Quantifying and modeling the strength of motion illusions perceived in static patterns

Johannes M. Zanker

Department of Psychology, Royal Holloway University of London, UK

Frouke Hermens

Department of Psychology, Royal Holloway University of London, UK

Robin Walker

Department of Psychology, Royal Holloway University of London, UK

The origin of motion illusions in simple black and white patterns such those as used by Op artists has been at the center of a lively scientific debate, relating motion processing mechanisms to involuntary eye movements that generate characteristic motion patterns. To overcome the limitations of using subjective ratings as a measure of illusory effects, we developed a new method to quantify the strength of the illusion for synthetic 'riloids' that were inspired by Bridget Riley's 'Fall'. In a 2AFC paradigm, test stimuli were compared to a reference set of patterns that elicit illusory motion of variable strength. We found that pattern parameters influencing the distribution of local orientation in the riloids (the amplitude and the spatial period of the line undulation) systematically affect illusion strength, whereas other parameters, such as the spatial period of the lines themselves, the duration of the stimulus, or fixation conditions, have little effect. These behavioral data are compared in computer simulations to the predicted activity generated by motion detector networks for displacements of the riloids that reflect small eye movements. The match between predicted illusion strength and experimental data support an explanation of the motion illusion in terms of retinal image shifts.

Introduction

The history of visual arts has seen numerous attempts to represent aspects from our external world which go beyond the inherently two-dimensional nature of a painting (Gombrich, 1977). For example, painters have developed a pictorial language to invoke clear impressions of depth and motion, which have no direct way of being captured on the flat and static surface of a canvas. In the twentieth century, Op artists began to experiment with simple black and white patterns that can create vivid dynamic illusions in static pictures (Riley, 1995; Wade, 2003), which allow artists to *elicit* particular percepts rather than just to *represent* aspects of a scene such as motion. Op Art paintings such as Bridget Riley's 'Fall' (1963, Tate Britain, London) create vivid sensations of shimmering and movement, despite the fact that they are nothing more than simple static patterns of paint on a static canvas. Similar phenomena related to compositions of repetitive lines in different orientations can be observed in R. Neal's painting 'Square of three' (Kupin, Haddad, & Steinman, 1973). The physiological and perceptual mechanisms responsible for motion illusions in such patterns have been a matter of debate for several decades (see, for

instance, Mon-Williams & Wann, 1996; Wade, 2003), reaching back to some early descriptions of dynamic deformations observed in patterns that are composed of fine lines (Purkinje, 1828 as discussed in von Helmholtz, 1924). An example of such a continuing debate concerns the mechanisms underlying the percepts in the 'Enigma' painting (Leviant, 1982, 1996), which consists of a pattern of radiating black and white lines (similar to the radial line pattern used by MacKay, 1957) superimposed by concentric rings of uniform color. This painting elicits two types of motion illusions, namely, circular motion in the concentric rings and a shimmering motion in the radiating lines. Scientists have speculated whether higher cortical mechanisms are required to explain such phenomena (see, for instance, MacKay, 1957; Zeki, 1994; Zeki & Lamb, 1994; Zeki, Watson, & Frackowiak, 1993), or whether the instability of the eyes, which are continuously moving and at the same time changing focus, could be responsible for the perceived motion (for instance, Pirenne, Campbell, Robson, & Mackay, 1958; Gregory, 1993, 1994; Kupin et al., 1973). The latter idea has gained some empirical support from studies that have directly compared the frequency of small eye movements with the strength of the motion illusion perceived in the rings of 'Enigma' (Troncoso, Macknik, Otero-Millan, & Martinez-Conde,

2008). Although different explanations are often stated as mutually exclusive alternatives, it is possible that the observed phenomena arise from a combination of both perceptual and oculomotor mechanisms.

In an attempt to assess the importance of gaze stability, in previous work (Zanker, Doyle, & Walker, 2003) we compared measurements of participants' eye movements made while looking at stimuli inspired by Bridget Riley's 'Fall' with the occurrence of illusory motion percepts. This type of stimulus differs from 'Enigma' in that it is composed purely from periodic line patterns, without any superimposed regions of homogeneous color, and consequently the generated motion illusion is restricted to the 'jazzing and shimmering' sensation similar to that seen for the radial line patterns. By contrast, the streaming inside the regions of different color experienced in 'Enigma' is absent—and in this sense Riley stimuli are simpler and therefore provide a useful tool to constrain the investigation of motion illusions in static patterns to a single phenomenon. This difference is particularly relevant because there are indications that the streaming sensation is preserved when the retinal image is stabilized, whereas the 'jazzing' sensation breaks down under such conditions (Hamburger, 2007; Kumar & Glaser, 2006), suggesting a different role of small involuntary eye movements in the two kinds of illusory motion. In our work on Riley's 'Fall', we observed a consistent pattern of small involuntary eye movements—or microsaccades (miniature excursions around the point of fixation) that are typically observed when participants are looking at such high-contrast line patterns and other stimuli—which could play an important role in the motion illusion (Zanker et al., 2003). The experimental work demonstrating the link between fixational eye movements and the emergence of the illusion was complemented by a computational study (Zanker, 2004) on the effect of small image shifts such as those induced by involuntary microsaccades on the low-level motion processing networks in the human brain. Earlier attempts to describe how the motion perception system responds to the information provided by Op Art paintings focussed on the Enigma motion illusion (Leviant, 1996) in relation to processing mechanisms for optic flow (Fermüller, Pless, & Aloimonos, 1997): small displacements of the Enigma image would lead to weak motion signal patterns that could be interpreted as typical motion fields by high-level mechanisms extracting flow components. A low-level, biologically motivated motion processing model as used in the present work, on the other hand, is based on early encoding mechanisms of motion information that have proven themselves useful for understanding a range of perceptual phenomena (Borst & Egelhaaf, 1989; Patzwahl & Zanker, 2000; Zanker, 2001; Zanker & Braddick, 1999). In order to gain some insight on the possible consequences of retinal image shifts, synthetic gratings that resemble Riley's 'Fall', so-called 'riloids' (see insets in Figure 1), were developed to be used as inputs for the computational model of early

motion processing (Zanker, 2004). This model generates response maps that represent the spatial distribution of motion signals generated by stimulus sequences, in this case riloids being displaced in small steps, as they would shift across the human retina during microsaccades. The patchy structure of the response maps—and more generally the discrepancy between overall motion energy and motion coherence in these signal distributions for riloids, but not for control patterns—resembles the motion illusion, which is not perceived as coherent shift of the whole pattern, but as a wobbling and jazzing of ill-defined regions (Zanker & Walker, 2004). Although other explanations are not excluded, these observations and theoretical considerations suggest that the puzzle of Op Art motion illusions could potentially have a rather simple solution in terms of small involuntary eye movements leading to image shifts that are picked up by well-known motion detectors in the early visual system.

