WITH THE EYE BEING A BALL, WHAT HAPPENS TO FIXATIONAL EYE MOVEMENTS IN THE PERIPHERY?

by

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RUNNING HEAD: FEM at the Periphery

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Abstract

Although the fact that the eye is moving constantly has been known for a long time, the role of fixational eye movements (FEM) is still in dispute. Whatever their role, it is structurally clear that, since the eye is a ball, the size of these movements diminishes for locations closer to the poles. Here we propose a new perspective on the role of FEM from which we derive a prediction for a three-way interaction of a stimulus' orientation, location, and spatial frequency. Measuring time-to-disappearance for gratings located in the periphery we find that, as predicted, gratings located to the left and right of fixation fade faster when horizontal than when vertical in low spatial frequencies and faster when vertical than when horizontal in high spatial frequencies. The opposite is true for gratings located above and below fixation.

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Introduction

Our eyes are never still; they flick, drift, and tremor, even while fixating (Ditchburn & Ginsborg, 1953; Ratliff & Riggs, 1950). Moreover, rather than interfere with vision, these fixational eye movements are indispensable: When eye movements are eliminated, e.g., by stabilizing the image on the retina, vision fails (Ditchburn & Ginsborg, 1952; Prichard, 1962; Yarbus, 1967).

Although these facts have been known for a long time - by Helmholtz if not earlier - the exact role of fixational eye movements (FEM) is still in dispute. Many regard the role of these movements as solely to counter adaptation in retinal receptors, their "fatigue" to use Helmholtz's expression (1911/1962), by providing a "fresh image" at every instant. Others, amongst them the authors of this paper, believe that FEM have a more specific role in the process of vision (e.g., Ahissar & Arieli, 2001; Avrahami, 2004; Hennig, Kerscher, Funke, & Wörgötter, 2002; Greschner, Bongard, Rujan, & Ammermüller, 2002; Martinez-Conde, Macknik & Hubel, 2004) but even they differ in the role they assign to these eye movements. In what follows, we shall present our own view of the role of FEM in vision and the results of a study designed to test predictions emerging from this view.

Firstly, it is obvious that FEM do not provide a "fresh image" to all receptors. Instead, they provide change in stimulation only to receptors facing contrast boundaries. As such, they provide a simple and ingenious mechanism for edge detection.

Secondly, movement in different directions produces different activation by differently oriented stimuli. For example, when viewing a vertical line, a horizontal movement causes change in stimulation to many more receptors than does a vertical movement. If the information available to the visual system includes not only retinal activation but also the eye movements that produced it, FEM could be instrumental in eliciting the *content* of the image being viewed.

Indeed, it has been shown that, when eye movements are restricted to only one direction, then only stimuli oriented orthogonally to that direction are perceived. Buisseret and colleagues tested the influence of the direction of eye movements on the distribution of orientation selectivity and found a preponderance of units tuned to the orientation orthogonal to the direction of movement that was left intact (see Buisseret, 1995, for a review of this work).

Thirdly, and as a result of the former, the *amplitude* of the movement must also play a role in vision. To illustrate, consider a stimulus consisting of a sinusoidal grating, namely, a grating with gradual transition between light and dark. It is easy to see that to produce maximal activation when viewing a sinusoidal grating, not only has the direction of eye movements to be orthogonal to the lines of the grating but the size of the movement also ought to ensure that receptors travel from areas of highest to areas of lowest illumination in the grating or vice versa (Figure 1): Movement of certain amplitude would produce maximal activation for a sinusoidal grating if its size matches exactly the distance from the highest to the lowest luminance of the grating, namely, if the grating's cycle is twice the size of the movement's amplitude[1]. Any other grating, with

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[1] A displacement of half a cycle produces maximal absolute change. Nevertheless, the optimal movement could be a quarter of the grating's cycle, whereby change, though less extreme, is more uniform in a greater number of receptors. With presently available evidence these and other options are all still viable. Note, however, that the prediction to be tested here does not depend on their resolution.

