



Illusory jitter in a static stimulus surrounded by a synchronously flickering pattern

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Abstract

The eyes are always moving even during fixation, making the retinal image move concomitantly. While these motions activate early visual stages, they are excluded from one's perception. A striking illusion reported here renders them visible: a static pattern surrounded by a synchronously flickering pattern appears to move coherently in random directions. There was a positive correlation between the illusion and fixational eye movements. A simulation revealed that motion computation artificially creates a motion difference between center and surround, which is usually a cue to object motion but now a wrong cue to seeing eye movements of oneself on-line. Therefore, this novel illusion indicates that the visual system normally counteracts shaky visual inputs due to small eye movements by using retinal, as opposed to extraretinal, motion signals. As long as they comprise common image motions over space, they are interpreted as coming from a static outer world viewed through moving eyes. Such visual stability fails in the condition of artificial flicker, because common image motions due to eye movements are registered differently between flickering and non-flickering regions.

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1. Introduction

As classical experiments on perceptual fading of stabilized retinal images have clearly shown, all visual scenes we normally enjoy are actually derived from moving retinal images. However hard we may try to keep the head and eyes stationary, small oscillatory movements of the eye relative to the orbit keep the image shaking on the retina (Krauskopf, Cornsweet, & Riggs, 1960; Steinman, Haddad, Skavenski, & Wyman, 1973). They are believed to play a critical role in constant visibility of visual stimuli, since artificially stabilized retinal images soon fade away from one's perception in seconds (Yarbus, 1967). These retinal motions indeed activate multiple cortical stages of visual processing (Bair & O'Keefe, 1998; Leopold & Logothetis, 1998; Martinez-Conde, Macknik, & Hubel, 2000, 2002; Snodderly, Kagan, & Gur, 2001). Paradoxically, however, these neural responses in normal observers do

not lead to corresponding and noxious perception of oscillation of the whole visual field. Thus, the visual system normally excludes them from one's veridical perception of the stable visual world in spite of random oscillations on the input stage. But how?

This question has long been addressed to visual stability during large-scale eye movements such as saccades and smooth pursuit. According to the "outflow theory," a copy of eye-movement commands is used by the visual system to subtract eye-originated image flow from retinal image motions (Helmholtz, 1866), whereas the "inflow theory" says that such a subtraction operation uses proprioceptive signals from eye muscles (Sherrington, 1918). However, it is unlikely that these extraretinal signals are compatible with the actual retinal image motions of fixating eyes. Random eye movements during fixation are partly derived from chaotic neuromuscular activities downstream of the oculomotor system (Eizenman, Hallett, & Frecker, 1985). If monitored by either outflow or inflow pathway conveying kinetic signals, they are not immediately usable for vectorial subtraction in vision within a practical interval of latency.

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The eye during fixation can also be moved by external force such as chewing behavior, and by head movement that vestibuloocular reflex cannot perfectly compensate for (Skavenski, Hansen, Steinman, & Winterson, 1979). These movements make retinal image slip that is inconsistent with what extraretinal signals could report. A psychophysical study also disproves the involvement of extraretinal signals for small eye movements in motion processing (Heidenreich & Turano, 1996). Accordingly, speed discrimination performance under stabilized and normal viewing conditions is equivalent if speed is described in retinal terms. A retinal-image model explains the results without needing to consider extraretinal signals.

As extraretinal signals seem invalid, an alternative approach is to use visual information *per se* for counteracting image motions due to small eye movements (Murakami & Cavanagh, 1998, 2001; Wertheim, 1994). At each instant, the visual system receives a two-dimensional retinal velocity field that is a mixture of components of three different origins, object motion, eye translation, and eye rotation. Recovering these components from the velocity field they cause is an ill-posed problem, and thus some constraints are necessary to nail it down. The key assumption is that, given a static outer world, small orbit-relative eye movements always give rise to the same image translation “everywhere.” On a spherical retina, this assumption is geometrically untrue but is locally acceptable in a certain spatial scale around the center of the visual field (Fermüller & Aloimonos, 1995; Rieger & Lawton, 1985). Further assuming that the head is approximately still during small eye movements and that the visual system knows it, the question is how much amount of common image translation should be ascribed to eye movements. The situation is conceptually analogous to lightness constancy: we are extremely sensitive to luminance contrast between objects but are normally unaware of subtle change of ambient light.

A new motion illusion has recently been reported to hint at the answer to this question. After adaptation to dynamic random noise, static-noise patterns are presented simultaneously in the adapted and unadapted regions. The one in the unadapted region appears to jitter in random directions for just a few seconds, essentially reflecting one’s own eye movements (Murakami & Cavanagh, 1998, 2001; Sasaki, Murakami, Cavanagh, & Tootell, 2002). Although further elaboration is undoubtedly necessary, this illusion strongly suggests a visual-motion-based scheme to solve the above mentioned question; accordingly the visual system compensates for small eye movements by keeping silent at common image motions unless they are clearly delineated from background motions by a difference in motion. Assuming that the adapted region has fatigued motion sensors whereas other regions remain unaffected,

this situation artificially creates a motion difference between regions, ending up with a jitter aftereffect—only the image motion in the unadapted region is interpreted to be moving whereas other regions are seen stationary, even though eye movements give rise to the same amount of retinal image motions in all regions.

There are a number of problems with this simple interpretation of the jitter aftereffect, however: (1) Adaptation produces the negative afterimage naturally moving with the eyes, which serves as a potential artifact. (2) The steep exponential decay of the aftereffect is unrelated to the explanation in terms of eye movements. (3) The duration measure being the only practical methodology, precise quantification is difficult. (4) The time-consuming adaptation paradigm is not welcomed when the illusion is applied to cell recordings, clinical tests, etc. However, probably the biggest problem is (5) that the aftereffect only gives us indirect evidence for a mechanism in a normally functioning system. One sees what happens after adaptation and only infers how the system would be working without artificial adaptation. If the proposed hypothesis of small-eye-movement compensation is true, one could find converging evidence using some different paradigm than adaptation.

The novel illusion reported in the present study overcomes all these difficulties. It demonstrates that image motions due to one’s own small eye movements are perceived in a static pattern surrounded by a synchronously flickering pattern, and that some artificial motion difference could indeed be created in the brain not only by adaptation but simply by presenting flicker. As such, the observer could monitor the impression of jitter “on-line” as long as the stimulus is viewed. This illusion therefore provides supporting evidence for the idea of visual-motion-based compensation of small eye movements, and newly demonstrate that spatiotemporally continuous accessibility to visual information is essential for the function of visual stability despite small eye movements.

The present study consists of phenomenology, psychophysics, and simulation. First, several phenomenal aspects of the illusion are reported by casually observing a typical stimulus configuration and its variants. Second, after establishing the similarity between perceived random motion and velocity white noise, a psychophysical matching procedure was used to find the perceptual match between the illusion and a stimulus in physical random motion. Third, the magnitude of the illusion was shown to have a positive correlation with eye-movement records during fixation. Fourth, an account for the illusory motion in terms of motion-energy detection was tested by computer simulation. Fifth, predictions from the motion-energy model were compared to psychophysical matching data for various settings of stimulus parameters.

2. General methods

This study followed Declaration of Helsinki guidelines and was approved by NTT Communication Science Laboratories Research Ethics Committee. Informed consent was obtained from all observers after explanation of the nature and possible consequences of the study. Two naive observers and the author (aged 21–33, with normal or corrected-to-normal vision) participated in formal experiments. Each observer had undertaken at least 100 practice trials before data acquisition.