A number of recent studies (Backus & Oruc, 2005; Conway, Kitaoka, Yazdanbakhsh, Pack, & Livingstone, 2005) have discussed the role of eye movements for one particularly strong motion illusion, known as the rotating snake illusion, which was created by the Japanese artist and psychologist A. Kitaoka (http://www.ritsumei.ac.jp/ ~akitaoka/rotsnake.gif). The asymmetries of the luminance profiles that are essential for the illusion in such patterns seem to suggest that the role of eye movements may be subsidiary whereas the nonlinearity of neurons in the early visual system and the physiological properties of motion detectors are crucial here (Backus & Oruc, 2005). Whereas there may be a range of possible—and not mutually exclusive—reasons why so many distinct static patterns (see also Fraser & Wilcox, 1979) can elicit vivid motion sensations, many authors emphasize the role of fixation stability for motion illusions induced by a range of simple geometric patterns (e.g., Murakami, Kitaoka, & Ashida, 2006; Troncoso et al., 2008). Maintaining a steady retinal image is crucial for making fine detail visual information available to the brain. However, a perfectly stabilized image would fade over time, and there is evidence that some small amount of displacement allows us to explore more and finer aspects of the scene (Martinez-Conde, Macknik, & Hubel, 2004; Rucci, Iovin, Poletti, & Santini, 2007). Recently, Murakami et al. (2006) pointed out that for the rotating snake patterns, the perceived illusion strength correlates with properties of slow fixational drifts, but not with those of small saccades. On the other hand, we have shown in previous work (Zanker & Walker, 2004) that for riloids microsaccades are a sufficient explanation for the perceived motion illusion. Because rotating snake patterns differ from riloids not only in their spatial layout that elicit motion illusions with a direction bias rather than random directions such as perceived for riloids, it is possible that the relative contribution of different types of eye movements differs for the two kinds of stimuli. In the context of a computational explanation of the motion illusion, the
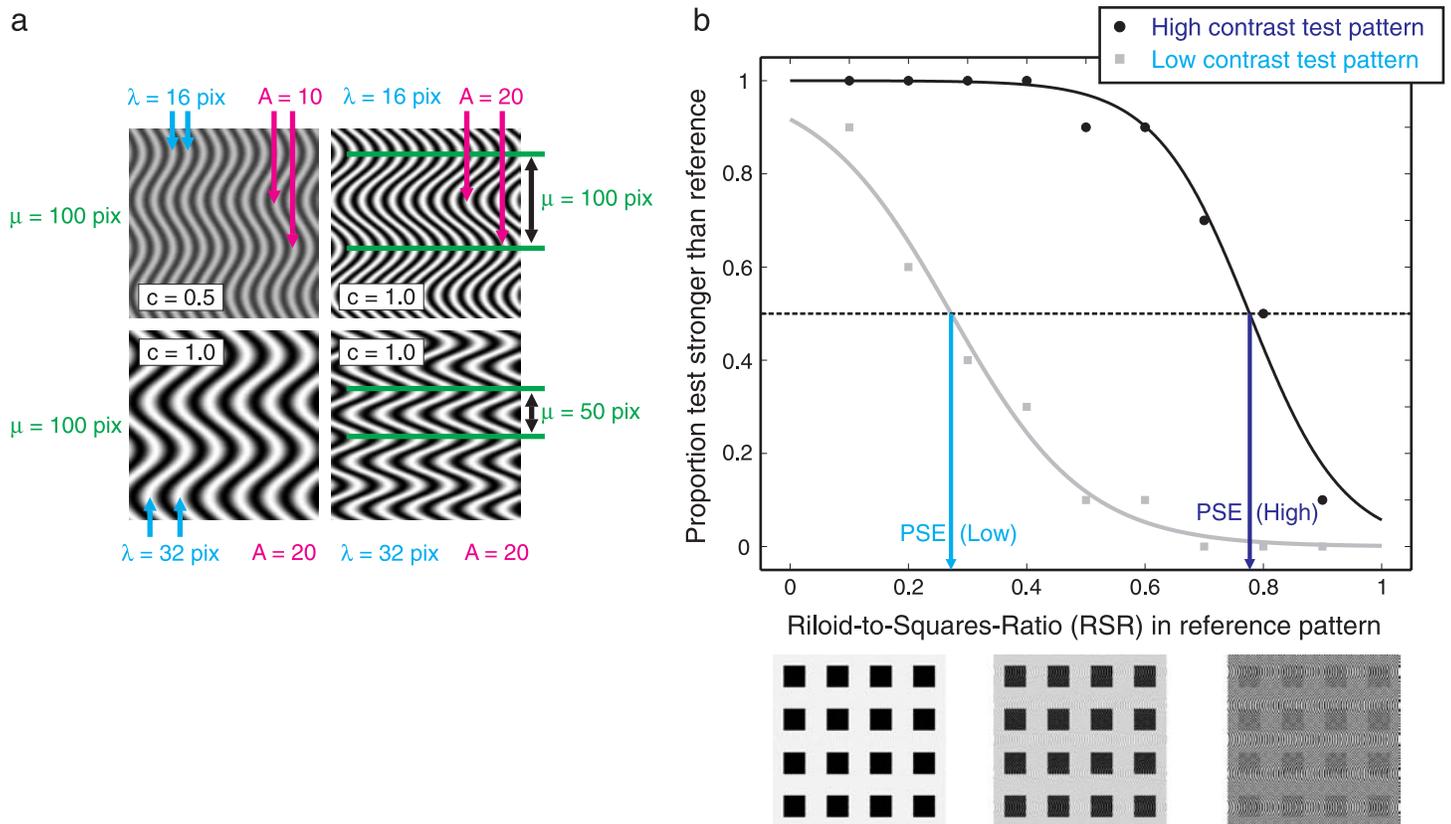
a

b

Figure 1. (a) Schematic illustration of the key pattern parameters: c (grating contrast), λ (grating wavelength), A (phase modulation amplitude), and μ (phase modulation period). (b) Two example psychometric curves for two test riloid patterns of different contrast. The proportions of decisions 'test is stronger than reference' are shown as function of RSR (relative contribution of riloids and squares to combined reference pattern) for two test stimuli. The low contrast test pattern (indicated by gray squares and line) leads to generally smaller proportions of 'test is stronger than reference' decisions, and a low point of subjective equivalence, PSE ('Low', light blue arrow), which is taken as quantitative measure of illusory strength, whereas the high contrast pattern (black dots and solid line) leads to generally higher proportions of decisions 'test is stronger than reference', and a larger PSE 'High', dark blue arrow). The insets below the graphs show examples of reference patterns at three difference levels of the Riloids-to-Squares-Ratio, RSR (0.3, 0.5, and 0.7), which varies the proportion of riloid and checker patterns, respectively, that make up the set of reference stimuli with increasing illusory strength.

exact origin of retinal image displacements is not crucial for the interpretation of the data, so here we do not pursue the question how different kinds of eye movement contribute to the phenomenon.

A fundamental problem for the field of research on motion illusions perceived in static images, including our own previous work, is the reliance on subjective reports from participants, in which they indicate whether or not they see an illusion, and the estimation of the perceived strength, reported using subjective rating scales. The lack of an objective quantitative method, that is not vulnerable to individual variations and criterion shifts to measure the strength of illusory percepts elicited by static patterns, raises the question whether such experimental findings are robust, how they depend on particular stimulus configu-rations, and whether there is a possibility to establish a quantitative relationship between motion signal distributions

predicted from modeling and the perceived strength of the illusion. We address this issue in the current study by generating sets of stimuli in which the strength of the illusion is systematically manipulated by superimposing checkerboards and riloids, in combination with a criterion-free psychophysical method—a two-alternative forced choice (2AFC)—to asses quantitatively the effectiveness of riloids in inducing illusory motion. This will establish a new method to measure illusion strength objectively that goes beyond the subjective ratings used so far. The new method will enable us to compare directly the properties of motion detector network responses with those of illusory percepts, and to manipulate and optimize the illusory strength of riloid patterns in a predictable manner in future studies. It also will enable us to design stimuli for oculomotor measurements which have well-defined perceptual effects and thus will allow us in future

experiments to interpret the statistics of fixational eye movements in relation to individual stimulus conditions.

Methods

Participants

Nine participants took part in the experiment and all gave their informed consent. The participants were split into three groups regarding their level of prior knowledge about the experiment. The first group of three participants (the authors) was fully informed about the purpose of the experiment and the stimulus conditions. The second group of three participants knew about the purpose of the experiment, but was unaware of the specific conditions in each experiment. The final three remaining participants were naive with respect to the purpose of the experiment. All participants had normal or corrected-to-normal vision. The study was approved by the local RHUL ethics committee.

Apparatus

The stimuli were presented on a 17″ TFT computer screen (Atyc systems) at a resolution of 1024 by 768 pixels, corresponding to screen size of 33.7 by 27.2 cm. The intensity of each image pixel was determined by the stimulus generation program in relative units, which was translated into brightness according to a concave function, as measured by a luminance meter. An intensity of 0 corresponded to a luminance of 0.6 cd/m^2, an intensity of 0.5 to a luminance of 34 cd/m^2 and an intensity of 1 to a luminance of 181 cd/m^2. Stimulus presentation was controlled by a Pentium 3 computer (AMD Athlon 1.8 GHz with 786 MB RAM) via an NVidia GForce4 MX graphics card. Participants' responses were recorded by an optical mouse.

