Frequency-Doubling Illusion under Scotopic Illumination and in Peripheral Vision

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Purpose. The authors sought to determine whether frequency-doubling illusion (FDI) could be perceived under scotopic illumination at central and peripheral retinal locations. For comparison, perception of the FDI at the central and peripheral retina under photopic illumination was also evaluated.

Methods. Five subjects matched the apparent spatial frequency of counterphase flickering sinusoidal gratings with stationary sinusoidal gratings presented foveally and out to 20° eccentricity under photopic and scotopic illumination conditions. Two spatial frequencies (0.25 and 0.50 cpd) were used at four temporal frequencies (2, 8, 15, and 25 Hz). Subsequent experiments explored the range of spatial and temporal frequency stimulus conditions under which the scotopic FDI might be observed.

Results. Under scotopic illumination conditions, the apparent spatial frequency of eccentrically presented 0.25- and 0.50-cpd flickering gratings gradually increased as a function of flicker frequency and approaches "doubling" at 15 Hz. Under photopic conditions, the apparent spatial frequency of 0.25-cpd flickering at 25 Hz was approximately doubled in all four primary meridians at central and peripheral eccentricities. The final experiment showed that the spatiotemporal range under which the scotopic FDI could be seen was similar to the photopic illumination condition reported earlier.

Conclusions. Scotopic FDI is similar to photopic FDI at the central and the peripheral retina. This suggests that similar mechanisms are responsible for generating the illusion under both photopic and scotopic illumination conditions. (*Invest Ophthalmol Vis Sci.* 2007;48:3413–3418) DOI:10.1167/iovs.06-1091

Spatial frequency-doubling illusion (FDI) occurs when the contrast of a low spatial frequency sinusoidal grating is counterphase modulated at high temporal frequencies. In other words, its apparent spatial frequency increases.[1] Earlier suggestions were that some form of nonlinear processing in our visual system is responsible for this illusion.[1] Maddess et al.[2] (Maddess T, et al. *IOVS* 1990;31:ARVO Abstract 230) attributed the source of this nonlinearity to a specific class of primate magnocellular (M) ganglion cells, M(y) cells, which resemble cat Y cells in their nonlinear spatial summation response characteristics.[3–6] However, the existence of such nonlinear responses in M cells is not universally agreed,[7–9] and a cortical locus has been suggested.[9]

There are several differences in the parvocellular (P) and M ganglion cells; it is generally agreed that M cells primarily convey information concerned with the perception of visual motion and luminance information, whereas P cells primarily convey information concerned with the perception of color and form.[10,11] These two types of cells also respond differently to luminance patterns at varying levels of retinal illumination. Purpura[12] reported that the responses of both types of cells decrease with reduction in mean retinal illumination, but P cells are affected relatively more than the M cells. As a result, in the scotopic ranges of mean retinal illumination, M cells are the predominant conveyor of spatial contrast information to the visual cortex.[12] Hence, if it is true that, at least under photopic conditions, the FDI is perceived because of inputs from the M cells, then the FDI should also be perceived under scotopic conditions. Until now, no psychophysical data have been published to suggest that the FDI can be perceived under scotopic conditions. One report[13] demonstrated increases of apparent spatial frequency with retinal illuminance levels as low as 8 photopic trolands. However, without the results of functional tests such as color vision or the demonstration of a central scotoma, it is not possible to rule out the influence of cone-based mechanisms in mediating these results. Hence, the first aim of this article is to provide further insight into this issue of perception of the FDI under scotopic conditions to add further insight into what neuronal mechanisms may be causing the illusion.

Of potential clinical relevance is the finding that patients with glaucoma experience greater loss of scotopic sensitivity than of photopic sensitivity.[14,15] A recent study using a rat model of experimental glaucoma confirms that, in the early stages of glaucoma, when no structural damage to the optic nerve is identifiable, some loss of scotopic functionality can occur before photopic functions are affected.[16] This raises the interesting possibility that, if the FDI can be perceived at scotopic levels and can be shown to arise from the same mechanisms responsible for the photopic FDI and if those mechanisms are themselves selectively damaged early in glaucoma in a way that raises their contrast threshold for detection (Maddess T, et al. *IOVS* 1990;31:ARVO Abstract 230),[2] glaucoma-related reductions in scotopic function might be more reliably sought by using stimuli that give rise to the scotopic FDI.