2.1. Stimulus

In a dark room, the stimulus was presented on a 21-inch color CRT monitor (Sony GDM-F500; 640×480 pixels, or $42.7 \text{ deg} \times 32 \text{ deg}$; scan rate 75 Hz; viewing distance 54 cm, constrained by the chinrest) controlled by a computer (Apple Power Macintosh). A circular “center” (diameter 13.3 deg) and an annular “surround” (outer diameter 26.7 deg) were placed concentrically on the uniform gray background of the mean luminance (36 cd/m^2). Borders between regions were softened by a cumulative-Gaussian-shaped contrast modulator (standard deviation 40 min). The surround was filled with a random-dot texture (50% of dots black, 50% white; each dot 16 min wide), which synchronously flickered at 9.4 Hz (with all dots visible for 80 ms and turned off to the mean luminance for next 27 ms, unless noted otherwise). The center was occupied by another random-dot texture (each dot consisting of a luminance profile of an isotropic two-dimensional Gaussian with the standard deviation of 8 min; dot density 3.5 dots/deg^2). The maximum Michelson contrasts of the center and surround patterns were both 99%. Throughout the experiment, the fixation spot was provided at 10 deg offset to the right from the center of the concentric stimulus. See Fig. 1 for the appearance of the stimulus.

In addition to the above setting, the central pattern was artificially moved in random directions in the matching experiments (see below). The velocity profile of random walk was generated by randomly sampling each instantaneous velocity (with the resolution of 13 ms) from an isotropic two-dimensional Gaussian probability density function with a variable standard deviation (σ in deg/s). Its center was 0 deg/s, its horizontal axis corresponded to leftward (negative) and rightward (positive) directions, and its vertical axis corresponded to downward (negative) and upward (positive) directions. Hence the generated profile was two-dimensional white noise with respect to velocity; this was equivalent to amplitude spectra with respect to position obeying “ $1/f$ ” (i.e., inversely proportional to frequency), such as seen in small eye movements of the human (Eizenman

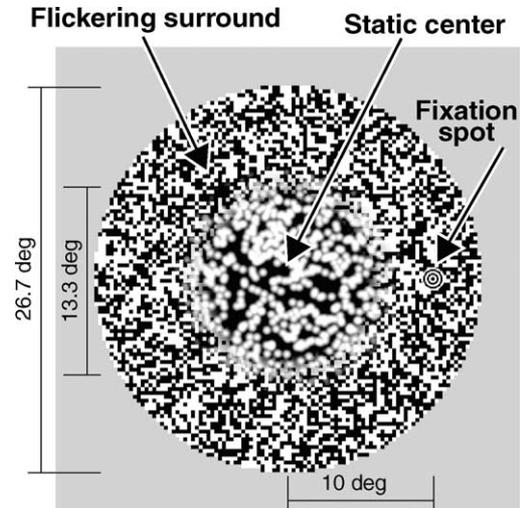


Fig. 1. Typical stimulus configuration for the illusion. The central pattern was static, whereas the surrounding annular region was synchronously flickering, i.e., periodically turned on (80 ms) and off (27 ms). Perceptually the central pattern appears to move in random directions. The illusion is more salient with peripheral viewing of the stimulus, presumably because the stationary center-surround border as a frame of reference becomes perceptually more obscure. However, the illusion persists if viewed centrally or if the stimulus is enlarged to cover tens of degrees.

et al., 1985).¹ According to the two-dimensional velocity profile generated as such, the central pattern as a whole was moved *coherently* (i.e., all dots in the same direction) within the center-surround border. The blurry microstructure of dots and center-surround border ensured anti-aliased sub-pixel animation. Ten different versions of movies had been generated for an identical level of physical-jitter amplitude and had been stored in disk before the experiment was executed.

2.2. Procedure

As the illusory motion occurred immediately and lasted as long as the stimulus was viewed, it was possible

¹ The actual time-series generation procedure utilized the equivalence between flat velocity amplitude spectra and $1/f$ -shaped position amplitude spectra. First, the position amplitude spectra were generated such that $y = 0$ for $f = 0$ and $y = s/f$ otherwise, where s is a scalar gain factor of amplitude and f is frequency. Second, a random angle was assigned to phase associated with each frequency. Third, by using inverse discrete Fourier transform, the frequency series of the amplitude-phase pairs was transformed back to horizontal position series for 64 frames. Since the DC component was nil, the position series did not contain any trend; the fundamental frequency corresponded to the sinusoidal wave with the wavelength of 64 frames. Fourth, the vertical position series was independently generated the same way, and finally the time series of two-dimensional position was made by combining the horizontal and vertical position series. The linear relationship between σ (standard deviation of the two-dimensional velocity distribution) and s (gain factor of position amplitude) was checked by Monte-Carlo simulation.

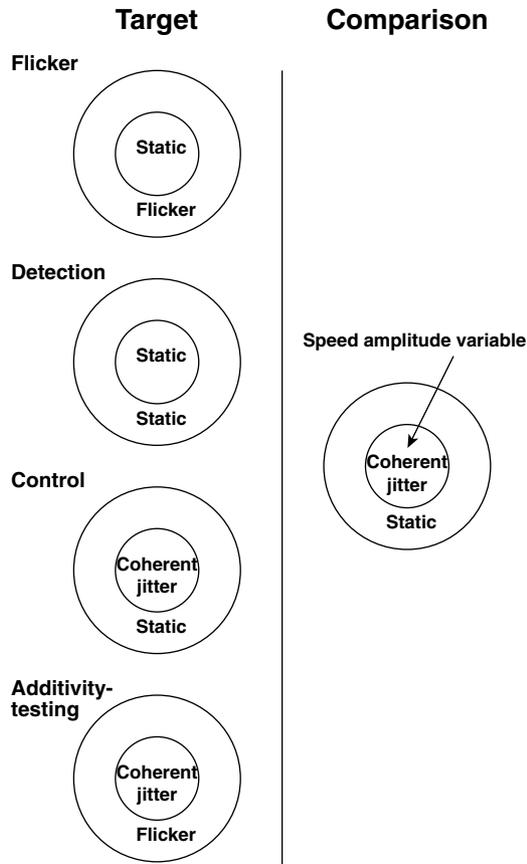


Fig. 2. Schematic views of the standard target stimulus and the comparison stimulus used in the perceptual matching experiments. As is shown in the right-hand column, the comparison stimulus always had the same shape throughout conditions: a static surround and a physically jittering center. The speed amplitude of the central jitter was variable. The left-hand column illustrates the shape of the target stimulus for four different conditions.

to find its perceptual match by presenting a stimulus that actually moved in random directions. In each trial, a standard *target* stimulus whose property was set appropriately was presented (its property depending on experimental conditions as described in detail in Section 3; see Fig. 2). Also presented within the same trial was a *comparison* stimulus consisting of a *static* surround and a *physically jittering* center, whose speed amplitude was variable. Actually, its amplitude was varied randomly from trial to trial, following the standard method of constant stimuli. The amplitude values of the comparison stimulus were chosen appropriately for each target stimulus and for each observer, on the basis of data from preliminary sessions, so that the range should be roughly centered at the true point of perceptual equality and the step size should be just small enough compared with the slope of the psychometric function (Fig. 3A). As a result, each increment of step was equivalent to speed amplitude multiplied by two, and there were