Stimuli

Riloid stimuli (i.e., a luminance function I(x,y) in horizontal and vertical dimension, varying between 0 and 1) were generated from vertically oriented sine wave gratings with a contrast c and a spatial wavelength λ, using the following equation:

$$I(x,y) = 0.5 * (1 + c * \sin[2 * \pi * (x - \phi(y))/\lambda]), \quad (1)$$

where the spatial phase of the grating, ϕ, can be modulated along the vertical axis by

$$\phi(y) = A * \sin[2 * \pi * (y/\mu(y))], \quad (2)$$

with an amplitude A of the grating phase modulation, and the spatial period of phase modulation, μ, being variable from the top to the bottom of the pattern, as given by

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

The values of the key pattern parameters (see Figure 1a), c (grating contrast), λ (grating wavelength), A (phase modulation amplitude), and μ_{top} and μ_{bottom} (phase modulation period at the top and the bottom of the image, respectively), were varied across experimental conditions, as stated and illustrated in the Results section. Besides the value of these parameters, we also varied the presentation duration, and tested the effect of the presence or absence of a fixation target at the center of the display. The size of the stimuli was 400 by 400 pixels, which corresponded to 13.2 by 14.2 cm on the computer screen.

Participants were asked to compare the test riloid patterns with individual elements of a set of nine reference patterns, which consisted of a standard riloid mixed with a checkerboard pattern, as illustrated in Figure 1b. The checkerboard pattern consisted of 4 × 4 squares measuring 50 by 50 pixels horizontally and vertically, respectively, that were spaced at a distance of 50 pixels (edge to edge). The distance from outer squares to the outer edges of the entire stimulus pattern was 25 pixels. The nine different reference patterns were obtained by varying the relative weight of the riloids and the squares in a linear superposition of the respective pixel intensity values. The resulting 'Riloid-to-Squares-Ratio' (RSR) for the reference patterns varied in steps of 0.1 from 0.1 (squares dominate the superimposed image, weak illusion in the reference) to 0.9 (riloid dominates the superimposed image, strong illusion in the reference). The standard riloid in the reference stimulus, which was constant across all conditions and similar to Bridget Riley's painting 'Fall', was constructed using the following parameter settings: c = 1.0, λ = 8, A = 32, μ_{top} = 400, and μ_{bottom} = 140.

Design

Participants were asked to make judgements in a 2AFC paradigm about the perceived relative strength of the illusion elicited by a test and a reference patterns presented side by side, using a method of constant stimuli. Each condition, in which one parameter setting of the riloid pattern was varied, was tested in one experimental session that lasted for approximately 30 minutes. A session consisted of four blocks in which two out of four values of the parameter under investigation were randomly interleaved. The order of presentation of the parameter values was counterbalanced across blocks to avoid practice and fatigue effects in the averaged data. Within each block each pair of test and reference pattern

was presented five times, leading to 10 decisions for each stimulus–test combination. The order of presentation of the parameter values as well as the blocks of parameter variations were randomized across participants.

Procedure

Participants were seated with a viewing distance of 50 cm from the computer screen, leading to an angular pixel size of 0.038 deg horizontally and 0.041 deg vertically. A chin rest was used to avoid head movements, and to maintain the head position and viewing distance across participants and experimental sessions. The stimuli were presented using a custom-made computer program (written in Visual C++) generating a display window that included two response buttons to be operated by mouse clicks. At the start of a trial, a pair of stimuli was shown, typically for a duration of one second. Participants were then required to indicate after the disappearance of the stimulus patterns which of the two stimuli elicited the stronger motion percept by clicking the corresponding button. Responses before the end of the stimulus presentation were not recorded. On each trial, new stimulus pairs were then presented until all pairs were shown five times. No fixation point was used in the standard configuration, which allowed participants to move their gaze between the stimuli before making a decision, although it is possible they did not move their eyes.

Data analysis

The proportions of decisions that a given test stimulus elicited a stronger illusory motion percept than the reference pattern were computed for each Riloid-to-Squares-Ratio, RSR, to generate a psychometric function (see Figure 1), with 10 trials per data point. For each parameter setting of the test stimulus, we estimated the RSR that yielded 50% decisions that the illusion from test is stronger than that from the reference—i.e., the point of subjective equality, PSE—by fitting a sigmoid function to the data. The following function was used as sigmoid:

$$\text{Predicted proportion} = 1/(1 + \exp(-(\text{RSR} - k1)/k2)), \qquad (4)$$

where k1 and k2 are the sigmoid parameters, k1 representing the estimated PSE and k2 being the slope at the PSE, respectively. The optimal fit of the function was obtained by minimizing the sum of the squared differences between the experimental data and the predicted proportions by means of a simplex search. The PSE was used as quantitative measure of the illusory strength of a given test pattern.

Unless stated otherwise, the results of the statistical analyses reported here present outcomes of univariate repeated measures analysis of variances ANOVAs. If the number of levels within one of the factors exceeded two, Greenhouse–Geisser corrected values are provided. The analyses were carried out in SPSS 14.0.

Results

Influence of a visible fixation target

In the first two experiments we established whether the use of a fixation target (to reduce scanning eye movements) would affect the strength of the perceived illusion, and whether the illusion would be affected by the duration of the stimulus presentation. First, the effect of presenting a fixation target between the test and reference images, as compared to allowing free eye movements was examined by measuring illusion strength with or without a small central fixation target. The fixation stimulus should influence gaze stability, and thus the amount of displacements of the riloid patterns across the retina, as well as maintaining their eccentricity. In one condition a small 'bulls eye' fixation stimulus was presented in the center between the two stimulus patterns, and participants were instructed to maintain fixation at its center as long as it was visible, starting approximately 1 sec before the stimulus pair was displayed and remaining visible throughout the stimulus presentation. In the alternative condition no fixation stimulus was used, and participants were allowed to move their gaze freely across the screen, and between the two stimulus patterns. We used standard riloid patterns with moderate contrast, c = 0.6, a fixed grating wavelength, λ = 8, and with a constant phase modulation period, $\mu_{\text{top}} = \mu_{\text{bottom}}$ = 200 pixels, and two levels of phase modulation amplitude, A = 6 and A = 24 pixels, which were randomly interleaved. The order of blocks (fixation target on/off) was counterbalanced for each participant and randomized across participants. Stimuli were presented for 1 second.

As can be seen in Figure 2, there is a small trend for the illusion strength to be slightly greater (by less than 10%) when the eyes were allowed to move across the screen. These differences, however were not statistically significant (main effect of the fixation condition: $F(1,8)$ = 2.74; p = 0.137; interaction with amplitude: $F(1,8)$ = 0.104; p = 0.755), and very small compared to the significant effect ($F(1,8)$ = 10.92; p = 0.011) of changing the modulation amplitude (about 30% increase when increasing from A = 6 pixels to A = 24 pixels). As indicated in the Methods section, participants differed in the level of prior knowledge regarding about the experiment. To test whether this knowledge had an effect, we compared the illusion strength for these three groups in a three way analysis of
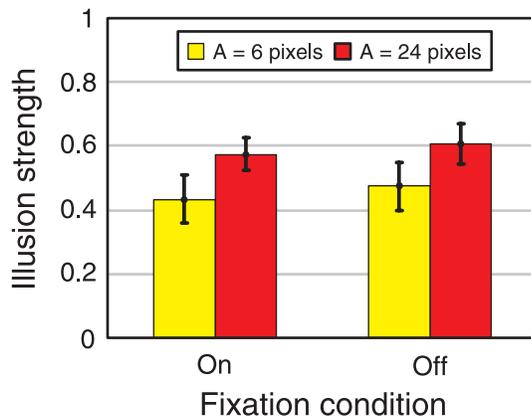
Figure 2. Strength of the perceived motion illusion (measured as PSE) for two different fixation conditions: stimulus presentations with a fixation target ('On') and without fixation target ('Off'), for which participants were allowed to make free eye movements, for two settings of phase modulation amplitude (A = 6 pixels and A = 24 pixels, yellow and red bars, respectively). The data are the averages across all nine observers, and error bars indicate the standard error of the mean.

variance, with participant group as a between-subject factor and amplitude and fixation condition as within subject factors. No significant effect of prior knowledge was found ($F(1,6) = 0.337$, $p = 0.726$), and no significant interaction with the other two factors was obtained ($p > 0.1$ for all interactions).

