Perception, 2000, volume 29, pages 325 – 335

DOI:10.1068/p3034

Perceptual dimorphism in visual motion from stationary patterns

Galit Naor-Raz
Department of Psychology, Brown University, Box 1853, Providence, RI 02912, USA;
e-mail: galit_naor@brown.edu
Robert Sekuler¶
Volen Center for Complex Systems, Brandeis University, Waltham, MA 02254, USA;
e-mail: sekuler@brandeis.edu
Received 13 April 1998, in revised form 8 July 1999

Abstract. Fraser and Wilcox [1979 *Nature (London)* **281** 565 – 566] devised a series of complex stationary patterns that provoked episodes of compelling illusory motion, but only in about two-thirds of people tested. Using simplified versions of their stimuli, we have confirmed their claim of perceptual dimorphism. We show that the strength of the illusory motion depends upon stimulus duration, eccentricity, and contrast. The illusory motion does not require fluctuations in accommodation, as has been suggested for some other forms of illusory motion. Finally, we consider the relation of Fraser-type motion to other forms of illusory motion.

1 Introduction

It is well-established that stationary stimuli can elicit compelling percepts of motion (Hunter 1915; Wade 1977). Typically, the most effective of such stimuli contain periodic high-spatial-frequency patterns at high contrast. MacKay (1961), to take one example, introduced the best-known of these patterns: tightly packed black and white 'spokes' radiating out from a central 'hub'. While viewing one of MacKay's patterns, after one or two seconds observers see illusory streaming motion, mainly at right angles to the pattern lines. It has not gone unnoticed that MacKay's stimuli resemble the paintings and prints of contemporary artists such as Bridget Riley (Wade 1995) and Isia Leviant (1996). Although the perceptual phenomena themselves are compelling, the mechanisms underlying the illusory motion remain controversial.

To determine whether this illusory motion is generated by the same brain mechanisms that produce motion under ordinary, non-illusory conditions, Zeki et al (1993) exploited one of Leviant's paintings, *Enigma*, as the stimulus in a brain imaging study. They found that this movement-evoking stimulus produced significant activation of area MT of the cerebral cortex. This tiny region of cortex is an important participant in the perception of visual motion (eg Salzman and Newsome 1994). Acknowledging that area MT is activated during perception of illusory motion, Gregory (1993) posed what might be considered a prior question: If motion requires temporal modulation, as seems to be the case, then what mechanisms are responsible for temporally modulating the periodic static patterns like the ones that Zeki et al examined? Gregory identified involuntary accommodative oscillations as a possible source of the required temporal modulation. Such fluctuations in the accommodative state of the eyes are concentrated in two frequency bands, one centered on 0.1 Hz and another on 2 Hz (Charman and Heron 1988; Winn et al 1990). This second band of microfluctuations produces temporal variations at frequencies to which human vision has considerable sensitivity (Snowden et al 1995). In reply to Gregory's suggestion, Zeki (1995) noted that aphakes experience the illusory motion in Leviant's *Enigma*. Accommodative

---

¶ Author to whom all correspondence and requests for reprints should be addressed.

fluctuations, which would be absent in these special observers, would therefore seem unlikely contributors to illusory motion, at least for the stimuli Zeki tested.

The Ouchi illusion provides another example of motion emerging from a stationary pattern. Hine et al (1995, 1997) explained illusory motion in the Ouchi stimulus as "a failure to integrate two motion signals into the single motion vector which characterizes rigid motion" (Hine et al 1995, page 3093). This illusion, like Leviant's *Enigma*, cannot be attributed to accommodative fluctuations, as aphakes experience the illusory motion.

Of course, MacKay's, Leviant's, and Ouchi's patterns are not the only stationary stimuli that can generate perceived motion. The artist-geneticist Alexander Fraser devised another, particularly interesting set of stimuli that also can provoke illusory motion (Fraser and Wilcox 1979). Two decades after these stimuli were first introduced into the scientific literature, Fraser's work is nearly unknown; one of our goals here is to call attention to that work. His stimuli comprised a series of adjacent sectors, which are shaded dark to light or light to dark. In Fraser's original paintings, the sectors were arranged in repeating sets, which formed a cochlea-like spiral. Fraser and Wilcox reported that these patterns produced illusory motion, usually movement in a direction dictated by the gradient of dark sectors to light ones. Although they did not investigate the effect systematically, they noted that the motion was appreciated best in peripheral viewing.