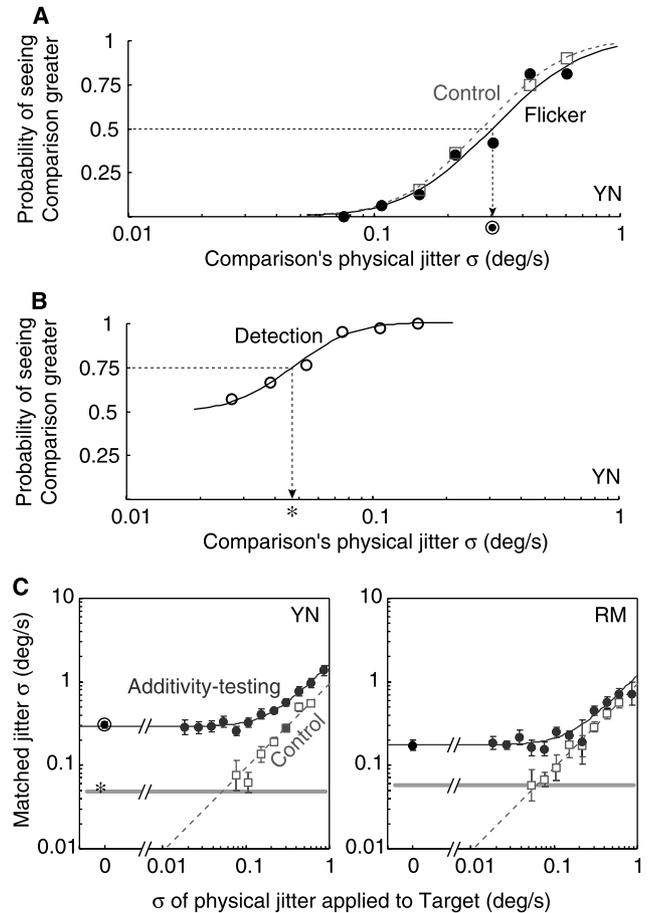


Fig. 3. Results of the matching experiments. (A) Psychometric functions for observer YN. Probability of seeing the comparison's jitter greater is plotted against the comparison's physical jitter amplitude. The comparison stimulus always consisted of a *static* surround and a *physically jittering* center, with its σ variable. In the condition designated "Flicker" (solid circles), the target stimulus consisted of a *flickering* surround and a *static* center. Any movement perceived in the center of the target stimulus was therefore illusory. The matched jitter is indicated by the bull's eye. In the condition designated "Control" (open squares), the target stimulus consisted of a *static* surround and a center physically jittering with σ of 0.3 deg/s. Therefore no illusion was involved. (B) The psychometric function for the detection threshold experiment; data for YN. The target stimulus consisted of a *static* surround and a *static* center. The threshold is indicated by the asterisk. (C) Matched jitter plotted as a function of *physical jitter* applied to the center of the target stimulus (error bar, ± 1 standard error). Its surround was *flickering* in the "additivity-testing" condition (solid circles) and was *static* in the "control" condition (open squares). The shaded baseline with an asterisk indicates the detection threshold, which is also depicted as the asterisk in (B). The bull's eye and the solid square indicate the matches obtained from the psychometric functions shown as "Flicker" and "Control", respectively, in (A). The solid curves indicate the best-fit variance-additivity model.

typically 6–7 separate data points to span a psychometric function.

The observer was sequentially presented with the target and comparison stimuli (inter-stimulus interval 333 ms; presentation order randomized) and was asked to judge which stimulus appeared more jittery. No

feedback was given. For each stimulus, the surround first appeared and remained for 2013 ms (151 frames), within which the center appeared (at a randomized timing) and remained for 853 ms (64 frames). For each target stimulus and for each observer, the frequency of seeing the comparison stimulus more jittery than the target stimulus was plotted against speed amplitude, and the best-fit cumulative-Gaussian psychometric function was estimated by the maximum likelihood method to determine the perceptual match (at the probability of 0.5). Its standard error was estimated by the bootstrap resampling procedure (Foster & Bischof, 1991; Maloney, 1990).

3. Results

3.1. Phenomenological observations

As the illusion is novel, its phenomenological aspects are briefly described before proceeding to psychophysical experiments.

A typical stimulus configuration was shown in Fig. 1. A static random-dot pattern was surrounded by another pattern that was periodically turned on (e.g., 80 ms) and off (e.g., 27 ms). The observer looked at the stimulus while maintaining gaze at the fixation spot as hard as possible. The central pattern appeared to move coherently in random directions. This phenomenon occurred immediately and lasted as long as the static center was accompanied by the synchronously flickering surround. The illusion changed in direction a few times per second and was described as tiny random oscillations of the center as a whole. The center-surround configuration was optimal, but the illusion was obtained in a grating or a checkerboard configuration where static and flickering dot patterns were intermingled in alternating regions.

The central pattern was blurred spatially for two reasons: to reduce retinal-velocity information from the stationary center-surround border and to realize anti-aliased smooth motion in perceptual matching experiments. However, presence/absence of high spatial-frequency components in the central pattern was not essential in producing the illusion. Eccentric viewing also perceptually blurred the border, but the illusion persisted even while fixating at the center. The fixation spot and the central pattern were presented apart for the more practical reason that the observer should not detect physical motion of the center in reference to the stationary fixation spot in matching experiments. The stimulus size was also flexible; at this eccentricity, the magnitude of the illusory motion did not change with further increasing size. When the same stimulus was front-projected on a screen subtending a few meters and was viewed centrally, the illusion still occurred despite

that the surround region would fall onto peripheral retinal regions as far as 20 deg or more.

Observations suggested relationship to eye movements: (1) The illusion was correlated with eye/head vibrations by external force (e.g., the cheek tapped gently by the hand). (2) Mild horizontal post-rotational nystagmus induced after body rotation biased the illusion toward horizontal (though the rest of the world did not appear to oscillate). (3) While tracking a slowly moving spot rather than the stationary fixation spot, the center appeared to move smoothly in the direction opposite to smooth pursuit or in the same direction as the retinal image motion. (4) The above observations were repeated with more than one static region embedded in the flickering surround (e.g., one in each quadrant of the visual field); these remote regions appeared to move together in the same direction and at the same velocity. Except for common image slip due to eye movements, there is no obvious reason that such synchronization should occur. In all these respects, the seen movement in the present illusion was phenomenally similar to that of the jitter aftereffect (Murakami & Cavanagh, 1998, 2001). However, the present illusion lasted as long as the stimulus was observed, whereas the jitter aftereffect ceases within a few seconds.

3.2. Perceptual matching

As different patterns of eye movements could modify the illusion, the illusory motion perceived during steady fixation might be related to small eye movements that are incessantly present but are normally unnoticeable. Small eye movements are known to follow Brownian random walk (Eizenman et al., 1985). Thus, if they give rise to the illusion, its replica should be obtainable by actually making the stimulus as such. To this end, the “comparison” stimulus was made otherwise identical to the standard “target” stimulus to be matched (Fig. 1), but with the *static* surround and with the center in *coherent jitter* simulating the eye’s random walk.

By varying the speed amplitude (σ in deg/s) of the central jitter of the comparison stimulus, the perceptual match to the illusion was established (see Fig. 2, “Flicker” for an illustration of two compared stimuli). It was at approximately 0.3 deg/s (Fig. 3A, bull’s-eye symbol), where the comparison stimulus appeared equivalent to the illusion in all phenomenological aspects (confirmed by naive verbal reports).

To ascertain that this perceptual match actually evoked suprathreshold jitter perception, the detection threshold of the physical jitter per se was also measured. The target stimulus was changed to a *static* surround and a *static* center (Fig. 2, “Detection”). Therefore, the task was reduced to detecting physical jitter in the center. As the lower asymptote of the psychometric function was theoretically 0.5 (i.e., the chance level of

two-alternative forced choice), the range-corrected cumulative Gaussian was fit to the data, and the detection threshold was defined as the speed amplitude corresponding to the probability of 0.75. The threshold was found at approximately 0.05 deg/s (Fig. 3B, asterisk). Therefore, the illusion-matched jitter was significantly greater than the detection threshold of the physical jitter per se.

The jitter matching data in Fig. 3A do not only establish the perceptual match but also provide an index of variability in the form of the slope of the psychometric function. If the illusory jitter perception was none in some trials, slight in some, and huge in others, the slope would become shallower than in the case in which perceived jitter was stable across trials. In the control experiment, the target stimulus consisted of a *static* surround and a *physically jittering* center with its σ constant at 0.3 deg/s (Fig. 2, “Control”). Therefore, the target and comparison stimuli were identical except that the speed amplitude of the latter was variable. Both were actually moving; no illusion was involved in this experiment. The resulting psychometric function (Fig. 3A, broken curve) was indistinguishable from the original illusion-matching data (solid curve). Therefore, the illusion is quite solid, and is a precisely measurable, perceptual event, rather than cognitive anecdote. These results support the eye-movement hypothesis that the illusion is related to retinal image slip due to incessant eye movements of fixation.