As there was no significant effect of the fixation condition, we chose not to use a fixation target in subsequent experiments, to make the task less demanding for participants who had verbally reported that maintaining prolonged fixation was less comfortable than free viewing.

Effect of stimulus duration

To test whether the strength of the illusion was affected by the length of time the participants viewed the stimulus pattern, we used a standard riloid patterns as test stimulus, with maximum contrast, c = 1, a fixed grating wavelength, $\lambda = 8$, and with a constant phase modulation period, $\mu_{top} = \mu_{bottom} = 200$ pixels, and two levels of phase modulation amplitude, A = 6 and A = 24 pixels. In each experimental block, the two modulation amplitudes were randomly interleaved, and the duration of the stimulus presentation was set to 250, 500, 1000, to 2000 msec in random order. No fixation stimulus was presented.

As can be seen in Figure 3, the duration of stimulus presentation, i.e. the time a participant would be able to move their gaze around and allowed them to inspect the two images separately, within the range tested here, did not systematically affect the measured strength of the motion illusion (main effect of duration: $F(2.39,14.46) = 0.673$, $p = 0.577$). As with the fixation condition tested in

(3.1), a main effect of the modulation amplitude was found ($F(1,8) = 20.59$, $p = 0.002$), but no interaction with the presentation duration ($F(3,1.81) = 1.84$, $p = 0.195$). The effect of the presentation duration was not dependent on whether participants were informed about the experiment before taking part (main effect of participant group in a 4WS*2WS*3BS, mixed within subjects, WS, and between subjects, BS, ANOVA: $F(2,6) = 0.489$, $p = 0.636$). The overall variation of illusion strength with changes in modulation amplitude demonstrates that the absence of any effect of presentation duration is not due to a lack of measurement sensitivity and demonstrates that the illusion is not affected by stimulus duration within the range tested.

As we did not observe an effect of stimulus duration, a duration of 1000 msec was used for all remaining experiments, which allowed participants sufficient time to look at the display without greatly extending the length of the experiment.

Variation of the amplitude of riloid phase modulation (A)

Riloids with maximum contrast, c = 1, a fixed grating wavelength, $\lambda = 8$ pixels, and constant phase modulation period, $\mu_{top} = \mu_{bottom} = 200$ pixels, were used as test patterns. The value of the horizontal phase modulation amplitude A was varied between 6, 12, 24, and 36 pixels (0.23, 0.45, 0.90, and 1.36 degrees of visual angle). In each experimental block, gratings with modulations of 6 and 24 pixels, or with 12 and 36 pixels, were presented. No fixation stimulus was used and stimuli were presented for 1 second.
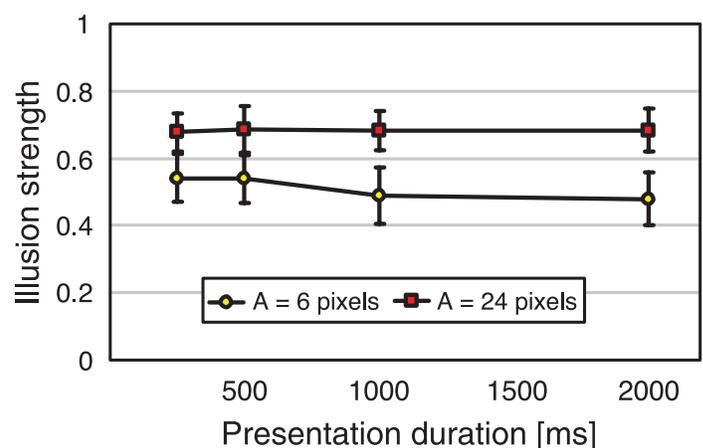

Figure 3. Illusion strength (points of subjective equality, PSE) as a function of the duration of the stimulus presentation (ranging from 250 to 2000 msec), for two levels of phase modulation amplitude (A = 6 pixels: yellow dots; A = 24 pixels: red squares). The curves show the averages results across all nine observers, and error bars indicate the standard error of the mean.
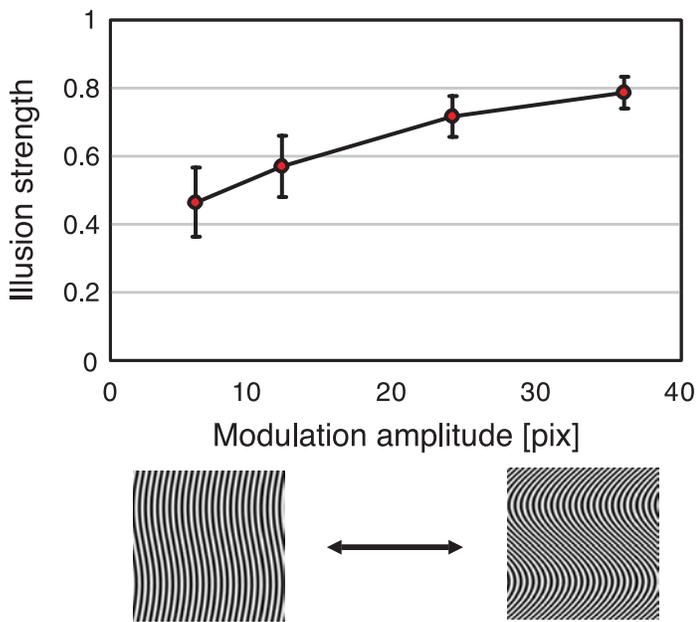
Figure 4. Illusion strength (points of subjective equality, PSE) as a function of the amplitude of phase modulation (A, ranging from 6 to 36 pixels, or 0.22 to 1.31 deg) of the riloid. The curve shows the average results across all nine observers, and error bars indicate the standard error of the mean. Example sections of two test stimuli (minimum and maximum A) are shown below the x-axis to illustrate the range of variation.

The effect of the phase modulation amplitude of the riloid pattern on the perceived illusion strength is shown in Figure 4 as average values for all 9 participants, with SEMs, demonstrating clearly that the perceived motion illusion grows stronger when the phase modulation is increased, i.e. when the periodic lines are less straight. Within the range of modulation amplitudes tested here, the illusion remained above a level of approximately 0.5, but for even smaller amplitudes the illusion would be expected to disappear completely, as the patterns approach the appearance of straight gratings. Between individual participants, the vertical position of the response curves can vary (data not shown), but all individuals consistently show a monotonic increase of illusion strength with larger modulation amplitudes. These individual differences can be interpreted as variations in how the motion illusion perceived by participants is affected, on average, by the superimposed squares. A repeated measures ANOVA was performed to determine whether these effects were statistically significant, with modulation amplitude as a within-subject factor (four levels) and prior knowledge group (3 levels) as a between-subject factor. The effect of modulation amplitude was significant ($F(1.11,6.65) = 12.34$, $p = 0.010$). No significant effect was found for the participants level of prior knowledge ($F(2,6) = 1.61$, $p = 0.276$). The interaction was not significant either ($F(2.22,6.65) = 0.073$, $p = 0.532$).

The effects of modulation amplitude resemble those found by Zanker et al. (2003), using subjective ratings to assess the strength of the motion illusion. It is important to note that the key change of appearance in the stimulus patterns when changing phase modulation amplitude is the deviation from straight vertical lines. Along each one of the periodic lines in the image, determined by the minimum of local intensity, the maximum deviation from vertical ranged between 11 deg in the case of A = 6 pixels to 48 deg in the case of A = 36 pixels. Due to the aperture problem the motion direction that is detected locally depends on the local contour orientation (Nakayama & Silverman, 1988). Therefore the variation of locally perceived direction of motion can be expected to be strongly sensitive to this manipulation of this riloid parameter.

Variation of the period of riloid phase modulation (μ)

Riloids with moderate contrast, c = 0.6, a fixed grating wavelength, $\lambda = 8$, and a constant modulation amplitude, A = 24 pixels, were used as test patterns. The vertical phase modulation period was identical for all regions of the stimulus, $\mu_{top} = \mu_{bottom}$, and was varied between 100, 200, 300, and 400 pixels for the 4 different test stimuli used (4.1, 8.1, 12.2, and 16.2 degrees of visual angle, respectively). In any given experimental block riloids with modulation period of 100 and 300 pixels, or with 200 and 400 pixels, were presented, in order to keep the duration of an experimental block comfortable to participants. No fixation stimulus was used and stimuli were presented for 1 second.

