c) Histogram of observed microsaccade amplitudes across all conditions and stimuli. (d) Microsaccade amplitude for each relative contrast and trial interval or stimulus sequence, for the high-contrast stimuli. (e) Directional microsaccade rate in the four cardinal directions (rightward, upward, leftward, downward) for the different intervals or stimulus sequences and stimulus conditions (relative contrast of $0.1, 0.5,$ and 0.9). Error bars and intervals show the standard error of the mean across participants.

the interval/fixation condition ($F_{2,14} = 4.52, p = 0.031$). This effect on the microsaccade rate was not due to the interval alone. When the two stimulus conditions (with and without a fixation symbol presented together with the stimulus pattern) were compared, a main effect of the fixation stimulus was found ($F_{1,7} = 15.07, p = 0.006$), whereas no effect of the relative contrast or an interaction was found (both p -values > 0.48). A repeated analysis of variance on the saccade amplitudes revealed a significant main effect of the interval/fixation condition (fixation target only versus composite stimulus with or without fixation target; $F_{2,14} = 7.18, p = 0.007$), as well as a main effect of relative contrast ($F_{2,14} = 3.76, p = 0.049$). The interaction between the two factors did not reach significance ($F_{4,28} = 1.91, p = 0.14$). When the two composite stimulus conditions were compared, a main effect of fixation target on microsaccade amplitude was found ($F_{1,7} = 7.70, p = 0.027$). The interaction with the relative contrast failed to reach significance ($F_{2,14} = 1.49, p = 0.259$). The main effect of the relative

contrast on microsaccade amplitudes, however, was significant ($F_{2,14} = 5.57, p = 0.017$). The pattern of results for microsaccade directions was similar to that found for the high-contrast stimuli, with one exception. Whereas for the high-contrast stimuli the difference between the rates for horizontal and vertical microsaccades did not reach significance, the main effect of direction was significant for the low-contrast stimuli ($F_{1,7} = 6.66, p = 0.036$). As for the high-contrast stimuli, the main effect of the interval/fixation stimulus was significant for the low-contrast stimuli ($F_{2,14} = 4.28, p = 0.036$). The remaining interaction and main effects were not significant.

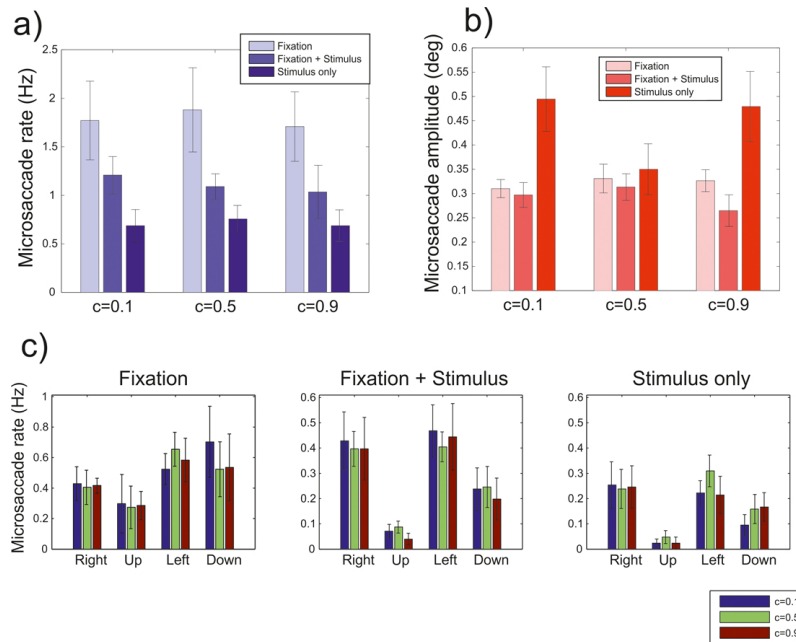


Figure 7. Microsaccade rate, amplitude, and direction for the low-contrast stimuli of Experiment 2. (a) Microsaccade rate for different relative contrasts ($c = 0.1, 0.5$, and 0.9) and trial interval (fixation or stimulus pattern) or stimulus sequence (composite stimulus with or without fixation symbol). (b) Microsaccade amplitude across stimulus conditions and trial interval or stimulus sequence. (c) Directional microsaccade rates (rightward, upward, leftward, downward) for the different intervals or stimulus sequences and relative stimulus contrasts. Error bars and intervals show the standard error of the mean across participants.

4 Experiment 3

One of the explanations of illusory motion in stimuli like Riley's *Fall* involves the shift of the retinal image caused by microsaccades. Such retinal shifts induce a complex pattern in the human motion system, which resembles the subjective experience of a shimmering motion in the illusion (Zanker 2004; Zanker et al 2010). To test this explanation of illusory motion in *Fall*, we investigated the relation between the illusion strength and properties of microsaccades occurring during the inspection of the image in Experiments 1 and 2. Stimuli with known illusion strengths from a previous study (from Zanker et al 2010) were used, and microsaccade properties were examined across the different images. No clear differences were found in the patterns of microsaccades for the different stimuli reflecting different motion illusion strengths, suggesting that rates, amplitudes and directions of microsaccades are not associated with the strength of the motion illusion. One possible issue, however, could be that by relying on stimuli with known illusion strengths, small trial by trial fluctuations in the perceived motion strength might not be detectable. In Experiment 3, we therefore took a

larger set of stimuli (by varying several parameters of the Rilooids, without any checkers in the background), so that we could ask participants to rate the perceived illusion strength on a trial by trial basis, without risking that participants would respond to each stimulus in a stereotyped way by memorizing the previously given response for a certain stimulus. This larger set of stimuli therefore had the advantage that participants might report trial by trial variations in the perceived motion strength, possibly caused by differences in the fixational eye movements made on that trial. By comparing trials with few and trials with many microsaccades, it can be investigated whether retinal shifts from microsaccades are an important factor in the motion illusion in Riley's *Fall* or whether other explanations of the illusion might be required.