Before entertaining thoughts on the development of a scotopic FDI-based clinical test for glaucoma, it is necessary to determine how scotopic FDI is perceived at central and peripheral retinal locations and how this relates to the FDI elicited under photopic conditions. In the photopic case, although early studies reported perception of the FDI only within 2° eccentricity,[17] McKendrick[18] and James[19] later confirmed that the FDI is perceived at retinal eccentricities up to 20°. The second aim of this article is thus to characterize and compare the FDI at different retinal eccentricities under photopic and scotopic conditions.

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Subjects and Methods

Subjects

Five subjects volunteered to participate in this study (age range, 21–26 years), and all had normal corrected or uncorrected visual acuity (20/20) in the tested eye. To be included in the study, subjects were required to have refractive error in the range of +4 D to −4 D of sphere and less than 2 D of astigmatism, normal findings on an eye examination, and normal color vision when tested on Ishihara and D-15 color vision tests under room (photopic) conditions. All experiments were performed monocularly using the eye with better best-corrected visual acuity or the right eye if both eyes had equal acuity. Two of the five subjects (IP, CT) were aware of the purposes of the experiments, and the other three subjects (JB, TD, OC) were naive to the purposes. All subjects read and signed informed consent documents before any testing, and all procedures were carried out in accordance with National Health and Medical Research Council guidelines for human observers, which is based on the tenets of the Declaration of Helsinki (approved by the National Vision Research Institute/Department of Optometry and Vision Sciences/Victorian College of Optometry Human Research Ethics Committee).

Subjects viewed the monitor screen at a viewing distance of 57 cm in dim ambient lighting conditions; their heads were left unrestrained. Pupils were dilated to 8 mm with tropicamide 0.5% drops. Each subject was involved in approximately 5 hours of data collection conducted in 30- to 60-minute blocks (beginning 15 to 20 minutes after instillation of mydriatic) over several weeks. At the beginning of each session, subjects were preadapted for 5 minutes for photopic experiments and at least 15 minutes for scotopic experiments. Before data collection for experiments, subjects were given sufficient practice on the task to ensure that any perceptual learning had stabilized and thus would not confound the results.

Apparatus

Stimuli were presented on a 35 × 26-cm computer monitor (DiamondView 1995; Mitsubishi Electric, Rydalmere, NSW, Australia) running at 120 Hz. The monitor's P22 phosphor consists of R, G, and B components that decay to 10% peak emission in 1.5, 6, and 4.8 ms, respectively. Mean background luminance was set to 36 cd/m^2 (1931 CIE chromaticity coordinates $[(x, y) = (0.3078, 0.3621)]$; nearest Plankian color temperature, 5600 K). Screen luminance was linearized by lookup table with a spectrophotometer (Photo Research 650; Photo Research Inc., Chatsworth, CA) and controlled with 10-bit accuracy using a graphics card (ThunderPower 30; Radius Inc., Belmont, MA) installed in a computer (Macintosh G4; Apple, Cupertino, CA) running EXPO software. A matte black cardboard surround was used to support fixation marks for peripheral eccentricities, which could not be displayed on the monitor.

Scotopic retinal illumination was achieved by fitting a modified set of commercially available protector gas welding goggles over the subject's spectacles that allowed a field of view greater than 30° in any direction. The goggle's ventilation holes were baffled with the use of black electrical tape to stop light entering, and one of the lenses was replaced by a thick black plastic occluder. The other goggle lens was replaced by two thin plano plastic lenses that acted as neutral density (ND) film holders. Photopic luminance of the display monitor was reduced by 4 log units using four layers of ND1 filters. The actual neutral density of this ND film/lens system measured with a spectrophotometer varied between 0.0032% and 0.1026% in the range of 400 and 700 nm with the average transmittance of 0.015%—that is, the effective ND value was 3.82 (ND value = −log(transmittance)). This ND film/lens system reduced luminance of the display monitor from 36 cd/m^2 to 0.0054 cd/m^2 so that retinal illuminance was reduced from 1809 to 0.27 photopic trolands with an 8-mm pupil. Another experiment was performed with a display luminance of 0.0396 cd/m^2 (retinal illuminance, 1.99 photopic trolands), achieved using three layers of ND1 filter (measured ND, 2.96; average transmittance, 0.11%). To ensure that cone pathways were rendered nonfunctional under the reduced illumination conditions (wearing goggles), all subjects were tested with the Ishihara and D-15 color vision tests after dark adaptation. None of the five subjects passed either of these color vision tests, confirming that both reduced illumination conditions can be considered scotopic.