The effect of the phase modulation period on the perceived illusion strength is shown in Figure 5, demonstrating a clear and highly significant decrease of the illusion strength with increasing μ ($F(1.82,14.56) = 19.83$, $p < 0.001$). For the two largest levels of μ, there seems to be little if any difference in the perceptual effect, but it would be expected that for much larger phase modulation period there should be further reduction, when the gratings approach straight vertical lines. As for the phase modulation amplitude tested in Variation of the amplitude of riloid phase modulation (A), apart from a vertical shift between individuals, the pattern of results was similar across participants, showing a consistent decrease of illusion strength when μ grows, independent of whether individuals knew about the purpose of the experiment or not (main effect of participant group in a 4WS*3BS ANOVA: $F(2,6) = 1.19$, $p = 0.366$; interaction with μ: $F(3.38,10.13) = 0.354$, $p = 0.808$).

Similar to the variation of modulation amplitude in Variation of the amplitude of riloid phase modulation (A), the most apparent change of appearance in the stimulus patterns is the deviation from straight vertical lines when the phase modulation period is reduced. The maximum
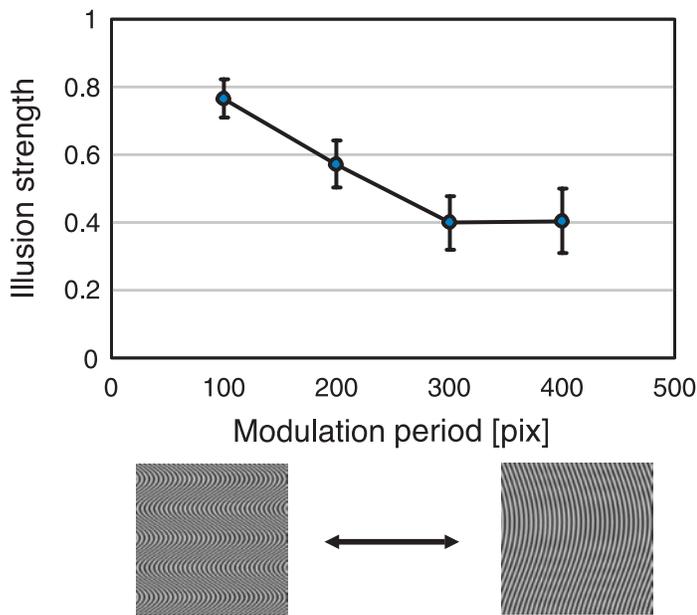
Figure 5. Illusion strength (points of subjective equality, PSE) as a function of the phase modulation period (μ, ranging from 100 to 400 pixels, or 4.1 to 16.2 deg) of the riloid. The curve shows the average results across all nine observers, and error bars indicate the standard error of the mean. Example sections of two test stimuli (minimum and maximum μ) are shown below the x-axis to illustrate the range of variation.

deviation from vertical orientation of the periodic lines ranged between 21 deg in the case of $\mu = 400$ pixels to 56 deg in the case of $\mu = 100$ pixels, which can be expected to strongly affect the variation of locally perceived direction of motion.

Variation of the contrast of the sinewave grating (c)

Riloids with a fixed grating wavelength, $\lambda = 8$, and a constant modulation amplitude, A = 24 pixels, and phase modulation period, $\mu_{top} = \mu_{bottom} = 200$ pixels, were used as test patterns. The nominal contrast, as given by the gray-level lookup table, of the pattern was varied from 0.1, 0.4, 0.7, to 1.0, where 1.0 is the maximum contrast for the computer screen, generated by using the full gray-level lookup table from 0 (corresponding to 0.6 cd/m^2) to 255 (corresponding to 181 cd/m^2). Because the monitor was not gamma-corrected, the actual contrast on the screen was 19%, 58%, 86%, and 99% of the maximum. In each experimental block, either riloids with nominal contrast 0.1 and 0.7, or with 0.4 and 1.0, were used. No fixation stimulus was presented and stimuli were presented for 1 second.

As shown in Figure 6, the strength of the motion illusion increases substantially and highly significantly ($F(2.43,19.45) = 72.54$, $p < 0.001$) when the nominal

contrast, c, of the riloid pattern is increased. Obviously, for even lower contrasts the illusion would be expected to disappear completely. This variation of perceived illusion strength is consistent across participants, although the curves for individual participants are shifted vertically (data not shown). This variability indicates a difference in the absolute strength of the illusion, but the small error bars in Figure 6 suggest that contrast dependence is much less susceptible to individual differences than the dependence on stimulus geometry tested in the previous two experiments. Moreover, the effect of the contrast on the illusion was independent of whether participants knew about the purpose of the experiment (main effect of participant group: $F(2,6) = 1.34$, $p = 0.330$; for between-group comparison; interaction with nominal contrast: $F(4.23,12.83) = 0.477$, $p = 0.763$).

Variation of the sinewave grating wavelength (λ)

Riloids with maximum contrast, c = 1, and with a constant phase modulation amplitude, A = 24 pixels, and phase modulation period, $\mu_{top} = \mu_{bottom} = 200$ pixels, were used as test patterns. The horizontal grating wavelength, λ, was varied from 4, 6, 16 to 32 pixels, corresponding to 0.15, 0.23, 0.60, and 1.21 degrees. In each experimental
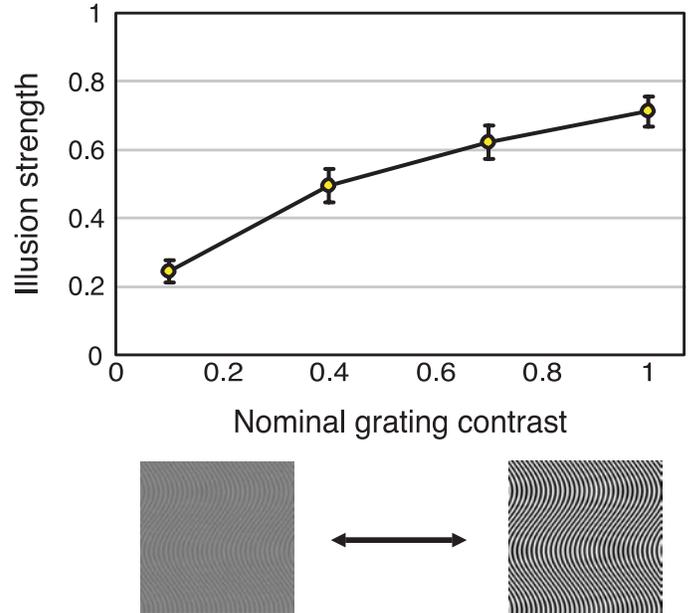

Figure 6. Illusion strength (points of subjective equality, PSE) as a function of the nominal grating contrast (c, ranging from nominal values of 0.1 to 1, corresponding to an actual screen contrast of 19% to 99%) of the riloid. The curve shows the average results across all nine observers, and error bars indicate the standard error of the mean. Example sections of two test stimuli (minimum and maximum c) are shown below the x-axis to illustrate the range of variation.
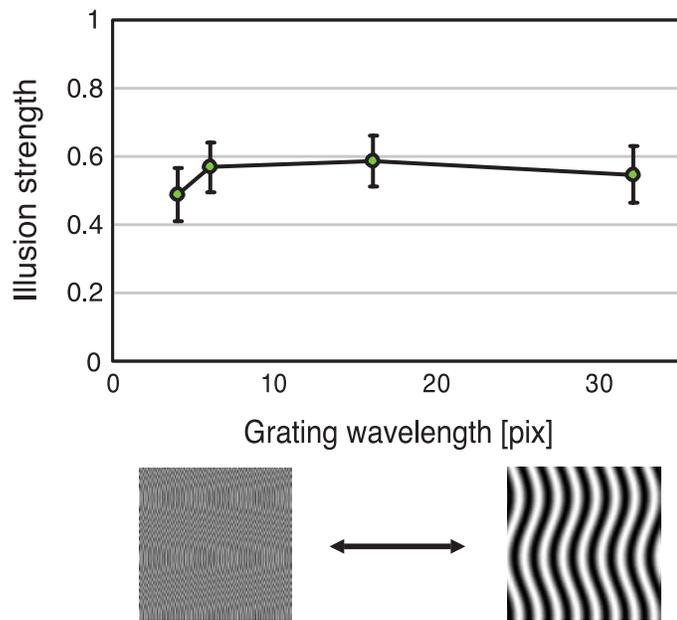
Figure 7. Illusion strength (points of subjective equality, PSE) as a function of the grating wavelength (λ, ranging from 4 to 32 pixels, or 0.15 to 1.16 deg) of the riloid. The curve shows the averages across all nine observers, and error bars indicate the standard error of the mean. Example sections of two test stimuli (minimum and maximum λ) are shown below the x-axis to illustrate the range of variation.

block, either riloids with a λ of 4 and 16 pixels, or with a λ of 6 and 32 pixels, were used. No fixation stimulus was presented and stimuli were presented for 1 second.

