

THE FINE-GRAIN MOVEMENT ILLUSION: A PERCEPTUAL PROBE OF NEURONAL CONNECTIVITY IN THE HUMAN VISUAL SYSTEM

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Abstract—In the visual periphery, brief presentation of two very closely spaced luminous point stimuli, in rapid sequence, causes the illusory impression that a single dot moves over a path of considerable extent. The interactions obtainable between two illusions near one another are described for various configurations of the inducing stimuli. Only when such illusions are codirectional are they found not to interfere with one another. The effective field position and extent of the illusion were measured by pitting two suitably separated illusions against one another. The extent varies from about 2° to 6° as stimulus eccentricity is increased from 10° to 24°. However, when mapped onto visual cortex by means of human cortical magnification factor, the illusion spans a patch of cortex about 3 mm dia, regardless of stimulus eccentricity; such a region in primate visual cortex corresponds approximately to the locus of cortical cells that “see” a given retinal point. Finally, it is suggested that these fine-grain effects may underlie certain perceptual responses to sequential random-dot displays.

INTRODUCTION

If two points on the human peripheral retina—separated by a few minutes of arc and hence not resolved spatially—are stimulated in sequence (about 50-msec interstimulus interval) by brief (duration a few msec) flashes of light, observers report “a moving dot that travels for a degree or more”, always in the direction dictated by the flash sequence (Thorson *et al.*, 1969; Biederman-Thorson *et al.*, 1971; Foster, 1977). The apparent travel time can be “an appreciable fraction of a second”. The two points stimulated simultaneously are perceived as a single flashing dot.

This “fine-grain movement illusion” has been shown to occur with stabilized retinal images and may represent the spatiotemporal two-impulse response of the peripheral movement-detection system (Biederman-Thorson *et al.*, 1971). It has been used to measure rate constants accounting for the range over which movement is perceived (Thorson *et al.*, 1969; Biederman-Thorson *et al.*, 1971) and to demonstrate rod- and cone-system interactions (Foster, 1977). The illusion can be elicited dichoptically but vanishes in dichogeniulate presentation (Thorson *et al.*, 1969; Biederman-Thorson *et al.*, 1971), suggesting that it could be used clinically to locate the meridian of nasotemporal division in the human retina (McIlwain, 1972). A theoretical treatment of the illusion in terms of the dynamics of neural arrays has also appeared (von Seelen, 1973).

The fine-grain movement illusion (FGMI) is a phenomenon quite distinct from classical apparent

movement (Graham, 1965; Kolers, 1972). Classical apparent movement (beta motion) is observed as an illusory impletion between sequentially flashed stimuli that may be spatially separated by angles of up to 18° (Zeeman and Roelofs, 1953). The FGMI is, moreover, unlike the effects seen when a stimulus light is simply given a very small and rapid displacement and then not turned off (Biederman-Thorson *et al.*, 1971; Scooby and Horowitz, 1976). There is, however, a short-range apparent movement effect obtained with alternating random-dot patterns (Braddick, 1974) that may be intimately related to the FGMI. When a region within the random-dot patterns is given a suitably small displacement it is perceived as a segregated coherently moving whole. It seems likely that the local motion-detecting process underlying the short-range apparent movement effect is the same as that underlying the FGMI (Braddick, 1974, p. 525; 1980, personal communication).

In this paper we describe the effects of pitting two FGMI's against one another in various ways, one of which provides an objective method of measuring, in terms of visual-field coordinates, the perceived position and extent *L* of the illusion. Our previous attempts to measure *L* proved unsatisfactory: matching real-moving stimuli elicited confounding FGMI effects (see the “on-move-off” case of Biederman-Thorson *et al.*, 1971), and steady adjustable markers introduced structure into the uniform field; the latter alters subjective estimates of the FGMI. The successful method described here requires that two FGMI's be experienced simultaneously and without interac-

tion. In Experiment 1 we examine the interactions which do occur when the two illusions are induced simultaneously near one another in visual space. In Experiment 2 we measure the perceived position and extent of the illusion as a function of stimulus eccentricity.