Stimuli

Stimuli consisted of vertically oriented sinusoidal gratings presented in the center of the CRT monitor within an 8°-diameter, software-generated circular window. Fixation spots were used on the monitor and on a surrounding black cardboard background. All stimuli were presented at 80% Michelson contrast. All combinations of spatial and temporal frequencies were randomized in a session. Only one retinal location was explored in a session.

FDI under Reduced Illumination

Two spatial frequencies (0.25 and 0.50 cpd) were used at three temporal frequencies (2, 8, and 15 Hz) under 0.27 photopic troland retinal illumination at 5° temporal retinal eccentricity and 1.99 photopic troland retinal illumination at 15° temporal retinal eccentricity. To avoid any confounding effects of the central 2° rod-free area, experiments under scotopic conditions were not performed with central fixation.

FDI under Photopic Illumination

For photopic experiments, only one spatial frequency (0.25 cpd) was explored at 25 Hz at five retinal eccentricities (0°, 5°, 10°, 15°, and 20°) in all four principal retinal meridians without any ND filter.

Spatiotemporal Range of the FDI under Reduced Illumination

Sinusoidal gratings of seven spatial frequencies (0.25, 0.50, 1, 1.50, 2, 4, and 6 cpd) counterphase flickering at 11 temporal frequencies (1, 2, 4, 8, 10, 12, 15, 17, 20, 25, and 30 Hz) were presented at 5° temporal retinal eccentricity under 1.99 photopic troland retinal illumination.

Procedure

Each trial consisted of two temporal intervals (raised cosine window) of 2.5 seconds with 0.5-second interstimulus intervals. The onset of each interval was accompanied by an audible tone. Counterphase flickering sinusoidal gratings (test grating) appeared in the first interval, and stationary sinusoidal gratings (match grating) appeared in the second interval. Test and match gratings were presented at same retinal location. To minimize spatially contingent adaptation effects, the spatial phases of test and match gratings were independently randomized at each presentation. Spatial frequency of the match grating was controlled by a QUEST staircase procedure[20] or by a method of adjustment (MoA; for characterizing the spatiotemporal range of the scotopic FDI) between 40% lower than the lowest test spatial frequency and 40% higher than the highest test spatial frequency used in the session.

The subject's task was to compare the spatial frequencies of the test and match gratings and then indicate whether that spatial frequency should be increased or decreased to match it with the spatial frequency of the test grating. In experiments using QUEST, subjects had to press the appropriate key. In experiments using MoA, subjects made spatial frequency matching judgments by rolling the scroll wheel of the computer mouse. The smallest rotation of the mouse wheel changed the spatial frequency of stationary match grating in steps of 0.04 cpd. Twenty trials were presented at each spatiotemporal combination for each experiment.

Statistical Analysis

For experiments using QUEST, the 75% performance thresholds for each spatiotemporal combination were determined by fitting psycho-