4.1 Methods

Fourteen new participants and author FH participated in Experiment 3, resulting in a total of fifteen participants (thirteen female, average age 19.3 years). The new participants were students from the University of Leuven taking part in return for course credit. The apparatus was very similar to that used in Experiments 1 and 2. An Eyelink II system (the same model as in Experiments 1 and 2) was used to record the eye movements. Stimuli were presented on a 21 inch CRT screen (Iiyama HM204DT), at a refresh rate of 75Hz (100Hz in Experiments 1 and 2). Participants were seated at a distance of 60 cm from the screen (57 cm in Experiments 1 and 2), maintained by a chin rest.

Stimuli were constructed using the equations from Zanker et al (2003), in which the modulation amplitude (A) was set to either of 6 or 36 pixels (minimum and maximum values tested by Zanker et al 2010, respectively), the modulation period (μ) to either 100 or 400 (top and the bottom had the same modulation periods), and the overall contrast (c) either to 0.1, 0.5, or 0.9 (10%, 50%, and 90% of maximum contrast, respectively). The grating wavelength (λ) was set to same values as in Experiments 1 and 2, namely 8 pixels. The size of the stimuli was kept at 600 pixels (22.9 by 22.9 deg of visual angle; cf, 23.0 by 23.0 degrees in Experiments 1 and 2). Each of the resulting 12 stimuli was presented six times to each participant, resulting in 72 trials per participant, three times with a fixation point superimposed on the image and three times without the fixation point.

Before the start of the experiment, participants performed at least 5 practice trials, randomly chosen from the set of 72 trials. During these practice trials, it was made sure that participants maintained fixation during the presentation of the stimuli. The practice trials also allowed participants to obtain an impression of the types of stimuli and their elicited motion illusions so that they could establish a baseline to determine what to consider as strong and weak motion illusions.

The trial structure was the same as in Experiment 2, with the fixation point presented for 1s, before the stimulus was presented for 3s (with or without the fixation point superimposed). After the offset of the stimulus, participants were asked to indicate the strength of the motion illusion induced by the stimulus on a three point scale (1 = weak, 2 = medium, 3 = strong motion illusion). Feedback after their button press confirmed their choice. Every 12 trials, participants were allowed a short break before continuing with the remainder of the trials.

4.2 Results

Figure 8 provides an overview of the motion illusion ratings of the participants. Generally, participants more often responded with lower values for the perceived motion strength (top left plot; $F_{1,14} = 7.37$, $p = 0.003$; linear contrast). The subsequent subplots of Figure 8 show how the average rating depended on the different parameters of the stimuli and presentation. In line with earlier studies (Zanker et al 2003; Zanker et al 2010), larger values for the modulation amplitude (A) resulted in higher ratings of the perceived illusion strength ($t_{14} = 2.45$, $p = 0.028$). Also in line with earlier observations (Zanker et al 2010), lower values for the

modulation period (μ) led to lower average ratings of the illusion ($t_{14} = 12.20$, $p < 0.001$). Higher contrasts (c) led to higher reported motion strengths ($F_{1,14} = 4.77$, $p = 0.046$; linear contrast), in agreement with earlier findings (Zanker et al 2010). The presence of the fixation symbol did not significantly influence the strength of the illusion ($t_{15} = 1.93$, $p = 0.074$), in agreement with earlier observations, showing that similar results are obtained when the fixation point is shown in between two stimuli (Zanker et al 2010) or in the centre of a single stimulus (present study).