METHODS

Stimuli and apparatus

The FGMI stimuli were produced by two matched pairs of miniature yellow light-emitting diodes (peak emission wavelength 570 nm) controlled by appropriate electronics. Each disc-shaped dot formed by an LED subtended 0.1° at the eye and the centre-to-centre separation of the two dots producing a FGMI stimulus subtended 0.2° . The LED pairs were mounted in matrix boards attached to a vertical X-Y machine cross-slide to allow independent and reproducible movement of the stimulus pairs.

The duration of the flash produced by each LED was fixed at 15 msec and the onset delay between the two flashes constituting each FGMI stimulus was fixed at 50 msec. (Rise and fall times of the flashes were less than $10 \mu\text{sec}$.) The two FGMI-stimulus pairs occurred simultaneously.

The stimuli were presented upon a uniform rectangular black field subtending $40^\circ \times 15^\circ$ at the eye and oriented horizontally. Outside this background field, the ambient field luminance was 0.33 cd m^{-2} . The intensity of each flash was fixed at 0.66 mod, which was between 2.5 and 3 log units above increment threshold. (These light levels were chosen to maximize the extent of the illusion; compare Biederman-Thorson *et al.*, 1971; Foster, 1977.)

A different experimental apparatus was used for a set of pilot experiments. There the two FGMI stimuli were generated at the ends of two bifurcated fibre-optic bundles, illuminated through slits by a small tungsten lamp swinging on a seconds pendulum. Stimulus parameters were, however, similar to those given above.

Procedure

Subjects viewed the stimuli monocularly with the right eye at a distance of 1.15 m. A small red fixation spot was located to the right of and horizontally in line with the LED array. Head position was stabilized with a head rest. No artificial pupil was used (see Virsu and Rovamo, 1979). Measurements were recorded after 20 min of dark-adaptation. Further details of the procedure are discussed below.

Subjects

The three subjects were R.J.M., F.M.F. and D.H.F. (one of the authors). Each had corrected-to-normal visual acuity of at least 6/5. Each was practised in making psychophysical judgements, and except for D.H.F. each was unaware of the purpose of the experiment. Two other subjects, J.T. and M.B.-T. (two

of the authors) participated in the pilot experiments described above, the results of which were confirmed and extended by the present study.

EXPERIMENT 1: INTERACTIONS BETWEEN TWO FGMIs

Figure 1(a) schematizes the basic single fine-grain movement illusion observed in response to the sequential brief flashing of the two small dots labelled 1 and 2 (in the sequence 1, then 2) in the visual periphery. The dashed line, with arrowhead to indicate perceived direction, represents qualitatively the "seen moving dot", which (with good fixation on a point 10° – 30° away from the stimulus dots) most observers say travels "a degree or more", even when the two stimulus dots are separated by less than 0.1° .

To determine how one FGMI might influence another, the two sets of two-flash stimuli were positioned 10° to the left of the fixation point and variously aligned relative to each other as in Figs 1(b)–(l). The dashed lines accompanied by question marks in (b)–(l) suggest what one might expect to occur if the two illusions simply superimposed and did not interact. (Vertical and horizontal scales in Fig. 1 are the same.) In fact, all subjects reported strong interactions between the effects of such stimuli presented as in Figs 1(b)–(i). That is, configuration (b) did not elicit the percept of two diverging moving dots but only a stationary blur and actually could not be distinguished from the reverse configuration (Fig. 1[h]).

Configuration (c) elicited neither the percept of two orthogonally moving dots expected on the basis of superposition, nor that of a single diagonal resultant movement; rather, all subjects reported a vague "smear" moving downward and to the right. (Contrast this result with the split motion obtained by Kolers (1972, Chap. 5) for classical apparent movement.) Configuration (d) is similar to (c), but with slightly greater separation; occasionally two orthogonally moving dots were seen, but not when flashes 1 and 2 were reversed in sequence.