3.3. Additivity testing

If the center of the target stimulus with surround flicker is physically making jittery motion instead of being static, the percept will be some mixture of illusory and physical motions. How are they mixed? If eye movements impose random motions in perception, they should constantly and independently do so irrespective of stimulus movement. Thus, the eye-movement hypothesis predicts that the illusion and the physically applied jitter should be perceptually additive, following the theorem that the variances of two independent noise sources simply add.

In the additivity-testing experiment, the target stimulus consisted of a *flickering* surround and a *physically jittering* center (Fig. 2, “Additivity-testing”), hence the perceived motion in the center was a mixture of illusory and real motions. In Fig. 3C (solid circles), the results are plotted as a function of speed amplitude of the target stimulus. The data were fit by the model assuming that the variances of illusory motion and real motion are perceptually additive:

$$y = m(x^2 + a^2)^{0.5}, \quad (1)$$

where y denotes matched jitter, x denotes physically applied jitter, a denotes magnitude of illusory jitter, and

m is proportionality constant. Similar forms of equations have often been used for estimating internal noise of the visual system, in which case y is usually signal strength at detection threshold, whereas m is related to efficiency or detectability (Doshier & Lu, 1998; Levi, Klein, Sharma, & Nguyen, 2000; Pelli & Farell, 1999). However, as the interest of the present study was in a suprathreshold motion phenomenon, y represents perceptual motion strength determined by matching. Parameter a specifies the magnitude of seen movement when there is no coherent jitter in the target stimulus (i.e., $x = 0$), and is related to purely illusory motion. Parameter m is simply related to response bias with which the observer tends to over-/under-estimate the perceived motion with surround flicker relative to the one without it. For example, consider the hypothetical case in which the flickering surround is functionally equivalent to the absence of the surround. Then the coherent jitter in the center would not have any relative-motion cue and thus would be harder to see than the comparison stimulus with a static surround. Response bias m in this case would be lower than unity. Alternatively, the observer might more frequently choose the stimulus with surround flicker as moving faster, even when the same motion is actually perceived in both intervals. Such cognitive bias would lead to m greater than unity.

Operationally, the model has two free parameters, m and a . Increasing m is equivalent to overall upward shift in log–log plot. The other parameter, a , characterizes the lower asymptote of the function. The model makes a flat function up to some level of the abscissa and then smoothly changes to a linearly increasing function in log–log plot. Additivity is met if data simply follow this profile. If, on the other hand, the illusion is a consequence of nonlinear interactions of visual stimuli (for example, the illusion might never occur unless the center is completely stationary, or alternatively the illusion might be persistent enough to mask whatever may be presented in the center), data should deviate from the prediction.

Additivity was indeed observed: the matching result plotted against physically applied jitter was extremely well fit by the variance-additivity model expressed in Eq. (1) (Fig. 3C, solid curve). For YN, $m = 159\%$ and $a = 0.183$ deg/s (determination coefficient $r^2 = 0.981$). For RM, $m = 118\%$ and $a = 0.148$ deg/s ($r^2 = 0.883$). For IM, $m = 138\%$ and $a = 0.081$ deg/s ($r^2 = 0.996$). Therefore, these data support the eye-movement hypothesis predicting that the noise source for the jitter illusion is independent of stimulus movement.

This procedure also factored out the response bias in comparing the target stimulus with flicker and the non-flickering comparison stimulus. Trials in the additivity-testing condition were actually intermingled with trials in the control condition in which the target stimulus

consisted of a *static* surround and a *physically jittering* center (Fig. 2, “Control”). In Fig. 3C (open squares), the results for the control condition are plotted as a function of speed amplitude of the target stimulus. The same jitter always appeared identical. Therefore, not surprisingly, $m = 100\%$ and $a = 0$, so that all the data were aligned on the identity function, $y = x$ (Fig. 3C, broken line). The target stimulus with flicker, however, tended to be overestimated by a constant proportion, as is shown by a slight upward deviation from the identity line at high enough levels of the abscissa (where perception must be dominated by real jitter rather than illusion). The model function, which trapped this small response bias in the form of parameter m , revealed a large amount of the additive factor a .

3.4. Correlation with small eye movements

Next, the observer’s eye movements were recorded to assess whether the magnitude of the illusory motion varies with statistics of eye movements. While the stimulus (with both *flickering* and *static* surrounds tested in separate sessions) was being passively observed (for 18 s) in the same viewing condition as in the matching experiments and while the observer was fixating at the fixation spot, the horizontal eye position of the observer’s right eye was recorded by an infrared-based limbus eye tracker (Iota Orbit 8) with the sampling resolution of 1 kHz. Just before and after the fixation period, calibration dots at 16 different positions (within ± 5 deg) were presented sequentially for 2 s each, and the observer was asked to make a reaching saccade to each of them. Trials were repeated 8–10 times, and 23–32 samples of blink-free 4-s periods were chosen from the fixation periods and were bandpass-filtered (1–31 Hz) to result in resampled velocity with the same resolution as the monitor (13 ms).² The velocity histogram with 0.1-s bin was plotted (the positive and negative of the abscissa being rightward and leftward directions, respectively) and the maximum likelihood method estimated the best-fit Gaussian, whose standard deviation was taken as the index of eye-velocity variability.

An across-observer analysis revealed that those who had the greater eye movements of fixation perceived the greater illusion, although the conclusion should be considered only tentative as the number of samples is limited (Fig. 4A). The abscissa indicates the perceptual match (parameter a of Eq. (1)), whereas the ordinate

indicates the standard deviation of eye velocity. There was a highly significant positive correlation between these quantities (correlation coefficient $r = 0.977$, $t_4 = 9.08$, $p < 0.001$). Linear regression in log–log plot revealed: $y = 1.128x + 0.957$ ($r^2 = 0.942$). Compared to the extreme and unlikely scheme where all eye velocity is translated into perceived motion without loss (broken line), the actual illusion had a gain of considerably less than unity, but it was roughly constant across observers. It is also important to note that eye velocity did not change depending on whether surround flicker was present (solid circles) or not (open triangles).³

There was no relationship between eye velocity and response bias (parameter m of Eq. (1)), as is shown in Fig. 4B ($p = 0.391$). Thus, those who had the greater eye movements do not necessarily overestimate motion embedded in surround flicker relative to motion without it. In Fig. 4C no relationship was found either, between eye velocity and detection threshold of physical jitter ($p = 0.864$), rejecting the idea that observers who were worse at maintaining fixation generally performed worse in every aspect of the experiments.

3.5. Simulation of motion-energy detection

Small eye movements occur incessantly and so does retinal image slip. Why is it perceived only in the presence of surround flicker, being suppressed otherwise? To test the hypothesis that surround flicker somehow confuses early motion-energy detection, computer simulation was performed.

An early stage of motion processing of the visual system is believed to detect spatiotemporal orientation of luminance contrast by linear filtering accompanied by simple nonlinear operation (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). Among interrelated computational models that have been proposed previously, Adelson and Bergen’s (1985) motion-energy model was implemented on a IBM-PC/AT-compatible computer (Dell Dimension 4100) by a custom program in MATLAB 6 (Mathworks Inc.), to see any change in outputs of motion-energy units depending on whether the pattern was flickering or not.

Under the assumption that the eye was moving to the left at 0.625 deg/s, the retinal image of a flickering random-dot pattern was rendered on a space–time surface

² Data were discarded if within 65 ms around each fixational saccade (determined by the velocity criterion of 10 deg/s) (Bair & O’Keefe, 1998; Snodderly et al., 2001), as the velocity profiles of microsaccades seemed distinct from the model of velocity white noise. However, their occasions were quite rare (0.2–1.5 times/s), and their presence or absence in data resulted in only a slight (< 0.03 deg/s) change in parameter estimation.