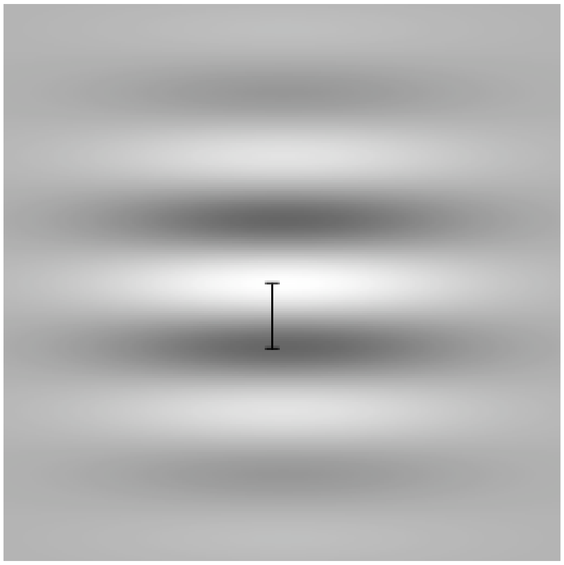

Figure 1: A grating with its optimal amplitude marked

a wider or narrower cycle (i.e., of lower or higher spatial frequency) would produce only partial activation. True, when the contrast of a grating is high, it can be detected even when its frequency is less than optimal; but when the contrast is low, detectability rapidly deteriorates for lower- and higher-than-optimal frequencies. This can explain the well-known shape of the contrast-sensitivity function (Campbell & Robson, 1968), which shows that sensitivity at the fovea is optimal at about four cycles per degree declining both for higher and lower frequencies. It can also explain why, in frequencies that are too low for fixational eye movements, it is the slope of the grating, not its overall contrast that determines its visibility (Campbell, Johnstone, & Ross, 1980).

Given the importance of the direction and amplitude of FEM for vision, one may wonder what happens to these movements outside the center of fixation, namely, in the periphery. To answer that, one should remember that the eye is a ball rotating on specific axiis.

When earth rotates on its axis for a full day, a point on the equator travels about 28,000 km while a point on either of the poles stays in its place. That is, the distance traveled by a point on earth decreases with the point's distance from the equator towards the pole. Unlike earth, the eye moves in relation to three axiis, corresponding to the three pairs of extra-ocular muscles responsible for its movement. The superior and inferior recti (the muscles connected at the top and bottom of the eye-ball) cause up and down movements around a horizontal axis orthogonal to the direction of gaze; the medial and lateral recti (the muscles connected at both sides of the eyeball) cause a left to right movement around a vertical axis and the superior and inferior oblique muscles (muscles connected at the top and bottom of the eye-ball but pulling the eye in opposite directions) cause a torsional movement around a horizontal axis coinciding with the direction of gaze. In what follows we consider only the first two axiis mentioned above.

To understand how these facts about the movements of the eyeball can affect vision in the periphery, consider a patch of sinusoidal grating to the right (or left) of the center of fixation (see Figure 2). If the grating is oriented vertically (Figure 2a) the direction of movement required for its detection is horizontal, namely, movement around the vertical axis. In relation to this axis, both the center of fixation and the patches on the left and right are on the equator, hence the horizontal movement of a receptor at the center and receptors at the periphery would have the same amplitude. The case is different for a grating in the same location that is oriented horizontally (Figure 2b). To detect a horizontal grating, a vertical movement is required and such a movement is around the horizontal axis. Relative to that axis, the center of fixation and the grating at the periphery share a meridian, not an equator. As a result, the amplitude of the vertical movement of receptors in the periphery would be smaller than that of receptors at the center.

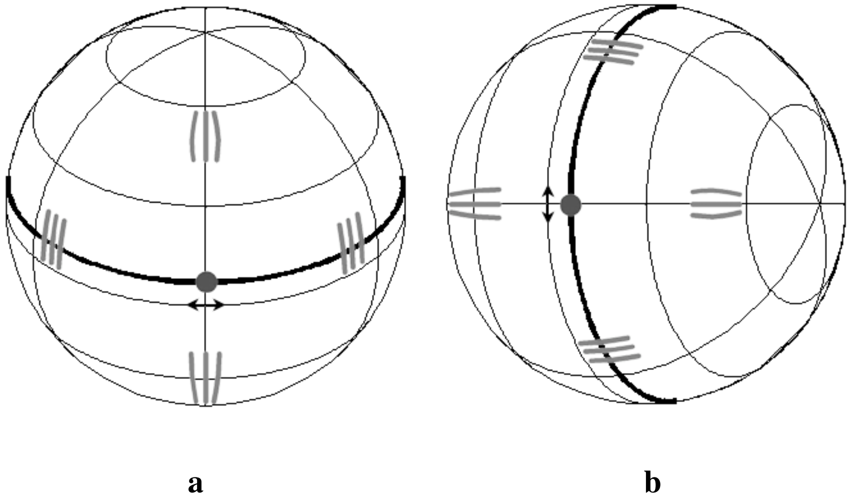

Figure 2: Meridian and Equator stimuli. 2a) For vertical stimuli, gratings to the right and left of fixation lie on the Equator of the axis of required movement while gratings above and below fixation they lie on the Meridian of that axis 2b) For horizontal stimuli, gratings to the right and left of fixation lie on the Meridian while gratings above and below fixation they lie on the Equator of that axis.