In configurations (e)–(h) we tried to make the two illusions collide. In (e), the converging illusory dots were distinct but with perhaps shorter travel than in (a); in (f) and (g) separate converging movement illusions still occurred but a dark gap was always perceived in the centre, between their terminations. Configuration (i) was an attempt to cross two illusory travelling dots, but the percept was only that of a "smear" moving toward the right. (Compare the similar effect of sequences of adjacent bars; Biederman-Thorson *et al.*, 1971.)

In configurations (j) and (k), the stimulus pairs were close to one another but codirectional and collinear; the response to both was reported as a pair of dots moving to the right. Configuration (l), like (j) and (k), elicited the strong percept of two travelling dots.

These findings—that FGMIs induced within about a half degree of one another interfere destructively

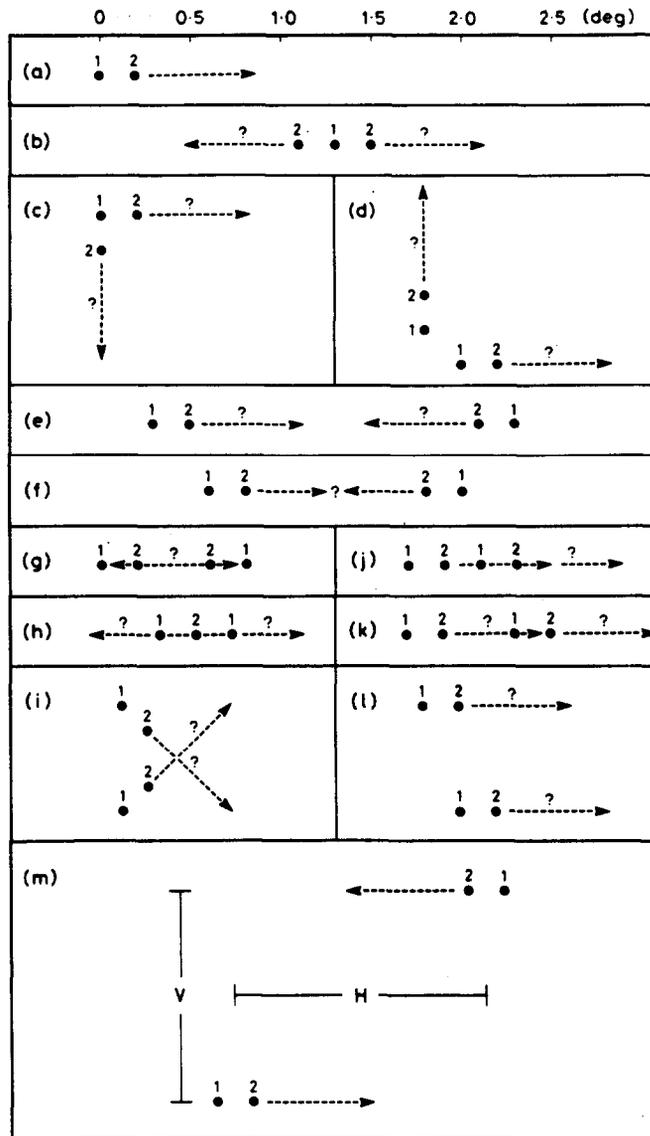


Fig. 1. Spatial arrangements of the stimulus flashes (indicated by the small solid circles, separated by 0.2° , dia 0.1°) generating the fine-grain movement illusion in the peripheral field (about 10° eccentricity). Numbers (1 or 2) over dots denote (1) flashed first, (2) flashed 50 msec later. In (a) and (m), dashed lines with arrowheads indicate qualitatively the perceived movement illusion. In (b)–(l), dashed lines with question marks show the illusion expected if superposition applies; for non-codirectional dot-pair stimuli within 0.5° of one another, (b)–(i), superposition does not occur (see text). In (m), two illusions coexist and can be compared as the horizontal distance H between stimulus pairs is varied. V, vertical separation which, if greater than about 1° , permits simultaneous perception of two non-codirectional, non-interacting illusions. Vertical scale same as horizontal.