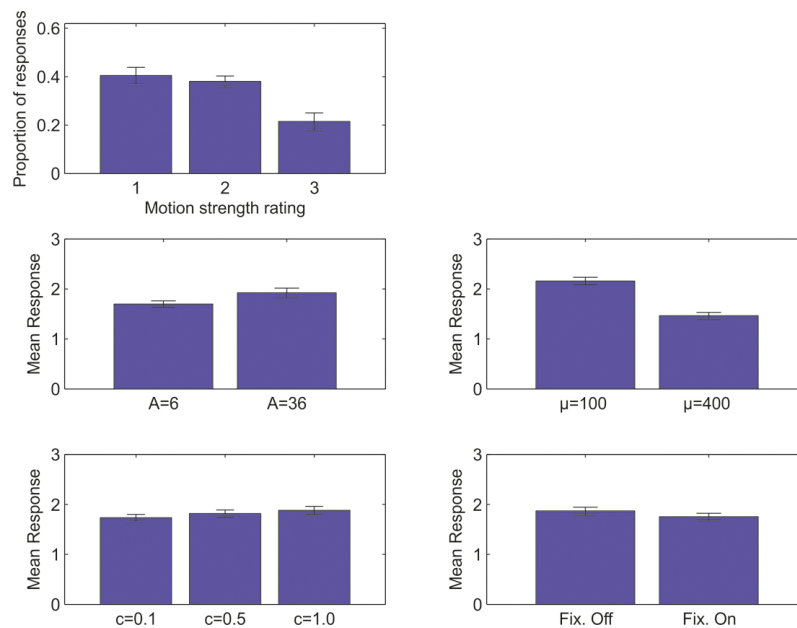


Figure 8. Average ratings and response frequencies for Experiment 3. The top-left plot shows the relative frequency of the different ratings across observers, showing a bias towards weaker (rating of 1 or 2) reported illusion strengths. The remaining plots show the average rating as a function of the different parameter values or conditions. The middle plots show that stronger ratings are obtained for stimuli with larger modulation amplitudes (' A ') and smaller modulation periods (' μ '). The bottom plots show a significant, but weaker effect of the contrast (' c '), and no significant effect of the presence (or absence) of a fixation point.

Figure 9 provides an overview of the microsaccade findings, linking the ratings on each trial to the frequency and amplitude of the microsaccades. The frequency of microsaccades during the trial (Figure 9a) showed a similar profile as in Experiment 2 (Figure 6a), showing two responses: One to the onset of the fixation symbol ($t = 0$ ms; left of red line) and one to the onset of the Rilloid stimulus ($t = 1000$ ms; right of red line). Whereas we found no influence of the strength of the illusion in the previous two experiments, the trial by trial analysis of Experiment 3 revealed an inverse relation between the perceived strength of the motion illusion and the microsaccade rate. For example, it was found that microsaccades were more often completely absent (0 microsaccades in a 3s interval; Figure 9b) when the illusion was rated more strongly ($F_{1,14} = 15.34$, $p = 0.002$; linear contrast). Furthermore, the more microsaccades were made, the lower the motion illusion ratings (Figure 9c; $F_{1,14} = 8.54$, $p = 0.011$; linear contrast). Pairwise comparisons between trials with zero microsaccades and trials with one, two, three, or four microsaccades show that only for trials with two microsaccades, the difference in the rating of the illusion strength compared to trials with zero microsaccades fails to reach significance ($t_{14} = 1.99$, $p = 0.066$). For trials with one ($t_{14} = 2.97$, $p = 0.010$), three ($t_{14} = 3.58$, $p = 0.0030$), and four microsaccades ($t_{14} = 2.45$, $p = 0.028$)—although this latter comparison fails to reach statistical significance if the stringent

Bonferroni correction is applied, setting the critical alpha level to 0.0125, for 4 comparisons), the average motion illusion rating was always significantly lower compared to trials without microsaccades.