Fraser and Wilcox's stimuli differ in several respects from the periodic stimuli described by MacKay and others. First, these stimuli comprise lower spatial frequencies than MacKay's, although luminance edges in Fraser and Wilcox's stimuli certainly do introduce high-frequency components; second, Fraser and Wilcox's stimuli depend upon graded repetitive variations in lightness, which was not the case for the stimuli used by others; and, third, Fraser and Wilcox's stimuli are most potent when viewed peripherally. Finally, to note the distinction that most intrigues us, the stimulus seemed to be effective only with some observers. Specifically, some 60%–75% of observers saw the motion, but other observers were immune, seeing either no motion or seeing weak, sporadic motion whose direction varied unpredictably from moment to moment. Further, these individual differences are not mere happenstance: with repeated testing, even when separated by some time, an individual's sensitivity or insensitivity to motion was consistent.

Perceptual dimorphism may not be unknown in the vision literature, but outside the domain of color vision it is quite rare. Evidence of aperceptual dimorphism led Fraser, with his training as a geneticist, to suspect that genetic differences might be at work. As a result, Fraser and Wilcox carried out a simple twin study. Testing pairs of monozygotic (MZ) and dizygotic (DZ) twins as well as non-twin siblings, they found striking variation in concordance. For MZ twins concordance was 0.90, but for DZ twins concordance was only 0.56, just about the same value as found for non-twin sibling pairs, 0.53. This pattern of concordances is a sign that some genetic influence might be at work.

To understand better the illusion described by Fraser and Wilcox, and to set the stage for possible future work on the genetics of seen motion, we examined various conditions that might promote or discourage the illusory motion, such as duration, eccentricity, and contrast.

2 General methods

2.1 *Screening of observers*

Although both authors of this paper experience the Fraser–Wilcox illusory motion, our first informal testing of friends and family members showed this ability was far from universal. This anecdotal confirmation of Fraser and Wilcox's original assertion encouraged us to carry out formal studies of the phenomenon.

Because we were primarily interested in the stimulus determinants of the illusory motion, we limited our testing to people who we knew would actually experience the illusion. Prior to formal testing, each volunteer was screened for sensitivity to the illusion with a large color version of the Fraser–Wilcox illusion.(1) Pilot testing showed that the illusory motion evoked by this display was strongest when the stimulus was viewed peripherally. We therefore used peripheral viewing in our screening.

Each volunteer was shown the large color stimulus and was asked to maintain fixation on the wall some 3 or 4 deg below the bottom of the stimulus, whose diameter subtended 8 deg. Screening began with a non-directive question: "As you look at the wall, do you notice anything about the striped disk above where you're looking?" About half the volunteers offered that they saw some movement in the disk. They were then asked to describe the motion, particularly its direction. All described the motion as going from dark to light sectors, which, from Fraser and Wilcox's work and from our own anecdotal observations, is the direction expected.

Volunteers who did not spontaneously report motion were asked directly if they saw any motion in the disk. Again, if they said they saw motion, they were required to state the direction. Only volunteers who reported motion in the expected direction were allowed to participate in the experiment. Several volunteers who failed to see the motion were brought back some days or weeks later and retested with the same stimulus. Each one failed again. Informal testing at the laboratory with abrupt stimulus onsets reconfirmed the fact that these subjects did not experience the illusion. Because we were interested in conditions that would modulate the strength of the Fraser–Wilcox illusion, we did not continue to test people who were unlikely to see the illusion under any of the conditions we would use. The number of volunteers screened out is given below for each experiment.

2.2 *Materials*

Stimuli were generated by a Macintosh computer and presented on a 17-inch monitor. The computer also recorded observers' responses for later analysis. A chin-rest and head support put the observer's eyes 57 cm away from the display on which stimuli were presented. Stimuli consisted of patterns adapted and much simplified from those used by Fraser and Wilcox. These patterns are shown in figures 1a and 1b. The direction of the systematic dark–light gradations contained in two stimuli was designed to evoke clockwise and counterclockwise motion, respectively, under optimum viewing conditions. Pilot tests confirmed Fraser and Wilcox's original observation: For each of these stimuli, movement was seen in a direction corresponding to the gradient from darkest to lightest segments. In the third, control, stimulus, shown in figure 1c, we reordered the gray-scale segments that made up the gradients in the other stimuli. Instead of segments arranged to produce gradients in only one direction all the way around the stimulus—either dark to light, or vice versa—segments were rearranged so that gradients in one direction were intermixed with gradients in the opposite direction. We expected that this arrangement would balance local movements in opposite directions, yielding little or no net movement.

3 Experiment 1

This experiment was done to determine optimal conditions for producing the Fraser–Wilcox illusion. The experiment consisted of several conditions in which stimulus duration, eccentricity, and direction of luminance gradients were varied factorially.

---

(1) This version of Fraser's stimulus is part of the permanent art display in the gallery of Brandeis University's Volen Center for Complex Systems. A facsimile of the stimulus can be viewed on the worldwide web at http://volen.ccs.brandeis.edu/~sekuler/volen_stimulus.html. It is also available on the *Perception* web site at http://perceptionweb.com/perc0300/naor_raz.html and will be archived on the CD-ROM provided with issue 12 of the journal.