unless they are codirectional—are interesting because existing theories of the illusion in terms of neural arrays (von Seelen, 1973) do not accommodate them. On the other hand, in the arrangement of Fig. 1(m), with the vertical separation V set at a degree or more, the two illusions were glimpsed simultaneously and appeared not to interact for any value of the horizontal separation H. This result allowed us to proceed with the above-mentioned measurement of the visual-field coordinates of the illusion.

EXPERIMENT 2:
EXTENT AND POSITION OF THE FGMI AS A
FUNCTION OF STIMULUS ECCENTRICITY

To describe the method, we must first anticipate the results by explaining that the visual-field position at which the movement illusion appears to start does not (as naively schematized in Fig. 1) coincide with the site of the dot stimuli. In Fig. 2, therefore, each of the two illusory trajectories, induced as in Fig. 1(m), is

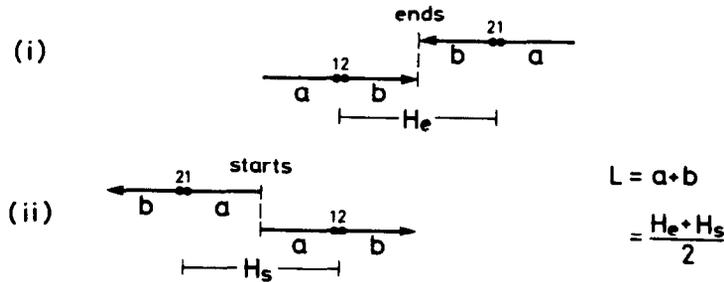


Fig. 2. Comparison procedure that measures the illusion. The dot-pair stimuli are shown by the small discs and the arrows represent the illusions. (i) Perceived end points of illusions aligned vertically to determine H_e . (ii) Perceived starting points of illusions aligned vertically to determine H_s . The extent L of the illusion is given by the formula shown.

represented for clarity in terms of a part a , between the start of the movement and the dots, and a part b , between the dots and the end of the movement.

Our method, then, is to find—by adjusting H —the setting H_e (Fig. 2 [i]) at which subjects indicate that the *ends* (denoted by arrowheads) of the two simultaneous illusions are just one above the other; similarly, the separation H_s (Fig. 2 [ii]) is found for the vertical alignment of the *starts*. Clearly, if the two illusions have identical shapes, the extent L is given by $a + b = (H_e + H_s)/2$, and the positions of the starts and ends (relative to the dot pairs) by $H_s/2$ and $H_e/2$, respectively.

At each eccentricity of the stimuli (from about 10° to 24° left of the fixation point) estimates of H_e and H_s were obtained by a method of ascending and descending limits. Subjects found this procedure easy to follow and results were reproducible. The starting value of H for each set of transits was randomized. H was then varied in 0.1° ascending (or descending) steps over a wide range; at each setting subjects judged (forced-choice) whether the “start” (and in other runs the “end”) of the upper illusion was to the right or to the left of the “start” (or “end”) of the lower illusion. The H settings at which the transition from “right” to “left” response occurred (points of vertical alignment as described above) were usually repeatable to within about 0.1° after a few practice runs. Values of the stimulus eccentricity θ are specified for the fixed dot pair (lower pair in Fig. 1[m]), and the upper pair was moved to vary H . (The vertical separation V of the dots was fixed at 1.2° throughout these measurements.) Because the measured extent L of the illusion varies with θ , a systematic error is thereby introduced which is here about 3% at most. The points plotted in Fig. 3 are determined by averaging H values for the last 4 or 6 transits in each run. Reproducibility of successive measurements of L values was within 5% during a session, about 5% on successive days and about 25% if weeks intervened.