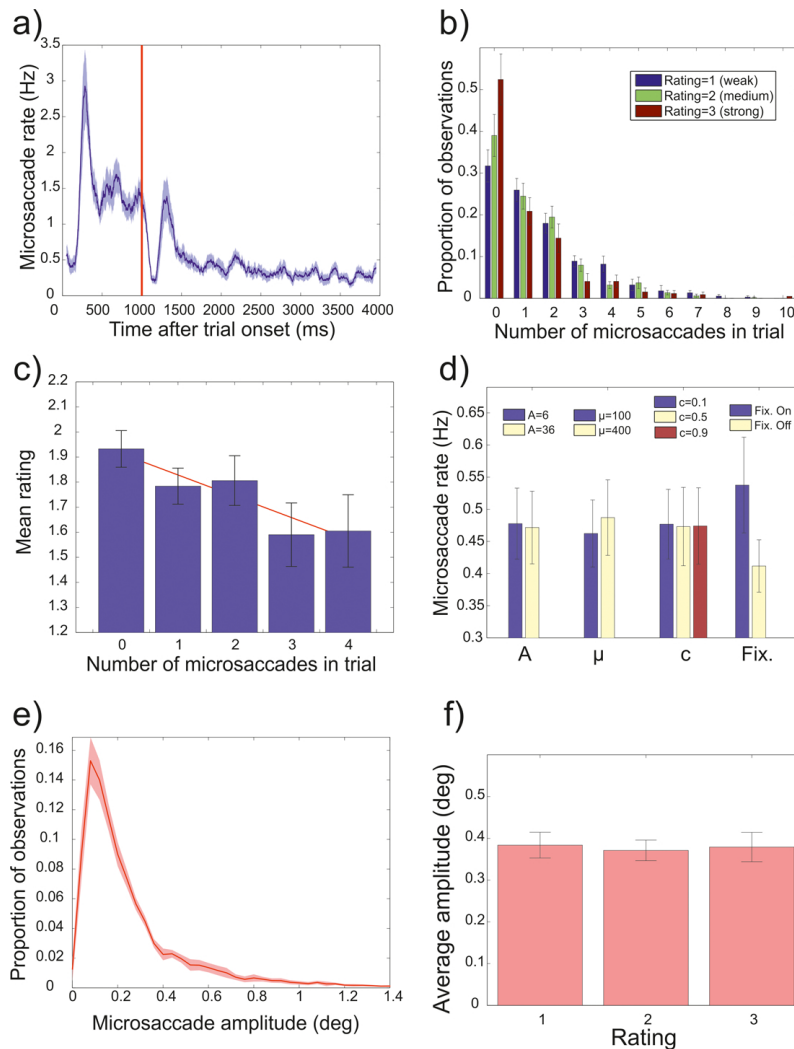


Figure 9. Microsaccade properties in Experiment 3. (a) Microsaccade rates show the typical ‘microsaccade signature’ (eg, Engbert and Kliegl 2003b and Experiments 1 and 2) after fixation ($t = 0$ ms) and stimulus onset ($t = 1000$ ms; red line), with a reduction in the rate followed by an increase above the initial rate. (b) The proportion of trials with 0, 1, ..., 10 microsaccades after stimulus onset ($t = 1000$ ms), showing that on many trials no single microsaccade was detected. The rate of trials without a microsaccade was larger for higher ratings of motion. (c) The average rating as a function of the number of microsaccades after stimulus onset ($t=1000$ ms), showing a downward trend (regression line in red, in the background). (d) Microsaccade rates as a function of the different stimulus parameters (modulation amplitude, A ; modulation period, μ ; contrast, c ; and fixation point presence), suggesting that only fixation presence influences the microsaccade rate. (e) The histogram of microsaccade amplitudes showing a similar pattern as in Experiments 1 and 2. (f) The average amplitude of microsaccades (on trials on which a microsaccade occurred) as a function of the motion illusion rating, showing no effect of the strength of the illusion.

An examination of the influence of the stimulus parameters on the microsaccade rates (Figure 9d) confirms the findings from the previous two experiments. Rates were no different for the different stimulus parameters (modulation amplitude, modulation period or contrast), but a significant influence of the presence of a fixation point was found ($t_{14} = 2.31$, $p = 0.037$).

A similar histogram of observed microsaccade amplitudes as in Experiment 1 and 2 was found in Experiment 3 (Figure 9e). A comparison of the microsaccade amplitudes (for trials in which at least one microsaccade was observed) did not reveal an effect of the rated motion illusion (Figure 9f— $F_{2,28} = 0.11$, $p = 0.90$).

5 General discussion

In three experiments, we investigated involuntary eye movements ('microsaccades') made by observers who were instructed to maintain fixation while watching parametric versions of Bridget Riley's *Fall* (called 'Riloids'). The stimulus presentation was varied in several respects. First, we investigated the influence of mixing the original Riloid with a regular pattern of squares (Experiments 1 and 2), which has been demonstrated to manipulate the strength of the motion illusion observed in the image (Zanker et al 2010). Second, the overall contrast of the image was varied (Experiment 2), another factor that has been shown to strongly influence the strength of perceived illusory motion (Zanker et al 2010). Third, the influence of a fixation target was determined, which was present or absent in different intervals (Experiment 1) or in half of the trials (Experiments 2 and 3) while the stimulus pattern was presented. Previous psychophysical experiments (Zanker et al 2010) have suggested that such a fixation target has little influence on the strength of the illusion. Finally, we also included Riloids without background checkers and varied the modulation amplitude, the modulation period, and the contrast of the pattern (Experiment 3).

Several properties of microsaccades were examined, including their frequency and amplitude (Experiments 1 and 2) and their relation to the perceived motion illusion judgements (Experiment 3). Earlier research (Zanker and Walker 2004) has suggested that whilst image instability is crucial for the perception of the illusion (the illusion is strongly reduced when retinal motion is eliminated and simulations with a computational model suggest that retinal shifts are essential to explain the patterns of motions perceived in the stimuli), the rate at which microsaccades occur is not directly related to stimulus that is shown. This observation was confirmed in the present study for a different set of stimuli which allowed for controlled variations of illusion strength (Experiments 1 and 2). Whether there is an association between microsaccade frequency and the illusion strength (rather than the stimulus) was examined in Experiment 3, in which participants were asked to rate the perceived strength of motion after each trial. This experiment revealed two important aspects. First, in many trials no microsaccades were detected at all, and even in the absence of such microsaccades, participants indicated that they perceived illusory motion. Second, trials with fewer microsaccades were associated with higher ratings for the perceived motion illusion. The more microsaccades were observed in an individual trial, the lower the average rating of the motion illusion strength. These observations support the idea raised earlier that illusion strength is not directly related to the frequency of microsaccades (Zanker and Walker 2004).

In our experiments, we replicated the effects of stimulus onsets on microsaccade rates. In agreement with earlier observations (eg, Engbert and Kliegl 2003b; Laubrock et al 2005), stimulus onsets—such as the onset of the fixation symbol or the Riloid—led to an initial decrease in the rate, followed by a pronounced increase and slow return to baseline. This pattern in microsaccade rates, known as the 'microsaccade signature', was also found for stimulus onsets in the auditory modality (Rolfs et al 2005, 2008) and for partial offsets of stimuli presented at fixation (Hermens et al 2010).

Another factor that influenced the microsaccade rate was the presence of a fixation target, which may provide some clues about the role of microsaccades in gaze control. Fewer microsaccades were found when the fixation target was absent. This was the case when