Given that the amplitude of the movement required for detecting a horizontal stimulus is decreased to the left or right of fixation, it would optimally serve only denser gratings, namely, gratings of higher frequency than that of gratings oriented vertically. The reverse is expected for gratings located above or below fixation, with the optimal spatial frequency of gratings oriented horizontally lower than that for gratings oriented vertically.

To test this prediction we relied on what is known as the Troxler effect. Troxler (1804) has noticed that, when the eyes fixate a small stimulus, low-contrast low-frequency stimuli at the periphery fade away. The effect has been explained by the fact that fixation on the small central stimulus restricts eye movements such that their amplitude is too small for the larger receptive fields in the periphery (e.g., Martinez-Conde et al., 2004). We suggest phrasing it somewhat differently, saying that the amplitude of the movements becomes too small for optimal activation of a low-frequency stimulus.

We asked whether time to fading would be sensitive not only to the spatial frequency of a peripheral grating but also to the combination of its location and orientation. Thus, gratings of low frequency, that are located along the meridian (relative to the axis of the movement they require for detection), would fade faster than when removed along the equator of that movement whereas gratings of high frequency, whose cycle is too small for optimal detection, would benefit (i.e., fade slower) from being on the meridian compared to being on the equator.

Our prediction is, then, that for low frequency gratings, gratings to the left and right of fixation would fade faster when horizontal than when vertical and gratings above and below fixation would fade faster when vertical than when horizontal. The opposite relation should hold for high frequency gratings.

To test this prediction, participants viewed displays containing a central fixation point and two low-contrast Gabor stimuli, i.e., sinusoidal gratings with a Gaussian envelope, located one to the left and the other to the right of fixation or two Gabor stimuli located one above and one below the fixation point. The orientation of simultaneously presented stimuli was the same, either horizontal or vertical. The distance between fixation point and the Gabors was 14^0. The spatial frequency of the Gabor stimuli was manipulated, assuming values between 0.60 cycles per degree and 2.15 cycles per degree.

Method

Participants

Sixteen students of the Hebrew University of Jerusalem participated in the experiment for a monetary reward. An additional participant, for whom fading hardly ever occurred (reaching the timeout of 20 seconds on 67% of the trials), was removed from the analysis.

Apparatus and Stimuli

The display consisted of a small black dot at the center of the computer monitor and two low-contrast Gabors located 14^0 of visual angle away from center either above and below or to its left and right (Figure 3). The luminance distribution of a Gabor stimulus is given by the following equation:

$$\mathrm{G} = \exp\left(-\left(\frac{x^2+y^2}{\sigma^2}\right)\right) \times \sin\left(2\pi\cos\theta \bullet \lambda x + 2\pi\sin\theta \bullet \lambda y\right)$$

Where x, y, the horizontal and vertical coordinates, go from -200 to +200, λ dictating the spatial frequency of the grating, and σ dictating the Gabor envelope.

With participants seated 28 cm away from the computer monitor and with $\sigma = 30$, the width of ±2 standard deviations of the Gabor envelope is 6.7 degrees of visual angle. The variable λ assumed values from .0300 to .1075 in steps adding 20% each, producing the following values for the spatial frequency (SF) of the Gabor: 0.60, 0.72, 0.86, 1.04, 1.24, 1.49, 1.79, 2.15, cycles per degree of visual angle.

The contrast of the stimuli was such that they were barely visible to facilitate their disappearance: The screen was grey (43 cd/m^2) and the contrast (±1 cd/m^2) was 0.023.

Figure 3: Example of a display in the experiment (with Gabors' contrast exaggerated for visibility).

The stimuli were produced and data collected in Matlab, using the Psychophysics Toolbox extensions (Brainard, 1997). The experiment run on a PC Intel Pentiuim III and were displayed on a 16 inch RGB monitor with a refresh rate of 75 Hz and a resolution of 1152*864.

Procedure

Participants were instructed that two low-contrast groups of lines and a black dot would appear on each trial; they were asked to fixate the black dot and note that the groups of lines start to fade and then disappear. Once the groups of lines disappeared they should press the space key. A block of trials contained 32 trials. Every participant performed one practice block and two experimental blocks.

Design

The experiment included two layouts with the stimuli either to the left and right of the central dot or above and below it. The grating of the Gabor stimulus was oriented either horizontally or vertically and it had one of eight spatial frequencies. The basic design thus consisted of Layout (2) x Angle (2) x SF (8) = 32. While Layout was blocked, Angle and SF appeared in random order.

Though layout and orientation were manipulated separately, the predictions to be tested concerned their combinations, which result in two, rather than four, conditions: Gratings were removed from the center of fixation either along a meridian of the axis of the movement required for their detection (stimuli oriented horizontally in the horizontal layout and stimuli oriented vertically in the vertical layout) or removed along the equator of that axis (stimuli oriented vertically in the horizontal layout and stimuli oriented horizontally in the vertical layout). The two conditions to be compared were, thus: Meridian versus Equator. Meridian stimuli were expected to fade faster than Equator stimuli in low frequencies but more slowly in high frequencies.