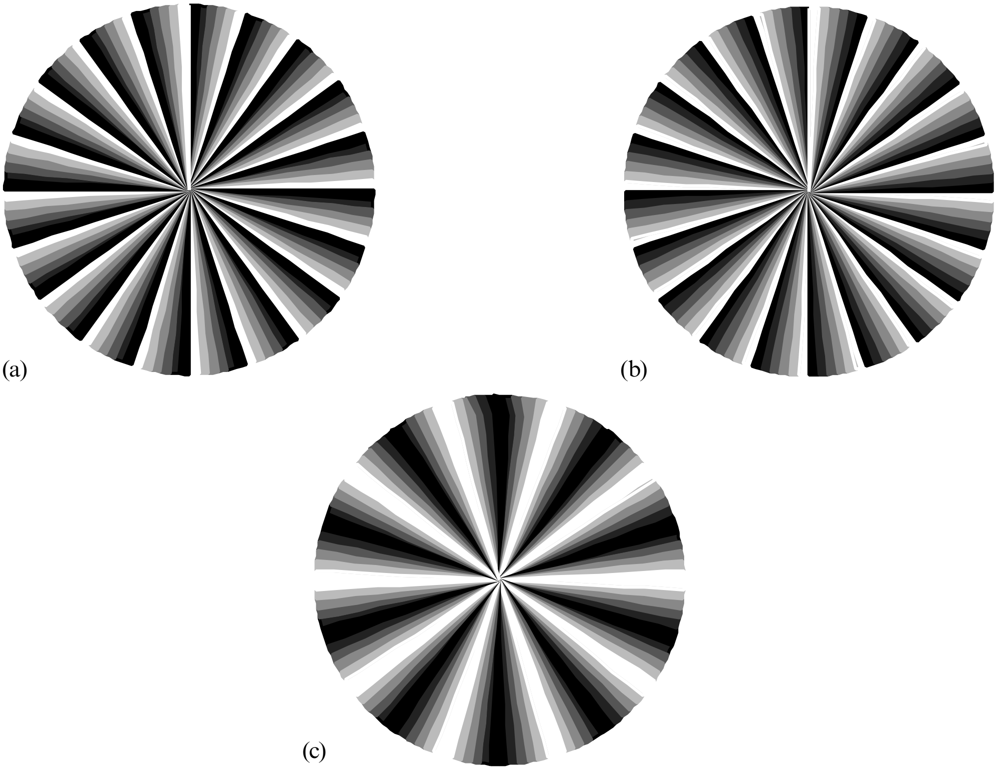

Figure 1. (a) A stimulus yielding an apparent motion in the clockwise direction. (b) A stimulus yielding an apparent motion in the counterclockwise direction. (c) A bidirectional, locally balanced control stimulus, which does not produce apparent motion. Illusory motion is most likely to be experienced when the disks are seen in peripheral vision; for best effect, fixate about two disk diameters below the stimulus. Note that when fixation is midway between and sufficiently below panels (a) and (b), it is possible to experience illusion simultaneously in opposite directions.

3.1 *Subjects*

Of ten volunteer observers, three failed to pass our screening test and were not tested further. Thus seven naive volunteers (mean age = 20 years) served as observers. All observers were undergraduate students at Brandeis University.

3.2 *Materials*

Before each trial, a small fixation cross appeared in the center of the computer display. The subject engaged fixation and initiated the trial when ready. Then, a stimulus disk, 10.5 deg in diameter, was presented at a position and for a duration appropriate to that trial.

If a spatially repetitive stimulus, like MacKay's, evokes illusory motion, the offset of the stimulus usually produces a complementary afterimage, and opposite direction, illusory motion. With presentations lasting a few seconds or longer, the offset of our stimuli produced precisely this effect—motion in the direction opposite to that which it evoked prior to offset. Most likely, the direction of motion at offset was controlled by the luminance gradient of the afterimage, which ran in a direction opposite to that of the original, inducing stimulus. Informal observations showed that test-field luminance actually influences the direction of motion in the afterimage (eg illusory motion is seen in the reverse direction when the field is bright, but in the forward direction when the field is dark), which suggests that the equivalent luminance distribution of the afterimage may be directly stimulating motion-sensitive mechanisms (Mather 1984).