The results plotted in Figure 7 show no clear effect of the grating wavelength on perceived illusion strength (main effect of λ in a 4WS*3BS ANOVA: $F(2.35,7.04) = 0.512$, $p = 0.679$). As with the previous conditions, we found no effect of previous knowledge of participants about the experiment (main effect of participant group: $F(2,6) = 1.71$, $p = 0.259$; no significant interaction with λ: $F(2.35,7.04) = 0.047$, $p = 0.608$). Post hoc tests, comparing the effects of the individual levels of the grating wavelength showed a small, but significant trend of initial increase of the illusion strength between the two smallest wavelengths ($t(8) = 2.65$, $p = 0.029$). This variation of illusion strength is, however, much smaller than those we have seen in the other experiments.

General discussion

This study aimed to develop and test a novel method to measure the perceived strength of motion illusions in static images. To this end, we used line patterns, or 'riloids' that were generated as systematic variations of Bridget Riley's painting 'Fall', inducing strong motion sensations in human observers. The strength of illusory motion was measured using a psychophysical procedure, in which a given test stimulus was compared to a set of reference stimuli in which illusion strength was manipulated by varying the relative contrast a static image component superimposed to a standard riloid. These comparisons led to the computation of the point of subjective equality—the point at which the strength of the illusion of the test pattern and the reference pattern is equal—which serves as a quantitative measure of the strength of the illusion perceived in the test pattern. To test this method, such measurements were performed for a range of experimental conditions and stimulus parameters. These stimulus manipulations can be summarized in the following three groups.

In the first group of experiments, we investigated the experimental conditions related to the fixation behavior of participants and the stimulus duration. No significant differences in the measured illusions strength were found when participants were allowed to freely scan the stimuli compared to when they were required to fixate a point in between the two stimuli (Influence of a visible fixation target section). This finding suggests that the motion illusion does not require foveal stimulation but can also be perceived in the periphery. Although we did not measure eye movements in the current experiments, and therefore cannot be sure to which extent the image is stabilized, it is well known (e.g., Martinez-Conde, 2006; e.g., Zanker et al., 2003) that observers frequently make microsaccades during visual fixation. Our current observation that the fixation condition did not influence the strength of the illusion suggests a rather simple explanation for the similarity of illusion strength under fixation and scanning conditions. Small image displacements caused by microsaccades are sufficient to elicit the illusion (Zanker & Walker, 2004), which is not further enhanced by the large displacements during image scanning. Indeed, previous computational modeling demonstrated that increasing displacement amplitudes did not affect the motion signals (Zanker, 2004). The illusion strength did not depend on stimulus duration, in the range from 250 to 2000 msec (Effect of stimulus duration section). This suggests that the comparison method is a powerful tool, robust against variations in the stimulus presentation method, and does not benefit from temporal integration (in the range of durations tested). This finding is important for future use of the method, because with brief presentation durations illusory effects can be assessed rather swiftly. It should be noted, however, that the number of microsaccades expected to occur during a single stimulus period can be rather low. With rarely more than 2–3 microsaccades per second being observed in steady state (e.g., Zanker et al., 2003), the illusory effect for short presentations may not exclusively depend on microsaccades, but could also involve other image displacements that have equivalent effects on motion detection, such as slow drifts, tremor, or larger fixation saccades. Gaze instability of any kind is

most likely immediately after stimulus onset, and microsaccade rates change most prominently after display changes (e.g., Engbert & Kliegl, 2003). Whereas this question deserves further experimental investigation, for the present purpose it seems sufficient to focus the computational analysis (see below) on the effects of microsaccades as one distinct representative case of involuntary image displacements.

In the second group of experiments, we investigated how the properties of the basic sinewave gratings used to construct the riloids affect the perceived illusion. A strong increase of illusion strength with increasing stimulus contrast (Variation of the contrast of the sinewave grating (c) section) was found, which can be easily understood from the basic properties of motion detectors. It is known from a wide range of computational, physiological, and psychophysical studies that motion detection depends strongly on stimulus contrast (Borst & Egelhaaf, 1989; Boulton & Hess, 1990; Tootell et al., 1995). As a direct consequence, local motion signals, assumed to contribute to the strength of the illusion, are expected to increase as the contrast of the riloid increases. Contrary to the effects of contrast, changing the spatial period of the basic line grating, λ, had little effect on the illusion strength within the range tested (from 0.2 to 1.2 degrees; Variation of the sinewave grating wavelength (λ) section). This finding provides valuable information about the range of motion detectors involved. Because motion detectors are inherently tuned to a preferred spatial frequency (Borst & Egelhaaf, 1989), the relative independence with regards to the spatial frequency suggests that a range of local motion detectors with different spatial tuning characteristics are contributing to the illusion. This obviously does not exclude the possibility that for a wider range of λ one could find a variation of illusion strength, because for very fine and for very coarse gratings local motion responses would be reduced, and as a consequence a weaker illusion would be observed. Varying contrast and spatial period directly affects the local motion detector responses through the tuning of its input elements, which is unrelated to the effect of the remaining set of stimulus parameters that influence the geometric configuration of the undulating lines which is crucial for the illusion.

The two key parameters affecting the geometric appearance of the riloid patterns, the amplitude and period of phase modulation, were investigated in the third group of experiments. We found an increase of perceived illusion strength with growing modulation amplitude, A, (Variation of the amplitude of riloid phase modulation (A) section) and a decrease with growing modulation period, μ (Variation of the period of riloid phase modulation (μ) section). Both of these manipulations affect the variation of local line orientation, which grows with A, up to a maximum deviation of ±48 deg from the vertical at A = 36 pixels and μ = 200 pixels; it also grows with the inverse of μ (which is the spatial frequency of phase modulation), up to a maximum deviation of ±56 deg from the vertical at

μ = 100 pixels and A = 24 pixels. This variation of local line orientation is known to substantially affect the distribution of local motion signals as result of the due 'aperture problem' (Adelson & Movshon, 1982; Hildreth & Koch, 1987; Nakayama & Silverman, 1988): the direction of motion cannot be detected for one-dimensional stimuli (such as lines) unambiguously at any given location, and can only be resolved by integrating responses from stimulus gradients oriented in two spatial dimensions. The discrepancy between strong local motion signals that vary incoherently in direction and weak integrated signals is the characteristic property of motion distributions generated by shifts of riloids, and was proposed to be crucial for the perception of illusory motion for such patterns (Zanker & Walker, 2004). This critical discrepancy is enhanced by stronger variations of local orientation, as will be illustrated by the following simulation results.