Results and Discussion

Average time-to-fading was calculated for every SF for the Meridian and for the Equator conditions, separately for every participant. Figure 4 presents a graph of the average time-to-fading for the two conditions in the eight values of SF.

As can be seen in the figure, both functions have the shape of an inverted U, corresponding, together, to the contrast-sensitivity function at the periphery - at a distance of 14^0 from center. Note that the whole function is shifted towards lower spatial frequencies relative to the known function at the fovea. This shift is in accordance with what is known about the size and density of receptors in the periphery.

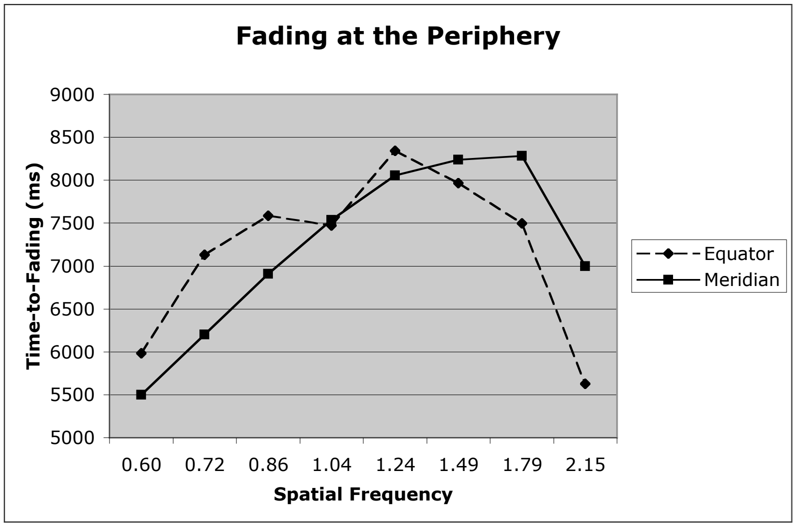

Figure 4: Time to Fading as a Function of SF, Separately for the two Location x Orientation

Most important to the issue at hand is the shift in the function for Meridian stimuli relative to the function of Equator stimuli: As predicted, the peak of the former occurs at higher spatial frequencies (1.79 c/d) than the peak of the latter (1.24 c/d).

To test for the quadratic nature of both functions and the shift of one relative to the other, an analysis of variance for repeated measures was conducted on Time-to-Disappearance with SF and Condition as independent measures. There is obviously a main effect of SF (*F*(7,105)=8.6, *MSE*=2961103, *p*<.001) with a significant quadratic component (*F*(1,15)=25.56, *MSE*=5651585, *p*<.001), confirming the quadratic nature of the functions. There is also an interaction between SF and Condition (*F*(7,105)=2.25, *MSE*=2133113, *p*=.036); here the linear-linear component of the interaction is significant

(*F*(1,15)=11.55, *MSE*=817410, *p*=.004), reflecting the shift in the function of one condition relative to the other.

The paper offers a reassembly of well known though loosely related facts about the visual system, from which a new conceptualization of the process of vision emerges. The process of vision is conceived of here as a dynamic combination of information gleaned from retinal activation and information about the eye movements that produced this activation. Together, these two sources of information can provide initial notions of the contents of the visual field: of contrast boundaries, their orientation, and their spatial frequencies.

The paper demonstrates that the new conceptualization can produce new, testable, predictions about visual phenomena, in this case about the complex relation between the visibility of a stimulus and its peripheral location, orientation, and spatial frequency.

As outlined here, the new conceptualization leaves, however, many questions unanswered. One concerns the role of torsional FEM: How do they combine with the horizontal and vertical FEM in the visual process? Another concerns the amplitude of FEM, which was regarded here as a given. It may be reasonable to assume default amplitude that is used for detection. But can the eye manipulate the amplitude of its FEM, tuning it to best fit the relevant stimulus? The question is of particular importance in view of abundant evidence showing that the visual system can tune to a particular spatial frequency following priming (Hübner, 1996; Tanaka & Sagi, 2000) or following prior experience (Davis, 1981; Schyns & Oliva, 1999). It has recently been shown that the visual system can tune even to the weight of the stroke by which a stimulus is drawn, namely, to the thickness of a stimulus' lines (Avrahami, in press). How is this accomplished? Is it by changing the amplitude of FEM? Is it by changing its direction through a combination of horizontal and vertical movements, or by a combination of these with torsional movement? Further research is needed to answer these questions. The present paper offers a framework for pursuing them.

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