In any case, to eliminate any illusory motion at stimulus offset, our stimulus disk was followed immediately by a spatially random masking stimulus that covered the entire display area. The intent was to overwrite any afterimage that would have been generated by the disk. This mask was a checkerboard, whose 6 min of arc square elements were drawn randomly from a palette that spanned the same luminance range as the levels comprising the stimulus disks. After a 3 s intertrial interval, the computer signaled that the observer was free to initiate the next trial. The mean luminance of all stimuli was 33 cd m^{-2}. In increasing order, the luminances of individual sectors were 0.1, 5, 15, 33, 55, and 90 cd m^{-2}, yielding a Michelson contrast of 0.91.

3.3 *Methods*

On each presentation, observers judged whether the stimulus disk seemed to move, and, if it did, whether it moved clockwise or counterclockwise. Judgments were signaled by pressing one of three buttons, corresponding to the two directions of motion—clockwise or counterclockwise—and to no motion.

Stimuli were presented for four different durations, 200, 400, 800, and 1600 ms, and at four different eccentricities, 7.2, 10.2, 13.2, and 16.2 deg. Eccentricity is defined as the distance between the stimulus center and fixation. Subjects wore their best optical correction while being tested, and were not given special correction at the most eccentric field position. All stimuli were presented in the superior visual field. The factorial combination of stimulus type, duration, and eccentricity produced a total of 48 different conditions, which were presented in block randomized order, once each in each of 20 blocks.

3.4 *Results and discussion*

For the stimulus disk whose dark-to-light gradients ran clockwise, we defined a correct movement response as one that indicated perception of clockwise motion; for the disk whose dark-to-light gradient ran counterclockwise, correct responses were those in a corresponding, counterclockwise direction. Preliminary inspection showed that for each subject clockwise and counterclockwise correct responses occurred with virtually identical frequencies. In all analyses, therefore, we combined subjects' clockwise and counterclockwise correct responses.

Figure 2 shows the mean percentage of correct movement responses for all seven subjects as a function of stimulus duration and eccentricity. The vertical bars indicate one standard error. As stimulus duration increased from 200 to 1600 ms, motion was seen increasingly in the stimulus-appropriate direction. Also, as stimulus eccentricity increased, so too did the frequency of seeing motion in the stimulus-appropriate direction. As the figure shows, reports of motion were highest when the disk was presented for the

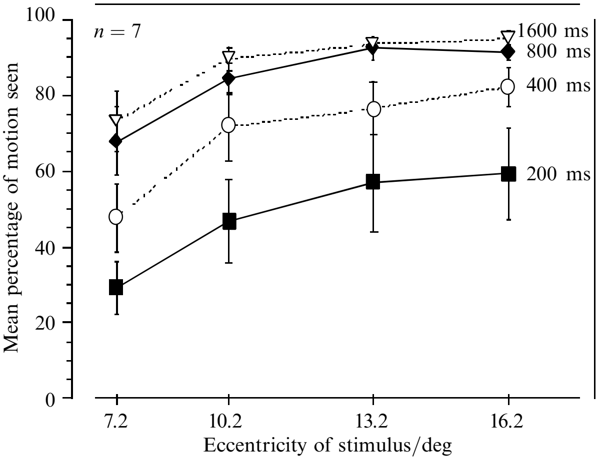

Figure 2. Mean percentage of correct movement responses for all subjects as a function of both stimulus duration and eccentricity.

longest duration (1600 ms) and at the greatest eccentricity (16.2 deg). Moreover, the parallelism of the curves shows that the effects of the two variables—duration and eccentricity—were largely additive. These results were confirmed in a repeated-measures analysis of variance, which showed significant main effects of stimulus duration and eccentricity ($F_{3,18} = 26.34$ and 19.78, respectively, and each $p < 0.01$). The interaction between duration and eccentricity was not statistically significant ($F_{9,54} = 0.68, p > 0.50$).

The parallelism of the curves for the four durations suggests that whatever the cause for the illusory motion might be, that cause is consistent for all durations tested, in spite of the fact that illusory motion can be detected more reliably at higher durations. We shall return to the effect of duration later, in the discussion section. Figure 2 also shows a flattening of the curves at the highest eccentricity. This could be related to the size of the operative spatial filter, so that at greater eccentricities the magnitude of the illusion slightly diminishes (or flattens).

Responses to the locally bidirectional control disk (figure 1c) provided a measure of the frequency with which motion would be seen in the absence of a consistent dark-to-light gradient. For convenience, we can call these reports of motion 'false positive' motion reports. Over all conditions, false positives occurred on 7.5% of trials (standard error of the mean = 2.5%).