Computational modeling

The overall pattern of results from the present experiments confirmed the observations made in previous work using on subjective rating of illusory motion (Zanker et al., 2003). However, the new method extends these finding by providing quantitative estimates of perceived illusion strength for a wide range of parameter values. This data set can be directly compared to simulations of motion responses in the 2DMD motion detector network (used previously by Zanker, 2004) to small displacements of riloid patterns, similar to those elicited by microsaccades. We restrict our comparisons between the model predictions and the psychophysical data to the parameters that directly influence the line orientations in the riloid patterns (Variation of the amplitude of riloid phase modulation (A) section and Variation of the period of riloid phase modulation (μ) section. Although other models (e.g., Hildreth & Koch, 1987), including some used in machine vision like the Lucas-Kanade algorithm (see Baker & Matthews, 2004), might generate similar results, the 2DMD model was chosen here as in our previous work because it directly provides local motion estimates at high spatial grain without the need of smoothing, and is closely associated with biological systems, accounting for a wide range of perceptual, behavioral, and physiological phenomena (cf. Borst & Egelhaaf, 1989; Zanker, 1994). The design of the model and all technical details are described in Zanker (2004). In essence, pairs of local, elementary motion detectors (EMDs, sometimes referred to as Reichardt detectors), which detect local image displacements in horizontal and vertical direction, respectively, are arranged in a two-dimensional network covering the complete stimulus area. Thus the network generates a two-dimensional map of local motion signals at high spatial resolution, with the relationship between horizontal and vertical responses

defining the direction and strength of the local motion response vector. The spatial and temporal tuning properties of the EMDs are determined by its standard sampling distance between neighboring input points, $\Delta\phi = 2$ pix, and standard time constant, $\tau = 2$ frames, respectively. The spatial and temporal tuning properties of the motion detector network are adjusted to the basic spatial frequency and frame rate of the stimulus, respectively, and as such are not directly related to the spatio-temporal tuning of individual motion detectors in the human visual system. This choice of tuning parameters is unproblematic because human motion processing is based on many parallel channels with different spatial and temporal tuning, and the perceptual response—the illusion—would necessarily be based on the channel best tuned to the stimulus in an analogous way.

From the distributions of local responses in the signal maps, we calculated a measure of the variation of local response direction relative to the average response direction for an extended image region. This 'incoherence measure' was estimated as the ratio of the average length of *local motion vectors* within a region of interest (ROI) and the length of the *average motion vector* for this ROI. To reduce noise and the effects of contrast-free image regions, responses below a threshold of 10% of the full response scale were excluded from calculating these averages. It has been argued that the discrepancy between motion coherence (length of average vector) and motion energy (average length of local vectors) critically reflects the conflicting information provided to the brain about local and global image displacement, and is therefore expected to be a reliable predictor of the perceived motion

illusion (Zanker & Walker, 2004). Whereas the previous computational work provided only a qualitative demonstration of the link between model output and the perceived illusion (Zanker, 2004), we are now in a position, to use this model, to study the quantitative relationships between the incoherence measure and perceived illusion strength, as they depend on stimulus parameters.

Riloid stimulus patterns with a size of 400×400 pixels, identical to those used in the psychophysical experiments, were generated as described in Stimuli section. For all simulations, the stimulus parameters were set to maximum contrast of 1.0 and grating period λ of 8 pixels. In the first set of simulations the phase modulation amplitude was kept constant at A = 24, whereas the phase modulation period was varied (μ = 100, 200, 300, and 400 pixels, as in the psychophysical experiments). In the other set of simulations, the modulation period was kept constant at μ = 200, and the modulation amplitude was varied (A = 6, 12, 24, 36 pixels, as used in the psychophysical experiments). The incoherence measure varies with the size of the ROI used for averaging the local responses and with size and direction of the pattern displacement. Two ROI sizes (100×100 pixels or 400×400 pixels) were used in combination with a range of image shifts. Patterns were generated with six steps of displacements corresponding to a zigzag trajectory. A range of amplitudes and directions was used: 10 pixels right and 10 pixels up; 20 pixels down; 20 pixels left and 20 pixels up; 30 pixels down; 30 pixels right and 30 pixels up; 40 pixels down. For any given pattern the model output (incoherence measure) for each displacement step was averaged for two ROIs, resulting in the average outputs shown in Figure 8.
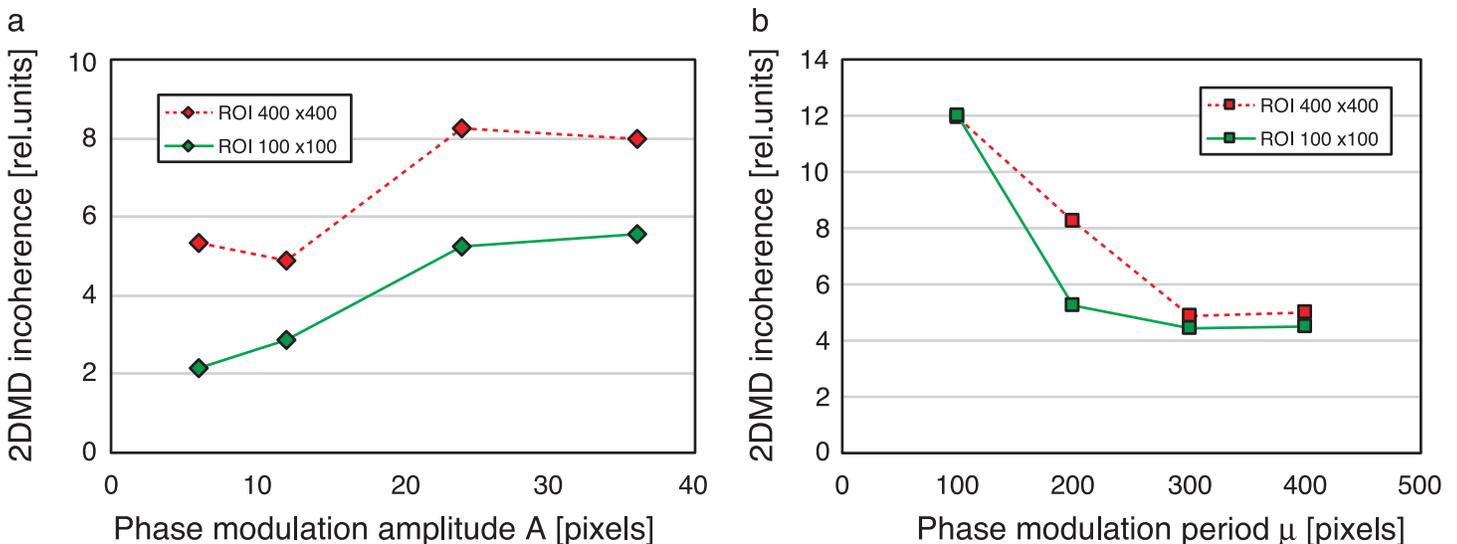

Figure 8. The incoherence measures derived from the 2DMD model output (see text), averaged for a range of displacement steps, is shown for two regions of interest (red/dotted and green/solid lines) as a function of the two stimulus parameters affecting the variation of line orientation in riloid patterns. (a) With increasing amplitude of the phase modulation of line gratings (diamonds, A, ranging from 6 to 36 pixels) the incoherence is increasing, predicting a stronger motion illusion. (b) With growing period of the phase modulation of line gratings (squares, μ, ranging from 100 to 400 pixels) the incoherence is decreasing, predicting a weaker motion illusion.

It is clear from Figure 8 that the average incoherence measures derived from 2DMD output reflect the psychophysical measurements for the same stimulus variations. There are some variations related to the ROI size, the effect of which needs to be tested more systematically. We also used only a small range of displacements, and it can be expected that using a wider variation of displacements, resembling closer the distribution of microsaccades, will present a more realistic simulation result. However, it is clear that when the amplitude of the phase modulation of line gratings, A, is increased, the response incoherence grows, similar to the illusion strength shown in Figure 4. When the period of the phase modulation of line gratings, μ, is increased, the response incoherence decreases, similar to the illusion strength shown in Figure 5. Within the limits of this modest range of image displacements and ROIs, it can therefore be concluded that the simple incoherence measure provides a good predictor of the change of motion sensation generated by riloids, at least for the stimulus parameters affecting the line orientations in riloid patterns.