the fixation target was present in the initial stimulus phase and was removed in the later stimulus phase (Experiment 1), and also, albeit to a lesser degree, when a direct comparison between trials with and without a fixation symbol was made (Experiments 2 and 3). This latter comparison excludes an explanation suggesting prolonged fixation as the cause of the reduction in microsaccades (Zanker and Walker 2004) rather than the presence of the fixation target. A possible explanation for the increased microsaccade rate with a fixation target could be that microsaccades serve to bring the eye back to fixation after periods of drift (Ditchburn and Ginsborg 1953; Poletti and Rucci 2010; Otero-Millan et al 2008). When a fixation target is present, such drifts are more obvious (one finds gaze is no longer directed towards the fixation symbol), which could explain why more microsaccades—as means of redirecting gaze to the point of origin after drifting away—occur. Such an explanation agrees with findings by Otero-Millan and colleagues (2008), who showed that microsaccades were less frequent when observers were viewing a blank screen, compared to when they were viewing an image, suggesting that microsaccades require visual stimuli to ‘anchor’ to (Otero-Millan et al 2008, page 8). Alternatively, participants might have performed two different tasks with or without a fixation target. When a fixation target was present, they might have tried to keep their direction of gaze as close as possible to the target. Without the fixation target, this might no longer be a tenable strategy, and instead, they might have tried to keep their eyes as still as possible. With these two different tasks, to maintain fixation or to try to keep the eyes still, different microsaccade rates have been observed previously (Steinman et al 1973), with lower microsaccade rates for keeping the eyes still than for maintaining fixation, which could therefore provide an explanation for our observed differences in rates. The importance of a fixation target for the occurrence of microsaccades was also demonstrated by Poletti and Rucci (2010), who found, in line with the work by Cornsweet (1956), that microsaccade rates were unaffected by the (perceived) fading of the retinal image, suggesting that the actual presence or absence of a visual stimulus is not what determines the microsaccade rate. Moreover, they observed that removing the fixation target and instead asking participants to maintain fixation within a certain region (‘relaxed fixation’ requirement) reduced the number of microsaccades. Furthermore, they found that the direction of microsaccades in the presence of a fixation target was negatively correlated with the direction of the preceding oculomotor drift, while such a correlation was not found without a fixation target. These observations suggest a possible role of microsaccades in correcting for fixation errors under high-accuracy fixation requirements (see, also, Engbert and Kliegl 2004).

A second aspect of the microsaccades that we investigated was their amplitude. Whereas microsaccade rates have been studied extensively, fewer studies have looked into microsaccade amplitudes. It has been suggested (eg, Steinmann et al 1973) that larger amplitude microsaccades are found under conditions with more oculomotor drift (suggesting a function to bring the eye back to the intended point of fixation). In addition, it has been found that when fewer microsaccades occur, for example, after the onset of a visual stimulus, their amplitudes tend to be smaller (Rolfs et al 2008). Furthermore, saccadic latencies were found to be longer when preceded by larger amplitude microsaccades (Rolfs et al 2008). Moreover, the size of microsaccades was found to depend on whether the microsaccade occurred as a single event or was part of a sequence of microsaccades (Laubrock et al 2010). Another study found that fading of the stimulus did not influence the amplitude of microsaccades (Poletti and Rucci 2010). Our study adds to these findings by investigating the role of a fixation stimulus and the type of visual stimulation (in particular, the strength of illusory motion induced by the stimulus). Whereas microsaccade rates were strongly influenced by the presence of a fixation stimulus, microsaccade amplitudes were only weakly affected. This suggests that a tight coupling between microsaccade amplitudes and rates (Rolfs et al 2008)

might not always occur. Moreover, it also suggests that larger amounts of oculomotor drift could be compensated for by more rather than larger amplitude microsaccades. With respect to visual stimulation, an opposite pattern of results was found. Whilst microsaccade rates were unaffected by patterns increasing the strength of the motion illusion, the microsaccade amplitude appeared to be modulated by this manipulation. The pattern of results, however, was complex. No modulation of the amplitude was found when the stimulus was presented at the end of a long interval of fixation (Experiment 1). When part of a shorter interval (Experiment 2), the influence appeared to be non-monotonically related to the strength of the illusion, with stronger influences for patterns inducing weak or strong motion illusion strengths. Experiment 3, however, suggests that the association between the illusion strength and microsaccade amplitude from Experiment 2 might actually be an association between the strength of the checker pattern and microsaccade amplitude. In this third experiment, in which participants rated the perceived motion illusion on each trial, the microsaccade amplitude appeared to be unrelated to ratings of perceived motion strength. Possibly, the checkers in the background acted as 'anchor points' for fixation stability, just like a fixation point, making it more obvious the eye has drifted. In this context, it should be noted, however, that computational simulations (Zanker 2004) suggest that all saccadic displacements larger than $\lambda/4$ (about 0.1 deg in the present stimuli) would lead to substantial motion illusions. Therefore the amplitude modulation in the range of 0.3 to 0.5 deg may have little effect on illusion strength, as displacements in this range are larger than the minimum displacement required for the illusion (about 0.1 deg).