4 Experiment 2

Students of motion perception have long been interested in the connection between visual processing of real motion and visual processing of illusory motion (Sekuler 1996). A number of years ago, a variety of motion paradigms suggested that responses to real motion were already quite robust at contrasts as low as two or three times detection threshold, and saturated at relatively low increments above such levels (Derrington and Goddard 1989; Keck et al 1976; Thompson 1983; Watson and Robson 1981). Some investigators attributed the early saturation to neurons in the magnocellular visual subsystem which tend to produce robust responses at relatively low levels of contrast (Tootell et al 1988). Recent work, however, suggests that these early claims may have been mistaken, and that motion responses do not invariably exhibit an early saturation as contrast varies. A few examples should make this point clear. With two different kinds of display geometries, induced movement showed no evidence of saturation at low stimulus contrast (Ohtani et al 1995; Raymond and Darcangelo 1990). With the motion aftereffect, Nishida et al (1997) confirmed that aftereffect duration did saturate, but only with low-contrast test stimuli, either static or flickering. Finally, with random-element cinematograms, perception of global flow either saturated early with contrast or did not, depending upon the homogeneity of contrasts for elements in the display (Edwards et al 1996). This last result may be especially important. Edwards et al suggest that saturation observed in performance with global-motion judgments does not necessarily mean that there was saturation at an earlier level where local-motion measurements are made. Clearly, the links between contrast and perceived movement are far from as simple as was first thought. Because neither in the original nor in the more recent studies had the impact of contrast on illusory motion generated by static patterns been examined, we decided to assess the strength of illusory motion generated by Fraser disks whose sectors varied in contrast.

We made all presentations at a duration and eccentricity that experiment 1 showed would produce strong movement on nearly every occasion. Using an anchored rating scale, subjects gave numerical estimates of the strength of motion produced by each stimulus.

4.1 *Subjects*

Eight new, naive subjects were recruited for this experiment. Our screening process rejected four of the twelve initial volunteers. Volunteers were either undergraduates or summer students at Brandeis (mean age = 17 years).

4.2 *Materials and methods*

In experiment 1, luminances of sectors in the stimulus disk varied nonlinearly with sector position in each collection of sectors. For experiment 2, we linearized the series, so that dark and light sectors comprised equal luminance steps below and above the mean luminance, 44.5 cd m^{-2}. This value was somewhat higher than the mean luminance used in experiment 1, a fact that pilot testing showed was of no discernible consequence. By varying the luminance of the sectors, we created a series of disks that differed in Michelson contrast but were constant in mean luminance. The smallest stepwise variations around the mean luminance produced an experimental disk whose contrast was 0.18; other disks had contrasts of 0.44, 0.72, and 0.99. For each contrast level, we created one disk whose dark-to-light gradients should produce clockwise motion, and one disk whose gradients should produce counterclockwise motion.

We assessed the baseline frequency of false positive movement reports with presentations of a uniform disk, which should produce few or no motion reports. This uniform disk had the same mean luminance as all other disks used in the experiment.

Observers used their own subjective scales to rate the perceived intensity of motion of the stimuli. To anchor this scale, observers were first presented with 'standard' stimuli, which we knew should produce illusory motion, either clockwise or counterclockwise. They were told to consider the intensity of motion produced by these standards to be 100 units and to compare whatever motion was evoked by a disk in the actual experiment with the motion evoked by the standard, scaling their numerical rating of motion intensity accordingly. In making their judgment, they were instructed to ignore the fraction of the trial during which motion was seen. A response of zero signified that no motion was seen.

In each block of trials, nine different disks were presented in randomized order. The nine disks comprised both clockwise and counterclockwise variants of the four disks of different contrast, as well as the uniform, unstructured disk. A session consisted of seven blocks of trials, the first two used for familiarizing the subjects with the rating procedure. We discarded data from those two blocks without analysis, leaving 45 analyzed trials per subject (5 blocks of trials, each block with 9 disks).

Duration and eccentricity were kept constant for all conditions in the experiment, duration being 800 ms, and eccentricity being 16.2 deg. The results of experiment 1 pointed to these values as being within the optimal range of effect. All other conditions, including viewing distance and checkerboard mask, were the same as in experiment 1.

4.3 *Results and discussion*

As figure 3 shows, over the entire range of stimulus contrast with which we worked, rated intensity of motion rose steadily as contrast increased. The homogeneous control

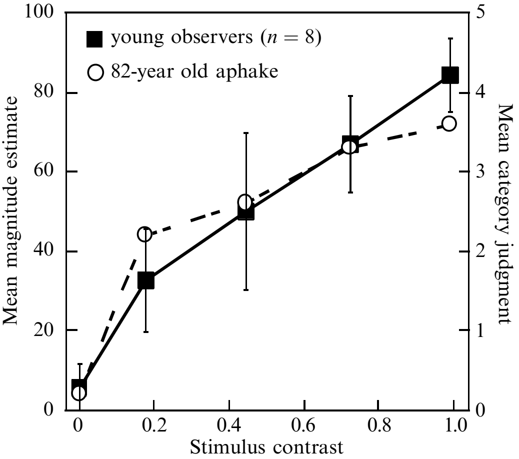

Figure 3. Rated intensity of illusory motion as a function of stimulus contrast in experiment 2. The dashed line shows the data of a single aphakic observer tested in the supplementary experiment.

stimulus, whose data are plotted at zero contrast, rarely evoked motion responses. In particular, observers reported motion on fewer than one trial out of a hundred with that stimulus. The error bars shown in figure 3 are sufficiently large that one cannot reject the proposition that the function relating strength of motion to contrast of the Fraser – Wilcox illusion is essentially linear. Moreover, there was no sign of saturation of response at low contrast.