Small adjustments of the intensity of the stimuli to provide at each eccentricity θ identical levels above increment threshold did not alter the results appreci-

ably. There is, however, a bias inward to the fovea in subjective extent of the illusion which is discernable at $\theta \geq 15^\circ$. For the large θ values, subjects estimate the ratio $L_{\text{inward}}/L_{\text{outward}}$ in the range 1.25–2; the effect of the matching procedure is to produce L values which are an average of the two. (The appearance of a single dot flashed peripherally differs greatly from that due to the dot pairs flashed in either inward- or outward-going sequence.) Reversing the standard procedure to find H_e and H_s , i.e. fixing the outward-going dot-pair and moving the inward-going dot-pair, does not change the computed L values by more than about 15%.

Figure 3(i) summarizes the measured trajectories with respect to the visual field position of the corresponding dot-pairs (horizontal arrows; all determinations for 3 subjects at 4 eccentricities). In these conditions, the trajectories are nearly centred about their dot pairs. A second significant finding is that the extent L (length of the arrows in Fig. 3[i]) plotted in Fig. 3(ii) varied systematically from about 2° to 6° as stimulus eccentricity was increased from about 10° to about 24° . The solid line in Fig. 3(ii) is a linear least-squares representation of the data (intercept 0.28° , slope 0.23, $r = 0.89$).

DISCUSSION

What do these psychophysical results tell us about their neural correlates? Previous observations have indicated that the spatial characteristics of the FGMI are determined at a stage of visual processing central to the retina. Since the illusion can be elicited dichoptically (Biederman-Thorson *et al.*, 1971), it cannot depend entirely on retinal interactions. Moreover, when the stimulus pair straddles the vertical midline, the illusion vanishes (Biederman-Thorson *et al.*, 1971), indicating that the underlying neural responses must occur in the same hemisphere, presumably in an area receiving binocular inputs such as the striate cortex.

One hypothesis—implicit in the theoretical study by von Seelen (1973)—has been that the “seen moving dot” may reflect the sequential activation of cells

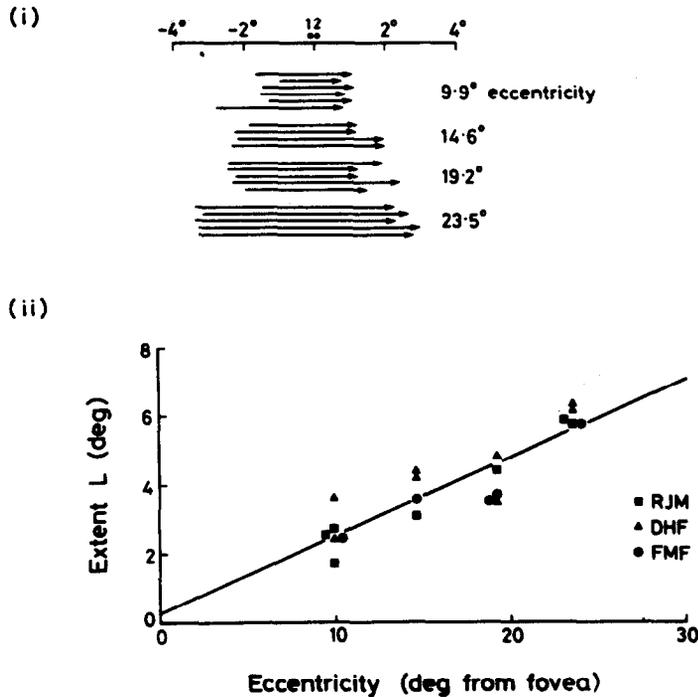


Fig. 3. Field position of the illusion with respect to the two-dot stimulus and extent of the illusion determined at various eccentricities of the stimuli in the field. (i) The arrows' tails and heads represent respectively the starts and ends of the illusions (relative to the dot-pair) computed from the measurements *a* and *b* obtained by the procedure indicated in Fig. 2. (ii) Extent *L* of the illusion (symbols) plotted against stimulus eccentricity. The solid line is a linear least-squares representation of the data (intercept 0.28°, slope 0.23, $r = 0.89$).