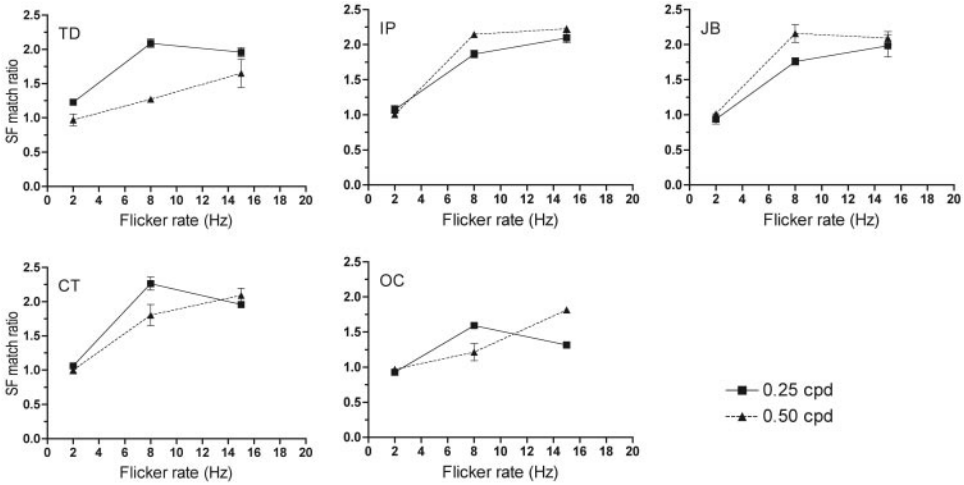

FIGURE 1. Apparent spatial frequency measurements performed by each subject at 5° temporal retinal eccentricity (nasal field) under scotopic conditions (0.27 photopic troland retinal illumination). Apparent spatial frequencies of 0.25- and 0.50-cpd gratings are measured as SF match ratios and plotted as a function of temporal frequency. The 0.25-cpd data are represented by *squares* and the *continuous line*. The 0.50-cpd data are represented by *triangles* and the *dashed line*. Error bars indicate SEMs.

metric response curves with base-2 Weibull functions with the use of least χ^2 metric and binomial estimates for the variance. For experiments using MoA, responses were averaged and variance surrounding them was calculated. To assess the significance of the various factors under investigation, analysis of variance (ANOVA) calculations were performed. All statistical analyses were performed with the use of graphing and data analysis software (KaleidaGraph version 3.5; Synergy Software, Inc. Reading, PA).

RESULTS

Investigation of the FDI under Scotopic Illumination

Figure 1 shows the results of the spatial frequency matching task for each subject at 5° temporal retinal eccentricity under 0.27 photopic troland retinal illumination. Perceived spatial frequency is quantified by the ratio of perceived to true spatial frequency, referred to as the SF match ratio. Figure 1 shows that as temporal frequency increased toward 15 Hz, each subject exhibited a variable amount of increase in the perceived spatial frequency from veridical (SF match ratio, 1.0) to "doubling" (SF match ratio, 2.0) for 0.25- and 0.50-cpd test gratings. Two-way ANOVA revealed no significant difference in the apparent spatial frequency of the 0.25 cpd- and 0.50-cpd test gratings ($P = 0.46$), but a significant influence of temporal frequency ($P < 0.0001$) was calculated.

Having established the existence of a scotopic FDI, we wanted to determine whether this illusion could be perceived at further peripheral retinal locations. Before investigating this question, however, we sought to establish the conditions under which, in our laboratory, the FDI could be perceived peripherally under photopic conditions.

Investigation of the FDI in Peripheral Retina under Photopic Illumination

This experiment was performed using 0.25-cpd test gratings and counterphase flickering at 25 Hz, which are similar to the stimulus conditions used in frequency doubling perimetry (FDP). Figure 2 shows that all five subjects perceived these gratings at doubled spatial frequency at all four primary meridians under photopic illumination. Apparent spatial frequencies were similar at retinal locations as far away as 20°. Two-way ANOVA did not reveal any significant difference between eccentric locations ($P = 0.5148$) or the four primary meridians ($P = 0.5346$). These results confirm that, under photopic conditions, perception of the FDI is similar at central and peripheral retinal locations in all four primary meridians.

Investigation of the FDI in Peripheral Retina under Reduced Illumination

The aim of this experiment was to determine whether the FDI can be perceived under scotopic illumination conditions in