5 Supplementary observations

Throughout one's life, until one descends into the depths of absolute presbyopia, one's accommodative state undergoes continuous microfluctuations. By minifying and magnifying the retinal image, such fluctuations temporally modulate the light distribution on the retina. But could this modulation generate the sort of directional signal that is essential for motion perception? In particular, how might temporal modulation affect our stimuli? Bülthoff and Götz (1979) modulated the mean luminance of a stimulus with steps of increasing and decreasing luminance, a step gradient like the ones that are at the heart of our stimuli. Slow temporal modulation produced illusory motion to and fro, varying with the modulation's phase. Informal observations in our laboratory showed that, when our stimuli were modulated in this way, the stimuli appeared to rotate—first in one direction, then in the other, depending upon the phase of the modulation and the direction of the step gradient.

Gregory (1993) asserted that fluctuations of accommodation might play a role in illusory motion, at least for certain stimuli. We wanted to see if accommodative fluctuations were crucial for the motion generated by the stimuli with which we had been working. We therefore tested a well-corrected, bilateral aphake (20/20 binocular visual acuity with refraction). Testing was carried out when the subject, 82 years of age, was one year post-op on one eye, and two years post-op on the other eye. We wanted to know whether a person with no accommodation would see the illusory motion.

5.1 *Methods*

The experimental design was identical to that of experiment 2: ratings were made of the intensity of motion produced by each of the 63 stimulus presentations. As before, the first two blocks of trials were discarded without analysis, leaving a total of 45 trials for analysis. At the aphakic observer's insistence, we altered the scale used to rate the intensity of perceived motion. To ease her choices, instead of using a continuous scale whose upper standard was anchored at 100, she adopted a rating scale of 1 – 5. The uppermost value on this scale was explicitly anchored to the same stimulus that had been equated to '100' for observers in experiment 2.

5.2 *Results and discussion*

The dashed line in figure 3 shows the aphake's ratings, which were similar to those of the younger subjects. As with the younger observers, the octogenerian's ratings increase steadily as stimulus contrast increases. This result is consistent with Zeki's (1995) report that aphakes see illusory motion in some spatially repetitive visual stimuli. Moreover, the result rules out the possibility that accommodative fluctuations are crucial for Fraser – Wilcox motion, or that they play any significant role in that experience.

6 General discussion

In the current study we explored the Fraser – Wilcox illusion in order to clarify the conditions under which this class of stationary stimuli produces motion. Results reveal that optimal conditions for seeing the motion are peripheral viewing, long duration, and high contrast. Experiment 1 shows that, unlike motion from MacKay-type stimuli, which takes a while to develop, Fraser – Wilcox illusory motion emerges relatively quickly, reaching asymptote somewhere between 400 and 800 ms (Leviant 1996). Experiment 2 and our supplementary experiment demonstrate that illusory motion increases steadily as the contrast increases and is relatively weak when stimulus contrast is low. Thus we can add Fraser – Wilcox motion to the list of motion phenomena that do not seem to saturate at low contrasts.

Experiment 1 showed that illusory motion varied with stimulus duration. This result stimulated our interest in the mechanism that lies behind this temporal integration. For example, might this duration dependence resemble the distinctly nonlinear functions obtained for summation in other motion phenomena (Festa and Welch 1997; McKee and Welch 1985)? To answer this question we used a simple summation model to predict, for each eccentricity, the probability of seeing motion at least once during presentations of varying duration. Starting with the empirical probability of seeing motion at the shortest duration, 200 ms, we calculated predicted probabilities for all longer durations. The calculations assumed that (i) each successive 200 ms increment in duration would result in another, independent opportunity to see the motion, and (ii) an observer would report motion if at least once during the presentation motion had been seen. The resulting values represent maximally efficient integration of successive samples. For all eccentricities, at long durations the empirical probability of seeing motion fell below predictions based on summation. There are several obvious candidate explanations for this discrepancy, in addition to imperfect summation. First, learning that sometimes motion is not immediately seen in the initial part of a trial, a subject may raise his or her criterion for reporting motion. Second, it may be that the transient at stimulus onset generates a particularly strong motion signal, which would not be produced later, during the steady state of the stimulus (Mather 1984). As a result, the probability of seeing motion during the initial 200 ms period would exceed the corresponding probability associated with succeeding 200 ms periods. This last possibility might be tested by ramping on the stimulus gradually rather than turning it on abruptly.