³ In many trials in the perceptual matching experiments (Fig. 3C), the center physically moved in random directions. To see whether the artificial jitter in the stimulus evokes optokinetic responses in random directions, eye-movement recording was repeated (for the author) at several levels of physical jitter (with σ of 0, 0.43, 0.86, and 1.71 deg/s). Both flickering and static surrounds were tested. The standard deviation of eye velocity did not change (0.497 ± 0.029 deg/s) across the range of physical jitter used in the matching experiment.

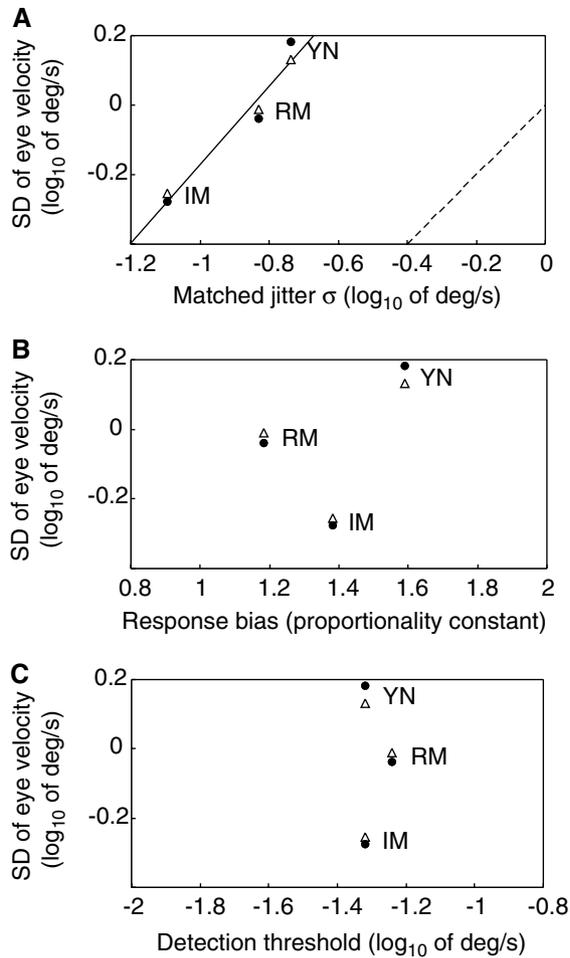


Fig. 4. Relationship between psychophysical data and statistics of small eye movements. In each panel, the ordinate indicates the standard deviation of instantaneous eye velocity during passive viewing of the stimulus with fixation (solid circle, flickering surround; open triangle, static surround). (A) The abscissa indicates the additive factor, a , of the matched jitter. The broken line indicates the identity function. The solid line indicates linear regression. (B) The abscissa indicates proportionality constant, m . (C) The abscissa indicates detection threshold of physical jitter per se.

with a simulation-pixel resolution of $2 \text{ arcmin} \times 1.667 \text{ ms}$ (Fig. 5A). The retinal image was filtered by biphasic temporal impulse response (TIR) functions (Fig. 5C),

$$\text{TIR}(t) = (0.2t)^n \exp(-0.2t) [1/n! - 0.95(0.2t)^2 / (n+2)!], \quad (2)$$

where t is time in ms, and $n = 6$ and 9 for non-lagged-like and lagged-like responses, respectively (McKee & Taylor, 1984; Pantle & Turano, 1992; Takeuchi & De Valois, 1997; Watson, 1982), and was also filtered by Gabor-shaped spatial impulse response (SIR) functions (Fig. 5D),

$$\text{SIR}(x) = \exp[-(x/\lambda)^2] \sin(\theta + 2\pi fx), \quad (3)$$

where x is horizontal position in arcmin, $\lambda = 3(\ln 2)^{0.5} / \pi f$, $f = 0.125$, and $\theta = 0$ and 0.5π for even- and odd-

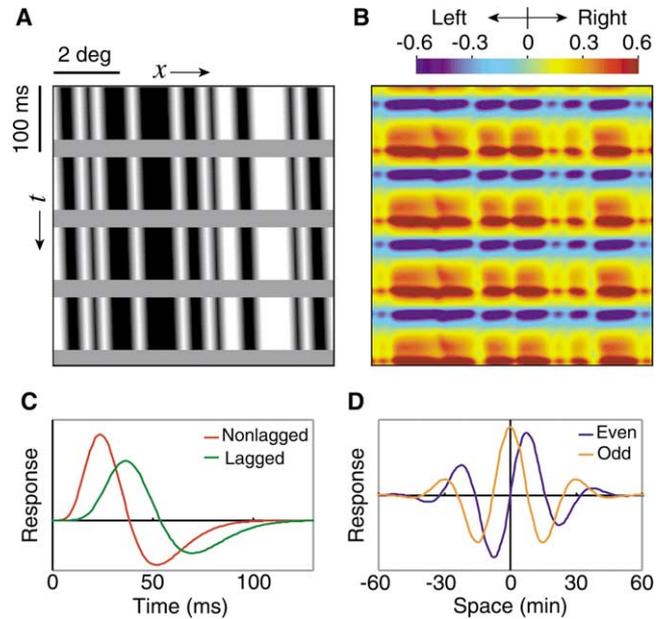


Fig. 5. Results of the simulation. (A) Spatiotemporal (horizontal \times time) plot of the retinal image motion (at 0.625 deg/s) of the flickering surround. Patterns are made oblique by eye velocity and are periodically interrupted by synchronous flicker. The input image actually had the size of 512×512 simulation-pixels, but only its central region of 256×256 simulation-pixels is shown. (B) Spatiotemporal plot of the outputs of motion-energy units. (C) Temporal impulse response functions used as a part of motion-energy computation. (D) Spatial impulse response functions used as a part of motion-energy computation.

symmetric responses, respectively (Watson & Ahumada, 1985). The simulation-pixel resolution of the filters was the same as that of the input image. Appropriate spatiotemporal combinations of the filtered outputs were squared and summed to yield motion-energy responses (Adelson & Bergen, 1985). The final bipolar motion responses (plotted by color scale in Fig. 5B) indicate the motion-energy contrast, i.e., the difference of leftward and rightward responses divided by their sum (Georgeon & Scott-Samuel, 1999).

The simulation was repeated while varying the three major parameters that governed spatiotemporal properties, namely eye velocity, the TIR's time constant, and the SIR's spatial frequency tuning. The outputs were essentially similar within a biologically plausible range of parameters, so only a representative example with the particular parameter values indicated above was shown in Fig. 5. The simulation revealed that biological units artificially create a motion difference between center and surround when eye movements produce common image motions in these regions. Although for more than half the period they correctly reported "right," the units occasionally reported "left" also, slightly ($\approx 50 \text{ ms}$) after the onset of each gray interval. This result is consistent with previous studies on the behavior of motion-energy processing units during the blank interstimulus interval

(Shioiri & Cavanagh, 1990; Pantle & Turano, 1992; Takeuchi & De Valois, 1997). These are critical occasions when center and surround are reported oppositely (because the non-flickering center moving at the same velocity is constantly reported “right”).

Thus, it is hypothesized that the visual system interprets this motion difference as (wrong) evidence for object motion in the center. When the stimulus is viewed with small eye movements, the static center is therefore perceived to jitter in the outer world. Possible mechanisms will be discussed in more detail in Section 4.

3.6. Effects of duty cycle and flicker frequency

The simulation results only qualitatively explain why one perceives illusory jitter in a static pattern surrounded by a synchronously flickering pattern. If the explanation given in the previous section is correct, perception and outputs of motion-energy units should covary with varying stimulus parameters. Preliminary observations suggested that flicker frequency and duty cycle are most relevant stimulus parameters that affect the magnitude of the illusion. Thus far they have been fixed at the particular values (on for 80 ms and off for next 27 ms) at which the illusion was seen most vigorously (to the author), hence perceptual matching data have been more or less restricted. It is unknown how these parameters quantitatively affect matching data as well as simulation outputs. Therefore, in a subsidiary experiment, psychophysical matching and computer simulation were repeated for several levels of flicker frequency and duty cycle, and human performance was compared with simulation outputs.