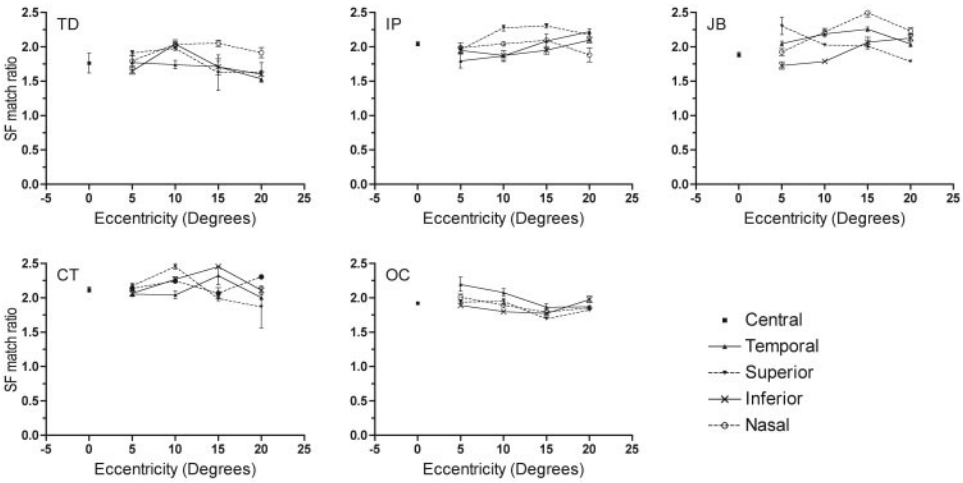

FIGURE 2. Apparent spatial frequency measurements performed by each subject at five eccentricities (0°, 5°, 10°, 15°, 20°) at all four principal retinal meridians under photopic conditions (1809 photopic troland retinal illumination). Apparent spatial frequencies of 0.25-cpd grating counterphase flickering at 25 Hz are measured as SF match ratios and plotted as a function of retinal eccentricity. Data at four primary meridians are shown with different symbols as indicated in the key. Data with central fixation are shown as *single isolated square*. Error bars indicate SEMs.

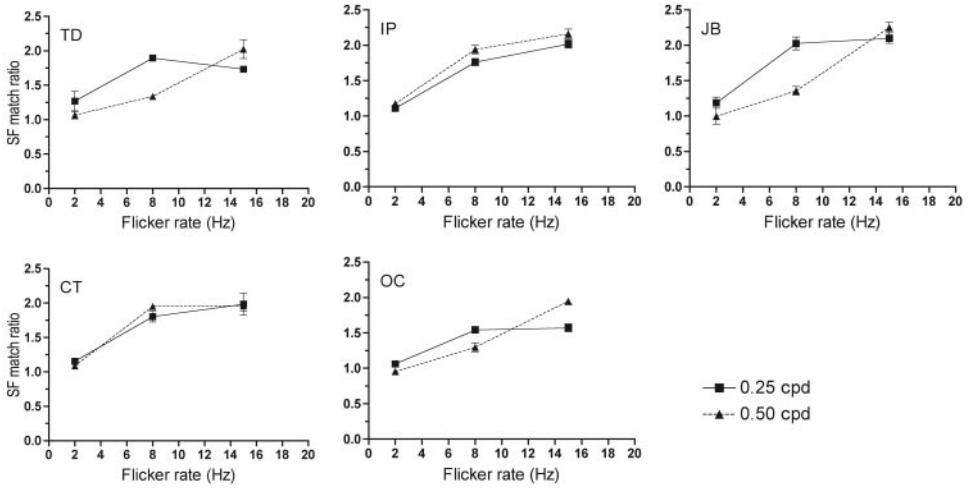

FIGURE 3. Apparent spatial frequency measurements made by each subject at 15° temporal retinal eccentricity (nasal field) under scotopic conditions (1.99 photopic troland retinal illumination). Apparent spatial frequencies of 0.25- and 0.50-cpd gratings are measured as SF match ratios and plotted as a function of temporal frequency. The 0.25-cpd data are represented by *squares* and the *continuous line*. The 0.50-cpd data are represented by *triangles* and the *dashed line*. Error bars indicate SEMs.

peripheral retina at 15° temporal retinal eccentricity. We first attempted this experiment using a retinal illuminance of 0.27 photopic troland, but subjects found the task difficult. Retinal illuminance levels were subsequently increased to 1.99 photopic troland.

Figure 3 shows that as temporal frequency increased, perceived spatial frequency gradually increased for 0.25- and 0.50-cpd test gratings and approached doubling at 15 Hz. At 15° temporal retinal eccentricity, two-way ANOVA showed no significant difference in the apparent spatial frequency of the 0.25-cpd and the 0.50-cpd test gratings ($P = 0.51$) but did show a significant influence of temporal frequency ($P < 0.0001$). Comparison of apparent spatial frequency results at two eccentricities (5° and 15°) under different levels of scotopic illumination conditions showed no difference for test spatial frequency or illumination conditions (0.25 cpd, $P = 0.94$; 0.5 cpd, $P = 0.96$), .implying that the FDI was similar at all retinal locations under all illumination levels.