Experiment 2 showed that, as assessed by direct scaling methods, the strength of Fraser – Wilcox illusory motion increases in a near-linear fashion as stimulus contrast increases from zero to over 90%. Because of the strong dependence of illusory motion on contrast, there is an opportunity to see whether the same dependence held for second-order motion stimuli. In that case, depth of modulation of spatial noise would be substituted for modulation of luminance. Indeed, it would be valuable to see whether the illusory motion can be evoked at all by second-order stimuli.

Our findings confirm the perceptual dimorphism reported by Fraser and Wilcox: about two-thirds of people we screened did experience the illusory motion. We now also have some idea of the conditions that best elicit illusory motion among those who do see Fraser – Wilcox motion. We have been able to rule out the possibility that accommodative fluctuations were necessary for the effect. As shown by the supplementary experiment, an individual with no accommodation could still see the motion.

Although we did confirm the existence of perceptual dimorphism for this illusion, we did not attempt to replicate the twin study that showed a genetic contribution to the illusion. Obviously, the earlier claim of a genetic contribution cries out for replication. But even when such a replication is done, there will be uncertainty about the mechanism or mechanisms that generate the experience of illusory motion. Assume, for sake of argument, that the experience of Fraser – Wilcox motion depended upon activation of directionally selective neurons such as those found in area MT and elsewhere in the cerebral cortex (Salzman and Newsome 1994). Activation of these neurons requires some mechanism that would introduce appropriate temporal modulation into our otherwise static stimuli. After all, temporal modulation does generate motion with other kinds of static stimuli (Anstis and Rogers 1986; Bülthoff and Götz 1979). In our case, the producers of temporal modulation might be eye movements, particularly movements associated with some systematic instability of gaze. To be more specific, suppose that a momentary fixation of the stimulus in figure 1a could generate a negative afterimage. Even if the afterimage were below threshold, for at least a short time it would interact with—adding to or subtracting from—whatever was fixated immediately thereafter (Leguire and Blake 1982). As a result, a small torsional movement of the eye would alter the neural response to the contrast profile of the stimulus. According to this hypothesis, this time- and gaze-dependent alteration of neural response would constitute the temporal modulation that underlies perception of movement (Anstis and Rogers 1986; Bülthoff and Götz 1979). One way to investigate this issue would be to use a mirrored contact lens in which the retinal image is stabilized and, in turn, the effect of eye movements greatly declines. If instability of gaze contributes to the illusory motion, it should be eliminated by this approach. It is true that eye movements tend to be relatively random in their direction, but they could still be partly responsible for triggering a direction-specific perception of illusory motion. The luminance gradients produced by sectors in each stimulus run in opposite directions. Overall, the luminance distribution of one stimulus is like a sawtooth function whose sloped component rises, for instance left to right, and the other is like a sawtooth function whose slope component decreases. As a result, the same direction of eye movement—saw left to right – would modulate the two retinal images in opposite directions, temporarily increasing local luminance in one, decreasing the other. This is most easily seen for an eye movement perpendicular to the direction of the gradient. Although our speculation might contain some truth, it clearly is incomplete. For example, it omits an explanation of why illusory motion proceeds only in one direction, from darker segments toward lighter segments. It also fails to explain why the motion is seen more easily with peripheral viewing. Most importantly, this speculation does not explain the perceptual dimorphism that makes Fraser – Wilcox motion interesting in the first place. Of course, known genetically determined differences in other forms of eye movements (Holzman 1989; Levy et al 1994), open the possibility that comparable, possibly linked, differences exist for fixational instability as well. It seems to us that any future research might profitably pursue two avenues: first, a focus on the role of eye movements in producing the Fraser – Wilcox illusion, and, second, an attempt to identify the mediating mechanisms that give rise to this striking perceptual dimorphism.

Acknowledgements. We thank Mary Sekuler for her conscientious and cheerful service as observer in our supplementary experiment. We also thank Patrick Bennett for supplying the computer code that generated our masking stimulus, and Elena Festa for thoughtful comments on our manuscript.