Conclusions

We found a quantitative similarity between the psychophysical measurements of the illusion strength perceived in static patterns resembling Bridget Riley's 'Fall' and the output of the 2DMD model responding to displacement of such patterns on a path resembling that of microsaccades occurring under natural viewing conditions. A similar effect of microsaccades on the activity of neurons in the motion processing pathway has been found in electrophysiological experiments (Martinez-Conde, Macknik, & Hubel, 2000). These findings add further support to the hypothesis presented previously (Zanker & Walker, 2004) that the image instability under fixation conditions is sufficient to predict the shimmering and jazzing sensations experienced when looking at such examples of Op Art and related simple black and white patterns. The simplicity of these patterns is an advantage in that the elicited illusion is a unique, confined phenomenon. This obviously does not exclude the possibility that different mechanisms play a crucial role (see, for example Troncoso et al., 2008) in other patterns that generate other sensations, such as the streaming experienced in Enigma (Leviant, 1996). Equally, we cannot exclude the possibility that the other kinds of eye movements occurring during visual fixation, including tremor and slow drifts (Martinez-Conde et al., 2004) or accommodation (Campbell, Robson, & Westheimer, 1959), could lead to similarly effective displacements of the retinal image and thus could account for the observed illusion (cf. Zanker et al., 2003). The question whether slow eye drifts could also contribute to illusions in riloids is theoretically interesting because it could shed new light on the role of internal signals reflecting eye position that could reduce the illusory effects, which are easier to retain for slow drift than for small saccades. Furthermore, for other stimuli that are based on asymmetric luminance profiles it is likely that additional nonlinearities in the early visual system and possibly adaptation mechanisms are crucial (e.g., Backus & Oruc, 2005). Therefore the current experimental and computational analysis is restricted to a simple form of Op Art patterns, suggesting that microsaccades in combination with well established motion detection mechanisms are sufficient to explain the illusion in riloids. The method developed here to obtain quantitative measures of illusory motion can be used for the design of optimized stimuli for other stimuli, for instance in a clinical context to study the interaction between eye movements and perception, and thus has considerable potential to advance our understanding of visual function.

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Corresponding author: Johannes M. Zanker.
Email: J.Zanker@rhul.ac.uk.
Address: Department of Psychology, Royal Holloway University of London, Egham, Surrey, TW20 0EX, England.

References

Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature, 300,* 523–525. [PubMed]

Backus, B., & Oruc, I. (2005). Illusory motion from change over time in the response to contrast and luminance. *Journal of Vision, 5*(11):10, 1055–1069, http://journalofvision.org/5/11/10/, doi:10.1167/5.11.10. [PubMed] [Article]

Baker, S., & Matthews, I. (2004). Lucas-Kanade 20 years on: A unifying framework. *International Journal of Computer Vision, 56,* 221–255.

Borst, A., & Egelhaaf, M. (1989). Principles of visual motion detection. *Trends in Neuroscience, 12,* 297–306. [PubMed]

Boulton, J. C., & Hess, R. F. (1990). Luminance contrast and motion detection. *Vision Research, 30,* 175–179. [PubMed]

Campbell, F. W., Robson, J. G., & Westheimer, G. (1959). Fluctuations of accommodation under steady viewing conditions. *The Journal of Physiology, 145,* 579–594. [PubMed] [Article]

Conway, B. R., Kitaoka, A., Yazdanbakhsh, A., Pack, C. C., & Livingstone, M. S. (2005). Neural basis for a powerful static motion illusion. *Journal of Neuroscience, 25,* 5651–5656. [PubMed] [Article]

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43,* 1035–1045. [PubMed]

Fermüller, C., Pless, R., & Aloimonos, Y. (1997). Families of stationary patterns producing illusory movement: Insights into the visual system. *Proceedings of the Royal Society London B, 264,* 795–806. [PubMed] [Article]

Fraser, A., & Wilcox, K. J. (1979). Perception of illusory movement. *Nature, 281,* 565–566. [PubMed]

Gombrich, E. H. (1977). *Art and illusion*. Oxford: Phaidon.

Gregory, R. L. (1993). A comment: Mackay Rays shimmer due to accommodation changes. *Proceedings of the Royal Society London B, 253,* 123. [PubMed]

Gregory, R. L. (1994). Under the carpet. *Perception, 23,* 741–744. [PubMed]

Hamburger, K. (2007). Apparent rotation and jazzing in Leviant's Enigma illusion. *Perception, 36,* 797–807. [PubMed]

Hildreth, E.-C., & Koch, C. (1987). The analysis of visual motion: From computational theory to neuronal mechanisms. *Annual Review of Neuroscience, 10,* 477–533. [PubMed]

Kumar, T., & Glaser, D. A. (2006). Illusory motion in Enigma: A psychophysical investigation. *PNAS, 103,* 1947–1952. [PubMed] [Article]

Kupin, J. J., Haddad, G. M., & Steinman, R. M. (1973). Saccades in Neal's 'Square of Three'. *Perception and Psychophysics, 14,* 298–300.

Leviant, I. (1982). Illusory motion within still pictures: The L-effect. *Leonardo, 15,* 222–223.

Leviant, I. (1996). Does 'brain-power' make Enigma spin? *Proceedings of the Royal Society London B, 263,* 997–1001.

MacKay, D. M. (1957). Moving images produced by regular stationary patterns. *Nature, 180,* 849–850. [PubMed]

Martinez-Conde, S. (2006). Fixational eye movements in normal and pathological vision. In S. L. Macknick, A. T. Martinez, J. M. Alonso, & P. U. Tse (Eds.), *Progress in brain research* (pp. 151–176).

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2000). Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. *Nature Neuroscience, 3,* 251–258. [PubMed]

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. [PubMed]

Mon-Williams, M., & Wann, J. P. (1996). An illusion that avoids focus. *Proceedings of the Royal Society London B, 263,* 573–578.

Murakami, I., Kitaoka, A., & Ashida, H. (2006). A positive correlation between fixation instability and the strength of illusory motion in a static display. *Vision Research, 46,* 2421–2431. [PubMed]

Nakayama, K., & Silverman, G. H. (1988). The aperture problem: I. Perception of nonrigidity and motion direction in translating sinusoidal lines. *Vision Research, 28,* 739–746. [PubMed]

Patzwahl, D. R., & Zanker, J. M. (2000). Mechanisms for human motion perception: Combining evidence from evoked potentials, behavioural performance and computational modelling. *European Journal of Neuroscience, 12,* 273–282. [PubMed]

Pirenne, M. H., Campbell, F. W., Robson, J. G., & Mackay, D. M. (1958). Moving visual images produced by regular stationary patterns. *Nature, 181,* 362–363. [PubMed]

Riley, B. (1995). *Dialogues on art*. London: Zwemmer.

Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine spatial detail. *Nature, 447,* 852–855. [PubMed]

Tootell, R. B., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., et al. (1995). Functional analysis of human mt and related visual cortex areas using Magnetic resonance imaging. *Journal of Neuroscience, 15,* 3215–3230.

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. [PubMed] [Article]

von Helmholtz, H. (1924). *Treatise on physiological optics*. New York: Dover.

Wade, N. J. (2003). Movements in art: From Rosso to Riley. *Perception, 32,* 1029–1036. [PubMed]

Zanker, J. M. (1994). Modeling human motion perception: I. Classical stimuli. *Naturwissenschaften, 81,* 156–163. [PubMed]

Zanker, J. M. (2001). Combining local motion signals: A computational study of segmentation and transparency. In J. M. Zanker & J. Zeil (Eds.), *Motion vision: Computational neural and ecological constraints*

(pp. 113–124). Berlin Heidelberg New York: Springer Verlag.

Zanker, J. M. (2004). Looking at op art from a computational viewpoint. *Spatial Vision, 17,* 75–94. [PubMed]

Zanker, J. M., & Braddick, O. J. (1999). How does noise influence the estimation of speed? *Vision Research, 39,* 2411–2420. [PubMed]

Zanker, J. M., Doyle, M., & Walker, R. (2003). Gaze stability of observers watching Op Art pictures. *Perception, 32,* 1037–1049.

Zanker, J. M., & Walker, R. (2004). A new look at Op art: Towards a simple explanation of illusory motion. *Naturwissenschaften, 91,* 149–156. [PubMed]

Zeki, S. (1994). The cortical Enigma: A reply to Professor Gregory. *Proceedings of the Royal Society London B, 257,* 243–245. [PubMed]

Zeki, S., & Lamb, M., (1994). The neurology of kinetic art. *Brain, 117,* 607–636. [PubMed]

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 London B, 252,* 215–222. [PubMed]