A third aspect we investigated was the direction of the microsaccades. Previous research has suggested that the direction of microsaccades is influenced by the direction of covert attention (Engbert and Kliegl 2003b; Laubrock et al 2005; Laubrock et al 2008). In addition, microsaccades have often been found to be biased towards the horizontal direction (eg, Engbert and Kliegl 2003a; Hermens and Walker 2010). In contrast, Zanker and colleagues (Zanker et al 2003; Zanker and Walker 2004) found a horizontal bias only for certain participants, whereas other observers displayed a bias towards vertical microsaccade directions. The present findings are in agreement with those from Engbert, Kliegl, and colleagues, showing a significant bias towards the horizontal direction, with leftward and rightward microsaccades being more frequent than upward and downward microsaccades. In addition, the direction of microsaccades was unrelated to the strength of the illusion elicited by particular stimulus patterns. The discrepancy of the results between Engbert, Kliegl, and colleagues; our present findings; and those from Zanker and colleagues could lie in the algorithm used to detect microsaccades. The former set of results were based on an algorithm detecting microsaccades on the basis of a velocity criterion applied to signals from both eyes, whereas the latter results were obtained using a detection criterion based on accelerations applied to the signal of one eye only. The difference in the algorithm is also reflected in a difference in the observed rates, with studies applying the algorithm by Engbert and Kliegl (2003b) reporting a rate of 1 microsaccade per second, and the study applying the acceleration criterion (Zanker et al 2003) observing a rate of 2 microsaccades per second. It is reassuring, however, that only the absolute rate and the distributions of directions seem to depend on the detection algorithm (see also Otero-Millan et al 2008; Poletti and Rucci 2010 and Troncoso et al 2008, who applied different algorithms to the same dataset and found no differences in results), whereas other aspects, such as differences in microsaccade rates across conditions, appear to be unaffected. Note, however, that our observation of no microsaccades in the presence of an illusion could possibly depend on the ability of the algorithm and eye tracking equipment to detect microsaccades. Possibly, microsaccades occurred on the relevant trials, but the

algorithm was not able to detect them (although the observed rates around 1Hz are well in line with earlier observations; Martinez-Conde et al 2009).

The present results cast doubts on an interpretation in which retinal shifts caused by microsaccades produce the illusion of shimmering motion perceived in parametric versions of *Fall*. First, we found that on a large number of trials, no microsaccades were observed (Experiment 3). On these trials, however, clear motion illusions were reported by participants. This finding quantifies an observation that already pointed at a possibility of motion illusions without microsaccades. Earlier, Zanker et al (2010) found that the strength of the illusion was relatively unaffected by the presentation duration of the stimulus. For stimuli presented as briefly as 250 ms, motion illusions were found—at a typical rate of 1 microsaccade per second (eg, Engbert and Kliegl 2003b), microsaccades might not have occurred on a few trials of such short presentation durations. Note, however, that the finding of motion illusions in the absence of microsaccades in itself is not sufficient to conclude that microsaccades do not play a role in the illusion. The reason is that it cannot be excluded that the presentation of the stimuli by itself might have contributed to the illusion. Possibly, the onset of the stimulus pattern induced a transient response of visual neurons, which could be involved in perceiving the illusion, similar to the recurrence of the percept of a faded stimulus after microsaccades (Martinez-Conde et al 2006). How exactly transients caused by stimulus onsets and induce a motion illusion, however, is less clear, and should be investigated further, for example, using computational modelling. Second, the occurrence of microsaccades was found to be either unrelated (Experiments 1 and 2) or inversely related (stronger motion percepts were found when fewer microsaccades occurred) to the motion illusion (Experiment 3). In particular this latter finding of weaker motion illusions with more microsaccades is difficult to reconcile with an explanation in which microsaccades generate the motion illusion.

Given the above observations, the present results suggest other causes than microsaccades for the illusion. For example, it could be possible that other types of fixational eye movements, such as oculomotor drift, are involved. Alternatively, there might be a role for perceptual transients, such as the onsets of stimulus patterns, in the illusion. Taking our findings as a reason to discard fixational eye movements altogether as a factor in the illusion might be a step too far, however, because earlier evidence strongly suggests the involvement of fixational eye movements. For example, it has been shown that if the retinal image is stabilized, the illusion is strongly reduced (Zanker and Walker 2004), which suggests that retinal instability plays a role in the illusion. Moreover the observed patterns of perceived motion are well in line with predictions from a motion perception model (Zanker 2004; Zanker et al 2010), assuming the involvement of retinal shifts, such as those occurring as a result of fixational eye movements. Oculomotor drift, rather than microsaccades might be a good candidate for offering an alternative or additional explanation for the illusion. These movements occur continuously, and therefore do not suffer from the problem of microsaccades that they might not occur on all trials, or for all presentation durations. Moreover, they are also relatively large movements of the eyes (Martinez-Conde and Macknik 2008), and could therefore provide the retinal shift assumed in computational models explaining the illusion (Zanker 2004). Whereas there is evidence that retinal shifts are important for the illusion (Zanker and Walker 2004), it cannot be excluded that perceptual transients, such as those caused by stimulus onsets and offsets, also play a role. The involvement of such perceptual transients in the motion illusion in Riley's *Fall* could be further investigated by presenting the stimuli for extended periods of time and to ask participants to indicate changes in aspects of the perceived motion, such as its speed or direction (Troncoso et al 2008). Such a presentation paradigm would eliminate perceptual transients and only leave signals arising from micro-movements of the eyes and eye-blinks.

Our experiments revealed no relation between the perceived illusion and the amplitude of the microsaccades. Such a lack of a relation is well in line with predictions from a motion detection model. Simulations with such a model (2DMD model, Zanker 2004) show that the amplitude of the microsaccades is not predicted to hugely influence the strength of the illusion, except if the microsaccade amplitude becomes very small with respect to the distance between stripes in the stimulus. The direction of microsaccades does not appear to be critical for the illusion either. Microsaccades are typically found to be biased towards the horizontal direction. If the direction of microsaccades would be of importance, it would therefore be expected that rotating the Riloid would change the strength of the illusion. Such an effect of the orientation of the pattern has not been observed (Zanker and Walker 2004).