Spatiotemporal Range of the FDI under Reduced Illumination

To gain an appreciation of what spatiotemporal stimulus combination could result in a measurable FDI under reduced illumination conditions, five subjects matched the apparent spatial frequency of flickering targets under 1.99 photopic troland retinal illumination at 5° temporal retinal eccentricity. Group results are shown in Figure 4. None of the subjects could perform the task at 25 and 30 Hz at any spatiotemporal combination. Moreover, as the spatial frequency of the test gratings increased, the task became more difficult and was not possible beyond 8 Hz for 6.00-cpd grating. The possible reason for these restrictions is addressed in the next section.

Figure 4 shows that test gratings of all spatial frequencies appeared veridical at low temporal frequency flicker. However, as the temporal frequency increased, apparent spatial frequencies of the low and intermediate spatial frequency test gratings increased but approached doubling only for 0.25-, 0.50-, 1.00-, and 1.50-cpd gratings. For 2.00-cpd grating, only partial increases in apparent spatial frequency were noted, whereas high spatial frequency (4.00 and 6.00 cpd) gratings were generally perceived with near veridical apparent spatial frequency.

DISCUSSION

Results of this study revealed that under scotopic conditions, and within the spatiotemporal parameters under which the spatial frequency matching task could be performed, the apparent spatial frequency of flickering gratings gradually increased as the temporal frequency of counterphase flicker increased. That the FDI could be perceived under scotopic conditions was a totally novel finding; it became important to consider whether the scotopic FDI identified by us was the same as the classical FDI reported earlier under photopic conditions.

Photopic FDI was first reported by Kelly.[1] If the temporal frequency of counterphase flicker is increased, the apparent spatial frequency of a low spatial frequency grating abruptly becomes doubled above 7 Hz and persists until the temporal frequency is increased above the critical flicker fusion (CFF) frequency. This issue of an abrupt onset of doubling has been criticized by several investigators (Demirel S, et al. *IOVS*. 1999; 40:ARVO Abstract 42).[17,18,21] Sufficient evidence (including from this laboratory; not reported here) now shows that under photopic conditions, apparent spatial frequency of a grating gradually increases before it doubles at approximately 8 to 12 Hz. We report similar results in this study under scotopic illumination conditions. Figure 4 shows that the 0.25-cpd grating appears with partially increased spatial frequency at 8 Hz but appears spatially doubled at 12 Hz. Kelly[1] also reported that the FDI is perceived at temporal frequencies as high as the CFF frequency. This is in contrast to our results because our

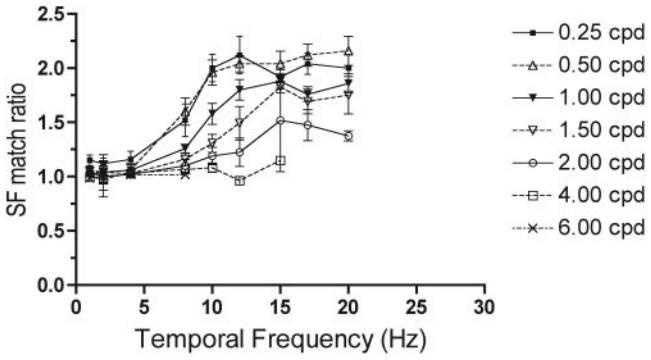

FIGURE 4. Group results of apparent spatial frequency measurements at 5° temporal retinal eccentricity (nasal field) under scotopic conditions (1.99 photopic troland retinal illumination). Apparent spatial frequencies of seven spatial frequencies (0.25, 0.50, 1.00, 1.50, 2.00, 4.00, and 6.00 cpd) counterphase flickering at eleven temporal frequencies (1, 2, 4, 8, 10, 12, 15, 17, 20, 25, and 30 Hz) are measured and plotted with different symbols and lines (see key). No data were available for 25- and 30-Hz flicker. Error bars indicate SEMs.

subjects could not perform the matching task at high spatial and temporal frequencies under scotopic illumination conditions (Fig. 4). However, this difference can be reconciled if we consider the dependence of spatial and temporal acuity on adapting illumination conditions. It has been shown for a normal trichromat and for a rod monochromat that spatial and temporal acuities vary with retinal illumination.[22,23] At low retinal illumination, spatial and temporal contrast sensitivity curves are low pass with lower spatial and temporal acuities. As the level of retinal illumination increases, both contrast sensitivity curves becomes bandpass, and simultaneously both acuities increase. This explains why our subjects could not perform the matching task at high spatial and temporal frequencies under reduced illumination conditions.