The cycle of flicker was 8 computer frames (107 ms) in the first condition (Fig. 6A). In each flicker cycle, the period during which the surround was displayed (hereafter called the on-duty period) was 0, 1, 2, . . . , 8 frames. The period during which the surround was not displayed (hereafter called the off-duty period) was simply the flicker cycle minus the on-duty period. In the second condition (Fig. 6B), the flicker cycle was set at 16 frames (213 ms) long, and the on-duty period was 0, 2, 4, . . . , 16 frames. In the third condition (Fig. 6C), the flicker cycle was 4 frames (53 ms) and the on-duty period was 0, 1, 2, 3, and 4 frames. These possible pairs of flicker cycle and on-duty period were presented in randomized order within an experimental session.

Psychophysical data for the three observers and simulation results are superimposed in Fig. 6. The (normalized) matched jitter is plotted as a function of on-duty period. Also, the most negative value (the most bluish point in Fig. 5B, where center and surround are reported most differently) of simulation outputs is superimposed. Data for three flicker frequencies are shown in separate panels, with differently scaled abscissas.

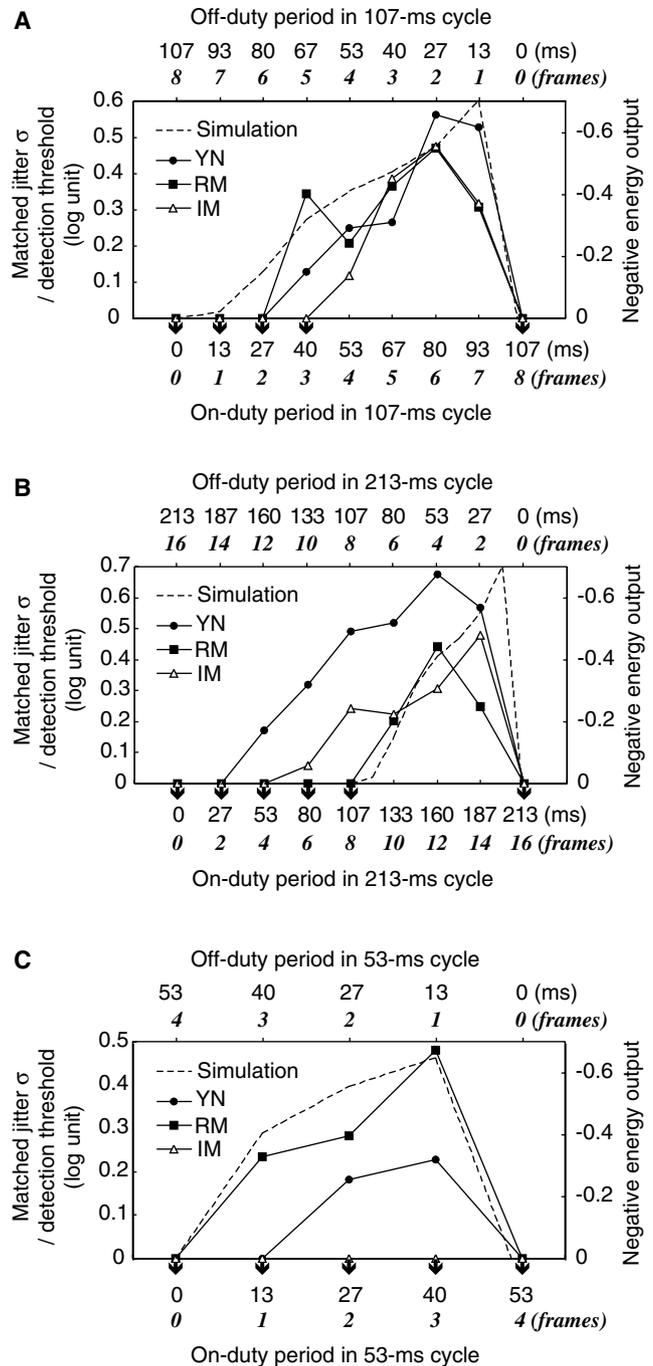


Fig. 6. Normalized magnitude (matched jitter divided by detection threshold) of the illusion as a function of on-duty period. The surround was visible for the period specified by “on-duty” and was invisible for the period “off-duty.” The downward arrows indicate that there was no measurable illusion. The data for the three observers are superimposed, and the most negative motion-energy output in the simulation is overlaid upside-down with the scale adjusted so that the maximum values of human data and simulation output roughly coincide. One flicker cycle was (A) 107 ms, (B) 213 ms, and (C) 53 ms.

In Fig. 6A, data for 107-ms flicker cycle are shown. There was a clear effect of on-duty period: the longer on-duty periods were far more effective in producing

the stronger illusion, its magnitude peaking at 80 ms. Interestingly, the simulation output also followed a similar function, peaking at 93 ms and gradually decreasing with decreasing on-duty period. As the on-duty and off-duty periods are complementary to each other, this result means that the peak is located at as short as 13–27 ms of the off-duty period. This pattern of results is counterintuitive. If the illusion simply depended on deprivation of visual information from the surround, longer off-duty periods should lead to longer deprivation and thus should be more effective. However, shorter off-duty periods were actually more effective.

This finding, however, agrees with the property of biphasic TIR function that is implemented as a part of a motion-energy unit. Let us consider that the negative lobe of the biphasic TIR brings about negative “afterimage” when the pattern is turned off. The motion-energy processing unit is sensitive to spurious spatiotemporal correlations in brightness between real stimulation (e.g., a *dark* dot) and an afterimage (e.g., a *dark* afterimage after a *bright* dot is turned off) (Pantle & Turano, 1992; Takeuchi & De Valois, 1997). The afterimage, however, gradually develops and gradually decays. If the stimulus reappears well before the afterimage develops, or well after the afterimage has completely faded out, the motion energy in the wrong direction is weakened. It becomes maximal when the stimulus reappears just after the afterimage has fully developed and just before it starts to disappear. The critical gray interval at which the response in the wrong direction is maximal is related to the interval between the positive and negative peaks of the TIR. In the functions used in the simulation, it was as short as approximately 30 ms.

The pattern of results was very similar when the one-cycle length of flicker was doubled (Fig. 6B) or halved (Fig. 6C). The simulation outputs were always the same, peaking at 13 ms off-duty period, whereas the human data for 213-ms flicker cycle (Fig. 6B) seem to prefer a slightly longer off-duty period. Also, there was a large inter-observer variability. The human data and simulation for 53-ms flicker cycle (Fig. 6C) were again more or less consistent with each other but variability across observers is even larger; in particular, observer IM did not perceive any illusory motion in this condition. Clearly, an explanation based on just a single type of motion-energy unit has a limitation. It is more reasonable that the visual system is equipped with multiple channels of temporal frequency tuning, each preferring a particular range of flicker frequency and being susceptible to individual sensitivity differences. Backward estimation of parameters such as the time constant of the TIR might be technically possible on the basis of the present psychophysical data, but it is beyond the scope of the present study.

4. Discussion

The present findings altogether suggest that perceptual stability of the visual world is impaired when spatiotemporally continuous access to retinal image motions is artificially interrupted by surround flicker. Classical theories of extraretinal signals cannot explain why (Helmholtz, 1866; Sherrington, 1918). By contrast, the visual-motion-based model of common-motion cancellation well explains the results. As eye movements produce common image motions on the retina, common motions are interpreted as coming from eye movements, whereas a motion difference is interpreted as evidence for object motion. However, synchronous flicker yields a spurious motion difference between flickering and non-flickering regions, even though eye movement actually moves them together on the retina.

Indeed, the simulation revealed that the stimulus used in the present study (Fig. 1), viewed with a certain eye movement, evokes abnormal outputs in early motion-energy detection. While the central stationary part of the stimulus is coded to move constantly, the flickering surround is coded to oscillate. As such, there is a spurious motion difference between regions. It is not obvious, however, how such a pattern of responses might be related to visibility of retinal image motions in the center.