Our conclusion that the rate of microsaccades is not directly related or could be even inversely related to the strength of the illusion may appear to be at odds with the findings of Troncoso et al (2008), who found a clear and distinct increase in the number of microsaccades before a perceived increase in the apparent speed of illusory motion. There are a number of issues to consider here. First, in our study we presented stimuli for a relatively brief duration, whereas Troncoso et al (2008) presented their stimuli for extended periods. The onset and offset of the stimuli in our experiments could have caused transient neural responses, which might have contributed to the illusion, in addition to the influence of retinal shifts generated by fixational eye movements implicated in earlier studies of the illusion (Zanker 2004; Zanker and Walker 2004). Second, in their study Troncoso and colleagues observed the increase in the microsaccade before the change in the perceived speed, rather than during the entire period of increased speed, and therefore the *rate change* rather than the rate itself could be responsible for the change in the perception (see Martinez-Conde et al 2006, for a similar increase in the microsaccade rate *before* the perceived reappearance of a faded stimulus). Third, the study by Troncoso et al (2008) might have investigated a different type of illusory motion. In their study, Troncoso and colleagues investigated the speed of a perceived streaming illusion elicited by patterns related to Leviant's 'Enigma' stimulus (Leviant 1996), which might be different in nature from the shimmering motion found for Riloids (eg, the streaming-like motion in Enigma is found in the bands without patterns, whereas the shimmering motion in Riloids is linked to clear patterns in the stimulus). Whereas the speed of illusory motion might be related to the strength of the illusion, as measured by Zanker and colleagues (Zanker et al 2010; Zanker and Walker 2004), these two measures do not necessarily need to correlate. Instead, stronger illusions could mean a larger range of directions, or more direction changes, rather than higher perceived speed. The possible difference between the two illusions might also involve the underlying mechanism. For example, to perceive a motion illusion in Riley's *Fall*, retinal shifts might be important. For the motion illusion in Leviant's 'Enigma', such shifts might be less important, and transients generated, for example, by microsaccades might be more strongly involved. Fourth, our psychophysical study (Zanker et al 2010), in which we found no effect of the fixation stimulus on the strength of the illusion (suggesting that microsaccades are not involved in the illusion, as their rate generally increases with the presentation of a fixation stimulus), did not control for eye movements. Whereas it was very unlikely that participants made large eye movements in the condition with the fixation target (only highly trained observers took part in the study, some of whom demonstrated in the present study that they could well maintain fixation when asked to do so), it can be expected that they did make eye movements in the condition without the fixation target. It can therefore not be excluded that the large-amplitude saccades likely to be made in this condition of the psychophysics experiment contributed to the motion percept and somehow counteracted the effects of the increased rate of microsaccades in the condition with the fixation symbol.

6 Conclusion

In summary, patterns, such as those used by Bridget Riley in her painting *Fall* provide a means of creating the perception of motion in a static image. Retinal shifts caused by eye movements made during visual fixation of the pattern, such as microsaccades and oculomotor drift, might be responsible for this motion percept. Whereas clear effects could be found of the presence of a fixation stimulus on the rate of the largest of these fixational eye movements, microsaccades, the relationship with the perceived strength of motion was more ambiguous. Two experiments suggested no relationship between microsaccade rates and the illusion, whereas a third experiment suggested an inverse relation. Interestingly, on many of the trials no microsaccades were detected, while the stimulus pattern still induced an illusion. In consideration of earlier results, these findings call for an alternative explanation of the motion illusion in Riley's *Fall*, possibly involving other types of fixational eye movements, such as oculomotor drift, or transients from other sources, such as the onset and offset of the stimuli. Future work should investigate these alternative explanations more closely—for example, by inspecting oculomotor recordings for slow drift and by computer models to further examine the underlying mechanisms of the perception of illusory motion.

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References

- Campbell F W, Robson J G, 1958 "Moving visual images produced by regular stationary patterns" *Nature* **181** 849–850 ◀
- Cornsweet T N, 1956 "Determination of the stimuli for involuntary drifts and saccadic eye movements" *Journal of the Optical Society of America* **46** 987–993 doi:10.1364/JOSA.46.000987 ◀
- Ditchburn R W, Ginsborg B L, 1953 "Involuntary eye movements during fixation" *Journal of Physiology* **119** 11–17 ◀
- Engbert R, Kliegl R, 2003a "Binocular coordination in microsaccades" in *The Mind's Eyes: Cognitive and Applied Aspects of Eye Movements* Eds J Hyönä, R Radach, H Deubel pp 103–117 (Oxford: Elsevier) ◀
- Engbert R, Kliegl R, 2003b "Microsaccades uncover the orientation of covert attention" *Vision Research* **43** 1035–1045 doi:10.1016/S0042-6989(03)00084-1 ◀
- Engbert R, Kliegl R, 2004 "Microsaccades keep the eyes' balance during fixation" *Psychological Science* **15** 431–436 doi:10.1111/j.0956-7976.2004.00697.x ◀
- Gregory R L, 1993 "A comment: Mackay Rays shimmer due to accommodation changes" *Proceedings of the Royal Society London B* **253** 123 ◀
- Gregory R L, 1994 "Under the carpet" *Perception* **23** 741–744 ◀
- Hafed Z M, Goffart L, Krauzlis R J, 2009 "A neural mechanism for microsaccade generation in the primate superior colliculus" *Science* **323** 940–943 doi:10.1126/science.1166112 ◀
- Hermens F, Zanker J M, Walker R, 2010 "Microsaccades and preparatory set: A comparison between delayed and immediate, exogenous and endogenous pro- and anti-saccades" *Experimental Brain Research* **201** 489–498 doi:10.1007/s00221-009-2061-5 ◀
- Hermens F, Walker R, 2010 "What determines the direction of microsaccades?" *Journal of Eye Movement Research* **3** 1–19 ◀
- Laubrock J, Engbert R, Kliegl R, 2005 "Microsaccade dynamics during covert attention" *Vision Research* **45** 721–730 doi:10.1016/j.visres.2004.09.029 ◀
- Laubrock J, Engbert R, Kliegl R, 2008 "Fixational eye movements influence the perceived direction of ambiguous apparent motion" *Journal of Vision* **8** 1–17 doi:10.1167/8.14.13 ◀
- Laubrock J, Kliegl R, Rolfs M, Engbert R, 2010 "When do microsaccades follow spatial attention?" *Attention, Perception, & Psychophysics* **72** 683–694 doi:10.3758/APP.72.3.683 ◀
- Leviant I, 1996 "Does 'brain-power' make Enigma spin?" *Proceedings of the Royal Society B: Biological Sciences* **263** 997–1001 doi:10.1098/rspb.1996.0147 ◀