In the spatial domain, there is no consensus on the cutoff spatial frequency below which the FDI is perceived. Most reports (Demirel S, et al. *IOVS*. 1999;40:ARVO Abstract 42)[17,21] suggest that photopic FDI is perceived only if the spatial frequencies are lower than approximately 2 or 3 cpd, an observation we also made under scotopic illumination conditions. Thus, the differences observed between the spatiotemporal ranges of FDI at different illumination levels only result from the differences in spatial and temporal acuities between scotopic and photopic vision.

Earlier evidence suggested that the photopic FDI is not perceived beyond 2° retinal eccentricity,[17] though later James et al.[19] and McKendrick et al.[18] reported that the photopic FDI can be perceived out to 10° and 20° eccentricity, respectively. Our results under photopic and scotopic conditions concur with these later reports that the FDI can indeed be perceived at peripheral retinal locations.

The spatial nature of the FDI at contrast levels near detection threshold, used in FDP, has been a matter of debate in the literature. It has been argued that the FDI is perceived as vague flicker[17] or is perceived at its doubled apparent spatial frequency only at low-contrast levels.[24,25] On the other hand, recent evidence suggests not that the spatial nature of the FDI varies with contrast levels but that the task of spatial frequency matching becomes difficult at low-contrast levels.[18,26] We have not performed any experiments at such low contrast levels; we have only shown that the FDI under the scotopic illumination is similar to the FDI under the photopic illumination. Given this similarity, we might predict that, as under photopic conditions, the FDI should be perceived at contrast levels as low as detection threshold contrast levels under scotopic illumination conditions.

Because the characteristics of the scotopic FDI are similar to those of classical photopic FDI, a simple hypothesis would be that the neural mechanisms responsible for both perceptual phenomena are the same. The differences recorded between the spatiotemporal range of the FDI at different illumination levels can be directly attributed to the visual units responsible for gathering and processing visual information and not the visual units generating the FDI percept. Thus, it is parsimonious to account for all the properties of the scotopic FDI using the current theory explaining photopic FDI. If indeed the nonlinearities in the magnocellular system are involved in the perception of the FDI under photopic conditions, as argued by Maddess et al. (Maddess T, et al. *IOVS* 1990;31:ARVO Abstract 230),[2] it would follow that the magnocellular system is also involved in the perception of the FDI under scotopic conditions. Three pieces of evidence support the theory proposed by Maddess et al. (Maddess T, et al. *IOVS* 1990;31:ARVO Abstract 230).[2] First, M cells have much greater contrast gain control than P cells, especially at low luminance levels.[12] Second, evidence shows that at low retinal illumination levels, the responses recorded from a Y-like M cell were more vigorous than from other recorded cells at a range of temporal frequencies.[27] Third, Maddess et al.[13] have shown that the units responsible for the production of the illusion have a spatial sampling density expected only from M(y) cells.

However, the theory that the M cells have significant nonlinear responses to generate the FDI is not universally accepted.[7–9] Findings of this study do not directly confirm or reject the current theory of M(y) cells as the neural basis of FDI. It is possible that neurones higher up in the visual pathway receive visual information from M and P cells under varying levels of illumination conditions and are responsible for the illusion. Additional psychophysical and physiological investigations are required to confirm the exact mechanisms responsible for generating the FDI.

It might be imagined that the scotopic FDI described in this article could be used in the development of a new clinical technique aimed at detecting glaucomatous visual function loss. The theoretical basis for the success of such a technique would rely on the veracity and combination of three key findings. The first is the success of FDP as it is currently applied. Although FDP does not explicitly require patients to identify when they can see the FDI, it uses stimuli for which the perception of the illusion is possible and is based on the premise that the mechanisms responsible for generating the illusion are the same as those selectively damaged in glaucoma. The second comes from this study that the FDI is similar under scotopic and photopic illumination conditions, both near the fovea and in the periphery, because it is underpinned by the same neural substrate. The third is the notion that patients with glaucoma undergo greater loss in scotopic sensitivity than photopic sensitivity,[14,15] a finding that has recently gained support from experiments using a rat model of induced glaucoma.[16] It might be that the scotopic FDI can be developed as a sensitive tool for early detection of glaucomatous visual function loss. However the limitations would include the clinical hurdle of requiring patients to dark adapt, which would make examination more time consuming.

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