First, why is the flickering surround not perceived to oscillate, when motion-energy units yield oscillatory responses? The timings of positive and negative response peaks of the motion-energy unit depend on the shape of TIR, which would have a large variability among real cells. Probably, such responses from a variety of cells are not reliable enough to support unitary percept of oscillatory motion. It seems more likely that they are interpreted as evidence for broadband noise in the stimulus and are the basis of perception of flicker.

Second, why is the stationary center perceived as jittering? Viewing the stimulus with small eye movements gives rise to retinal image motions in all regions. They are interpreted as coming from eye movements, not from motions in the outer world, if a region has common image motions with its neighborhood. However, the presence of surround flicker creates a motion difference between center and surround in the stage of early motion-energy detection. As the image motions in the center become “uncommon” with respect to its surround, they are not interpreted as coming from eye movements but from object motions. A physiological support of this idea may be found in extrastriate motion areas, where responses to the preferred direction are suppressed for many cells when moving stimuli in the same direction extend beyond the classical receptive field (Allman, Miezin, & McGuinness, 1985; Tanaka et al., 1986). These cells respond only weakly to common motions covering the inside and outside of the classical

receptive field, but vigorously fire when early energy units submit opposite directions between inside and outside. In area MT of the macaque, the classical receptive field of the cell is typically as wide as 10 deg at the eccentricity used in the present study (Murakami & Cavanagh, 2001). Thus, the stimulus size in the present study is roughly compatible with the explanation in terms of receptive-field property of MT cells. This is consistent with the previous findings that the jitter aftereffect is strongest when the stimulus size is comparable to the average receptive field size of the macaque MT cells (Murakami & Cavanagh, 2001), and that there is a specific increase in magnetic resonance signals from the human MT+ when the observer perceives the jitter aftereffect (Sasaki et al., 2002).

Third, why is only the center, not the surround, perceived to jitter when both are “uncommon” with respect to each other? Possibly some jitter is attributed to the center and some to the surround, but perception of salient flicker in the surround could distract from seeing jitter in it. Also, there is a general principle that our perception of object motion is relative to a certain frame of reference, such that larger backgrounds tend to appear stationary in the visual field (Wallach, 1959). Accordingly, when a motion-energy detection stage suggests a motion difference between center and surround, the center is interpreted to move relative to the larger surround. This is probably why the stimulus illustrated in Fig. 1 is the best configuration for the illusion.

The present findings are consistent with the characteristics of the jitter aftereffect that has previously been reported as supporting evidence for the visual-motion-based model of common-motion cancellation. We see a shaky pattern of movement corresponding to our own small eye movements when the retinal image slip they cause is internally represented as different from surrounding motions. In the case of jitter aftereffect, it was by adaptation that the surround is coded to have weaker motion signals than the center has, when both regions are stimulated by the same amount of retinal image slip. In the present case, it was by synchronous flicker that the surround is coded to have different motion signals than the center's once every cycle of flicker. The novel illusion reported here clearly demonstrates that the jitter perception is not specific to adaptation to dynamic noise but is a generic phenomenon when eye-originated retinal motions are coded differently. Moreover, the tight correlation between perception and velocity distribution of small eye movements (Fig. 4A) is suggestive of an application of this illusion as a convenient method of *measuring* them without an expensive eye tracker with high spatial and temporal resolutions.

Phenomenological observations described in Section 3 included the condition in which the observer made smooth pursuit eye movement instead of fixation. The

central static pattern surrounded by a synchronously flickering pattern clearly appeared to move in the direction opposite to smooth pursuit. Such a motion illusion, referred to as the Filehne illusion, is known to occur even when the central static pattern alone is presented (Filehne, 1922). The Filehne illusion also occurs when stimuli are presented in dark environment. If visual stability were established solely by the proposed mechanism based on retinal motion signals, this illusion should not happen. Therefore, it is agreed that the Filehne illusion is evidence for visual stabilization assisted by extraretinal signals for smooth pursuit (Freeman, 1999, 2001; Freeman & Banks, 1998; Freeman, Banks, & Crowell, 2000; Haarmeier, Bunjes, Lindner, Berret, & Thier, 2001; Haarmeier & Thier, 1996; Mack & Herman, 1978; Turano & Massof, 2001; Wertheim, 1987, 1994). That is, the illusion is interpreted as undercompensation of visual motion signals by extraretinal signals with a smaller gain. Without surround flicker, however, the Filehne illusion was severely reduced to almost none in the present stimulus configuration. This observation was made under unlimited inspection time, hence this seems consistent with the previous finding that the Filehne illusion is compromised or even inverted for stimulus durations longer than 1 s (de Graaf & Wertheim, 1988; Mack & Herman, 1978; Wertheim, 1987). Either the proposed visual-motion-based model or extraretinal signals with a perfect gain can explain the absence of the illusion. But why does introducing surround flicker boost the Filehne illusion? Either the gain of visual motion signals must be increased, or the gain of extraretinal signals must be decreased, by surround flicker. If the second idea were correct, the Filehne illusion in one hemifield should be enhanced by a flickering pattern in the other hemifield (because extraretinal signals must be global). This was not observed. The enhancement of the Filehne illusion was only seen in a static pattern adjacent to the flickering pattern. This suggests that visual motion signals are enhanced by local processing that is sensitive to a motion difference between adjacent regions.

Though a stationary scene is normally perceived to be stationary despite eye movements, the whole visual field appears to move by gentling pressing the eyeball with the finger (Helmholtz, 1866). However, when the same observation is made under stroboscopic illumination at 5–6 Hz, the world does not appear to move; if self-luminous objects are added to the scene, only those objects appear to move by pressing the eye (MacKay, 1958). One might argue that this demonstration has a phenomenal similarity to the present illusion, because in both cases, retinal image motions due to the movement of the eye are visible only in objects that are presented constantly, whereas flickering surrounds do not appear to move. However, the present jitter illusion is not a simple variant of this demonstration. When the surround

was presented stroboscopically (i.e., the on-duty period of 1–2 frames every flicker cycle), neither the center nor the surround appeared to jitter (Fig. 6). In MacKay's demonstration, stroboscopically lit things are very poor stimuli to activate motion sensors (Nakayama, 1985). On the other hand, the surround flicker in the present illusion strongly activates motion-energy units in a wrong direction.

A static pattern in rapid contrast reversal appears to move in the same direction as smooth pursuit, or in the opposite direction to the retinal image slip (Anstis, 1970; Spillmann, Anstis, Kurtenbach, & Howard, 1997). As the stimulation is retinally equivalent to the situation of "reversed-phi" (Anstis, 1970), the perception is consistent with what motion-energy units would constantly report. However, when the optimal stimulus for this was applied to the surround of the present stimulus (Fig. 1), no motion perception occurred during fixation. Therefore, the present illusion and the retinal reversed-phi are distinct phenomena delineated by eye-movement type (fixation vs. pursuit), flicker type (gray-interval insertion vs. contrast reversal), and preferred frequency range (<10 Hz vs. >10 Hz). Nevertheless, both illusions critically point out the major problem the visual system is confronted with in modern artificial illuminations (Peli & García-Pérez, 2000). Through the process of evolution in the natural environment, the visual system has acquired the ability of counteracting eye movements under the assumption that they should cause early visual cortex to show common motion responses in neighboring cells—so that "uncommon" motions in any place are interpreted as coming from object motion (e.g., a predator). However, flicker illuminations can invade this assumption, causing us to see something not to see, i.e., our own eye movements. The present report is the first to demonstrate that, in order to establish the visual stability despite incessant eye movements of fixation, spatiotemporally continuous access to the retinal velocity is essential.

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References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2, 284–299.