- Martinez-Conde S, 2006 "Fixational eye movements in normal and pathological vision" *Progress in Brain Research* **154** 151–176 doi:10.1016/S0079-6123(06)54008-7 ◀
- Martinez-Conde S, Macknik S L, 2008 "Fixational eye movements across vertebrates: Comparative dynamics, physiology, and perception" *Journal of Vision* **8** 1–16 ◀
- Martinez-Conde S, Macknik S L, Hubel D H, 2004 "The role of fixational eye movements in visual perception" *Nature Reviews Neuroscience* **5** 229–240 doi:10.1038/nrn1348 ◀
- Martinez-Conde S, Macknik S L, Troncoso X G, Dyar T A, 2006 "Microsaccades counteract visual fading during fixation" *Neuron* **49** 297–305 doi:10.1016/j.neuron.2005.11.033 ◀
- Martinez-Conde S, Macknik S L, Troncoso X G, Hubel D H, 2009 "Microsaccades: a neurophysiological analysis" *Trends in Neurosciences* **32** 463–475 doi:10.1016/j.tins.2009.05.006 ◀
- Otero-Millan J, Troncoso X G, Macknik S L, Serrano-Pedraza I, Martinez-Conde S, 2008 "Saccades and microsaccades during visual fixation, exploration, and search: Foundations for a common saccadic generator" *Journal of Vision* **8** 1–18 doi:10.1167/8.14.21 ◀
- Rolfs M, 2009 "Microsaccades: Small steps on a long way" *Vision Research* **49** 2415–2441 doi:10.1016/j.visres.2009.08.010 ◀
- Rolfs M, Engbert R, Kliegl R, 2005 "Crossmodal coupling of oculomotor control and spatial attention in vision and audition" *Experimental Brain Research* **166** 427–439 doi:10.1007/s00221-005-2382-y ◀
- Rolfs M, Kliegl R, Engbert R, 2008 "Towards a model of microsaccade generation: The case of microsaccadic inhibition" *Journal of Vision* **8** 1–23 doi:10.1167/8.11.5 ◀
- Poletti M, Rucci M, 2010 "Eye movements under various conditions of image fading" *Journal of Vision* **10** 1–18 doi:10.1167/10.3.6 ◀
- Steinman R M, Haddad G M, Skavenski A A, Wyman D, 1973 "Miniature Eye Movement" *Science* **181** 810–819 doi:10.1126/science.181.4102.810 ◀
- Troncoso X G, Macknik S L, Otero-Millan J, Martinez-Conde S, 2008 "Microsaccades drive illusory motion in the Enigma illusion" *Proceedings of the National Academy of Sciences* **105** 16033–16038 doi:10.1073/pnas.0709389105 ◀
- Zanker J M, Doyle M, Walker R, 2003 "Gaze stability of observers watching Op Art pictures" *Perception* **32** 1037–1049 doi:10.1068/p5128 ◀
- Zanker J M, Hermens F, Walker R, 2010 "Quantifying and modeling the strength of motion illusions perceived in static patterns" *Journal of Vision* **10** (2): 1–14 ◀
- Zanker J M, Walker R, 2004 "A new look at Op art: towards a simple explanation of illusory motion" *Naturwissenschaften* 75–94 ◀
- Zanker J M, 2004 "Looking at Op Art from a Computational Viewpoint" *Spatial Vision* **17** 75–94 doi:10.1163/156856804322778279 ◀
- Zeki S, 1994 "The cortical Enigma: a reply to Professor Gregory" *Proceedings of the Royal Society B: Biological Sciences* **257** 243–245 doi:10.1098/rspb.1994.0121 ◀
- Zeki S, Watson J D G, Frackowiak R S J, 1993 "Going beyond the information given: The relation of illusory visual motion to brain activity" *Proceedings of the Royal Society B: Biological Sciences* **252** 215–222 doi:10.1098/rspb.1993.0068 ◀
- Zuber B L, Stark L, Cook G, 1965 "Microsaccades and the velocity-amplitude relationship for saccadic eye movements" *Science* **150** 1459–1460 doi:10.1126/science.150.3702.1459 ◀