References

Anstis S M, Rogers B J, 1986 "Illusory continuous motion from oscillating positive – negative patterns: implications for motion perception" *Perception* **15** 627 – 640

Bülthoff H, Götz K G, 1979 "Analogous motion illusion in man and fly" *Nature (London)* **278** 636 – 638

Charman W N, Heron G, 1988 "Fluctuations in accommodation: a review" *Ophthalmic and Physiological Optics* **8** 153 – 164

Derrington A M, Goddard P A, 1989 "Failure of motion discrimination at high contrasts: evidence for saturation" *Vision Research* **29** 1767 – 1776

Edwards M, Badcock D R, Nishida S, 1996 "Contrast sensitivity of the motion system" *Vision Research* **36** 2411 – 2422

Festa E K, Welch L, 1997 "Recruitment mechanisms in speed and fine direction discrimination tasks" *Vision Research* **37** 3129 – 3143

Fraser A, Wilcox K, 1979 "Perception of illusory movement" *Nature (London)* **281** 565 – 566

Gregory R L, 1993 "A comment: Mackay Rays shimmer due to accommodation changes"*Proceedings of the Royal Society of London, Series B* **253** 123

Hine T J, Cook M, Rogers G T, 1995 "An illusion of relative motion dependent upon spatial frequency and orientation" *Vision Research* **35** 3093 – 3102

Hine T J, Cook M, Rogers G T, 1997 "The Ouchi illusion: an anomaly in the perception of rigid motion for limited spatial frequencies and angles" *Perception & Psychophysics* **59** 448 – 455

Holzman P S, 1989 "The use of eye movement dysfunctions in exploring the genetic transmission of schizophrenia" *European Archives of Psychiatry and Neurological Science* **239** 43 – 48

Hunter W S, 1915 "Regional factors in visual after-movement" *Psychological Review* **22** 479 – 489

Keck M J, Palella T D, Pantle A, 1976 "Motion aftereffect as a function of the contrast of sinusoidal gratings" *Vision Research* **16** 187 – 191

Leguire L E, Blake R, 1982 "Role of threshold in afterimage visibility" *Journal of the Optical Society of America* **72** 1232 – 1237

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

Levy D L, Holzman P S, Matthysse S, Mendell N R, 1994 "Eye tracking and schizophrenia: a selective review" *Schizophrenia Bulletin* **20** 47 – 62

MacKay D, 1961 "Interactive processes in visual perception", in *Sensory Communication* Ed. W A Rosenblith (Cambridge, MA: MIT Press) pp 339 – 355

McKee S P, Welch L, 1985 "Sequential recruitment in the discrimination of velocity" *Journal of the Optical Society of America A* **2** 243 – 251

Mather G, 1984 "Luminance change generates apparent movement: Implications for models of directional specificity in the human visual system" *Vision Research* **24** 1399 – 1405

Nishida S, Ashida H, Sato T, 1997 "Contrast dependencies of two types of motion aftereffect" *Vision Research* **37** 553 – 563

Ohtani Y, Ido K, Ejima Y, 1995 "Effects of luminance contrast and phase difference on motion assimilation for sinusoidal gratings" *Vision Research* **35** 2277 – 2286

Raymond J E, Darcangelo S M, 1990 "The effect of local luminance contrast on induced motion" *Vision Research* **30** 751 – 756

Salzman C D, Newsome W T, 1994 "Neural mechanisms for forming a perceptual decision" *Science* **264** 231 – 237

Sekuler R, 1996 "Motion perception: a modern view of Wertheimer's 1912 monograph" *Perception* **25** 1243 – 1258

Snowden R J, Hess R F, Waugh S J, 1995 "The processing of temporal modulation at different levels of retinal illuminance" *Vision Research* **35** 775 – 789

Thompson P, 1983 "Discrimination of moving gratings at and above detection threshold" *Vision Research* **23** 1533 – 1538

Tootell R B, Hamilton S L, Switkes E, 1988 "Functional anatomy of macaque striate cortex. IV: Contrast and magno-parvo streams" *Journal of Neuroscience* **8** 1594 – 1609

Wade N J, 1977 "Distortions and disappearances of geometrical patterns" *Perception* **6** 407 – 433

Wade N J, 1995 "Portraits of artists and scientists", in *The Artful Eye* Eds R Gregory, J Harris, P Heard, D Rose (Oxford: Oxford University Press) pp 399 – 425

Watson A B, Robson J G, 1981 "Discrimination of moving gratings at and above detection threshold" *Vision Research* **21** 1115 – 1122

Winn B, Pugh J R, Gilmartin B, Owens H, 1990 "Arterial pulse modulates steady-state ocular accommodation" *Current Eye Research* **9** 971 – 975

Zeki S, 1995 "Phenomenal motion seen through artificial intra-ocular lenses" *Proceedings of the Royal Society of London, Series B* **260** 165 – 166

Zeki S, Watson J D G, Frackowiak R S, 1993 "Going beyond the information given: The relation of illusory visual motion to brain activity" *Proceedings of the Royal Society of London, Series B* **252** 215 – 222