- Allman, J., Miezin, F., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception*, 14, 105–126.
- Anstis, S. M. (1970). Phi movement as a subtraction process. *Vision Research*, 10, 1411–1430.
- Bair, W., & O'Keefe, L. P. (1998). The influence of fixational eye movements on the response of neurons in area MT of the macaque. *Visual Neuroscience*, 15, 779–786.
- de Graaf, B., & Wertheim, A. H. (1988). The perception of object motion during smooth pursuit eye movements: adjacency is not a factor contributing to the Filehne illusion. *Vision Research*, 28, 497–502.
- Dosher, B. A., & Lu, Z.-L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the USA*, 95, 13988–13993.
- Eizenman, M., Hallett, P. E., & Frecker, R. C. (1985). Power spectra for ocular drift and tremor. *Vision Research*, 25, 1635–1640.
- Fermüller, C., & Aloimonos, Y. (1995). Direct perception of three-dimensional motion from patterns of visual motion. *Science*, 270, 1973–1976.
- Filehne, W. (1922). Über das optische Wahrnehmen von Bewegungen. *Zeitschrift für Sinnesphysiologie*, 53, 134–145.
- Foster, D. H., & Bischof, W. F. (1991). Thresholds from psychometric functions: superiority of bootstrap to incremental and variance estimates. *Psychological Bulletin*, 109, 152–159.
- Freeman, T. C. A. (1999). Path perception and Filehne illusion compared: model and data. *Vision Research*, 39, 2659–2667.
- Freeman, T. C. A. (2001). Transducer models of head-centred motion perception. *Vision Research*, 41, 2741–2755.
- Freeman, T. C. A., & Banks, M. S. (1998). Perceived head-centric speed is affected by both extra-retinal and retinal errors. *Vision Research*, 38, 941–945.
- Freeman, T. C. A., Banks, M. S., & Crowell, J. A. (2000). Extraretinal and retinal amplitude and phase errors during Filehne illusion and path perception. *Perception and Psychophysics*, 62, 900–909.
- Georgeson, M. A., & Scott-Samuel, N. E. (1999). Motion contrast: a new metric for direction discrimination. *Vision Research*, 39, 4393–4402.
- Haarmeier, T., Bunjes, F., Lindner, A., Berret, E., & Thier, P. (2001). Optimizing visual motion perception during eye movements. *Neuron*, 32, 527–535.
- Haarmeier, T., & Thier, P. (1996). Modification of the Filehne illusion by conditioning visual stimuli. *Vision Research*, 36, 741–750.
- Heidenreich, S. M., & Turano, K. A. (1996). Speed discrimination under stabilized and normal viewing conditions. *Vision Research*, 36, 1819–1825.
- Helmholtz, H. v. (1866). *Handbuch der physiologischen Optik*. Leipzig: Voss.
- Krauskopf, J., Cornsweet, T. N., & Riggs, L. A. (1960). Analysis of eye movements during monocular and binocular fixation. *Journal of the Optical Society of America*, 50, 572–578.
- Leopold, D. A., & Logothetis, N. K. (1998). Microsaccades differentially modulate neural activity in the striate and extrastriate visual cortex. *Experimental Brain Research*, 123, 341–345.
- Levi, D. M., Klein, S. A., Sharma, V., & Nguyen, L. (2000). Detecting disorder in spatial vision. *Vision Research*, 40, 2307–2327.
- Mack, A., & Herman, E. (1978). The loss of position constancy during pursuit eye movements. *Vision Research*, 18, 55–62.
- MacKay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature*, 181, 507–508.
- Maloney, L. T. (1990). Confidence intervals for the parameters of psychometric functions. *Perception and Psychophysics*, 47, 127–134.
- 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.

- Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2002). The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *Proceedings of the National Academy of Sciences of the USA*, *99*, 13920–13925.
- McKee, S. P., & Taylor, D. G. (1984). Discrimination of time: comparison of foveal and peripheral sensitivity. *Journal of the Optical Society of America A*, *1*, 620–627.
- Murakami, I. (2002a). An adaptation-free jitter illusion perceived in a static random-dot disk surrounded by a flickering random-dot field. *Vision Science Society Annual Meeting Abstracts*, *2*, 254.
- Murakami, I. (2002b). Additive and multiplicative factors of the simultaneous jitter illusion. *Asian Conference on Vision Abstracts*, *2*, 7.
- Murakami, I. (2002c). Illusory jitter induced by flickering surround texture: correlations with small eye movements. *Society for Neuroscience Annual Meeting Abstracts, CD-ROM*, #457.11.
- Murakami, I. (2002d). Illusory jitter induced by flickering surround texture: effects of flicker frequency and duty cycle. *European Conference on Visual Perception Abstracts*, *31*, 161.
- Murakami, I., & Cavanagh, P. (1998). A jitter after-effect reveals motion-based stabilization of vision. *Nature*, *395*, 798–801.
- Murakami, I., & Cavanagh, P. (2001). Visual jitter: evidence for visual-motion-based compensation of retinal slip due to small eye movements. *Vision Research*, *41*, 173–186.
- Nakayama, K. (1985). Biological image motion processing: a review. *Vision Research*, *25*, 625–660.
- Pantle, A., & Turano, K. (1992). Visual resolution of motion ambiguity with periodic luminance- and contrast-domain stimuli. *Vision Research*, *32*, 2093–2106.
- Peli, E., & García-Pérez, M. A. (2000). Motion perception under vibration. *Investigative Ophthalmology and Visual Science*, *41*, S792.
- Pelli, D. G., & Farell, B. (1999). Why use noise? *Journal of the Optical Society of America A*, *16*, 647–653.
- Rieger, J. H., & Lawton, D. T. (1985). Processing differential image motion. *Journal of the Optical Society of America A*, *2*, 354–360.
- Sasaki, Y., Murakami, I., Cavanagh, P., & Tootell, R. B. H. (2002). Human brain activity during illusory visual jitter as revealed by functional magnetic resonance imaging. *Neuron*, *35*, 1147–1156.
- Sherrington, C. S. (1918). Observations on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles. *Brain*, *41*, 332–343.
- Shioiri, S., & Cavanagh, P. (1990). ISI produces reverse apparent motion. *Vision Research*, *30*, 757–768.
- Skavenski, A. A., Hansen, R. M., Steinman, R. M., & Winterson, B. J. (1979). Quality of retinal image stabilization during small natural and artificial body rotations in man. *Vision Research*, *19*, 675–683.
- Snodderly, D. M., Kagan, I., & Gur, M. (2001). Selective activation of visual cortex neurons by fixational eye movements: implications for neural coding. *Visual Neuroscience*, *18*, 259–277.
- Spillmann, L., Anstis, S., Kurtenbach, A., & Howard, I. (1997). Reversed visual motion and self-sustaining eye oscillations. *Perception*, *26*, 823–830.
- Steinman, R. M., Haddad, G. M., Skavenski, A. A., & Wyman, D. (1973). Miniature eye movement. *Science*, *181*, 810–819.
- Takeuchi, T., & De Valois, K. K. (1997). Motion-reversal reveals two motion mechanisms functioning in scotopic vision. *Vision Research*, *37*, 745–755.
- Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., & Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *Journal of Neuroscience*, *6*, 134–144.
- Turano, K. A., & Massof, R. W. (2001). Nonlinear contribution of eye velocity to motion perception. *Vision Research*, *41*, 385–393.
- van Santen, J. P. H., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A*, *2*, 300–321.
- Wallach, H. (1959). The perception of motion. *Scientific American*, *201*, 56–60.
- Watson, A. B. (1982). Derivation of the impulse response: comments on the method of Roufs and Blommaert. *Vision Research*, *22*, 1335–1337.
- Watson, A. B., & Ahumada, A. J. J. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, *2*, 322–342.
- Wertheim, A. H. (1987). Retinal and extraretinal information in movement perception: how to invert the Filehne illusion. *Perception*, *16*, 299–308.
- Wertheim, A. H. (1994). Motion perception during self-motion: the direct versus inferential controversy revisited. *Behavioral and Brain Sciences*, *17*, 293–355.
- Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum Press.