within a central array of movement-sensitive cells. An implication of this notion is that the extent *L* of the FGMI should be related to the region of a central visual map spanned by these discharging cells. One

estimate of the size of this region of activation can be obtained by multiplying *L* by the appropriate magnification factor, *M* (mm of central map per degree of visual angle; Daniel and Whitteridge, 1961). Assuming for the moment that the critical events occur in striate cortex, we may use estimates of *M* derived by Cowey and Rolls (1974) from human phosphene measurements of Brindley and Lewin (1968). When the extent *L* of the FGMI obtained in Experiment 2 is multiplied by the corresponding value of *M*, the product is a relatively constant cortical distance of about 3 mm (Table 1).

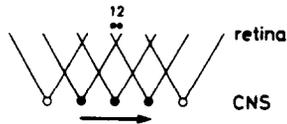
Table 1. Relationship between stimulus eccentricity, extent *L* of the FGMI and striate-cortex magnification factor *M*

Eccentricity (deg)	<i>L</i> (deg)	<i>M</i> (mm deg ⁻¹)	<i>M</i> × <i>L</i> (mm)
9.9	2.6	1.33	3.5
14.6	3.8	0.94	3.6
19.2	4.0	0.73	2.9
23.5	6.0	0.60	3.6

It is known that spatial acuity and some contrast sensitivity functions which vary with eccentricity in the visual field also become invariant when multiplied by the appropriate *M* (Cowey and Rolls, 1974; Virsu and Rovamo, 1979; Rovamo and Virsu, 1979). The 3-mm cortical "unit" defined by the FGMI is, however, far larger than that derived from these spatial acuity measures (e.g. 0.084 mm for minimum angle of resolution, see Cowey and Rolls, 1974; compare Virsu and Rovamo, 1979; Rovamo and Virsu, 1979), even though the spatial separation of the two dots of the FGMI stimulus is below the spatial resolution limit (see Schwartz, 1980).

L: means of data in Fig. 3(ii); *M*: see Cowey and Rolls, 1974; *M* × *L*: estimated cortical span of the illusion. The values of *M* were obtained from a linear regression on the data of Fig. 3A (filled circles) in the paper by Cowey and Rolls (1974). The equation of the regression line (with *M* in mm deg⁻¹ and eccentricity θ in deg) is $1/M = 0.067\theta + 0.091$, $r = 0.84$. The data given by Cowey and Rolls are the most direct estimates available of *M* for the human visual system, being derived from the phosphene data of Brindley and Lewin (1968) for mainly the lower left octant of the visual field. An indirect estimate of *M* may be obtained by making use of data on primate retinal ganglion-cell densities, receptive-field densities, and human visual acuity. The values of *M* for the nasal field obtained by Drasdo (1977) who used such an approach yielded values of *M* × *L* close to 5 mm. A similar method was used by Rovamo and Virsu (1979) whose values of *M* for the nasal field also yielded values of *M* × *L* close to 5 mm.

Significantly, the region of striate cortex which responds to a given point stimulus, the neural point image, is about 3 mm dia in primates (see McIlwain, 1976); this translationally invariant distance is close



Overlapping fields

Fig. 4. Spatial relationship of the fine-grain stimulus (1, 2) and the overlapping receptive fields of a hypothesized central array of movement-sensitive neurones. If response latency varies with stimulus position in the receptive field, then a single fine-grain stimulus could produce sequential activation (arrow) along a row of cells, with length determined by receptive-field size and overlap.

to that obtained by M-scaling the FGMI. This distance also corresponds approximately to the lateral extent of direct intracortical connections in macaque visual cortex (Fisken *et al.*, 1973).

With these ideas in mind, we have considered two possible explanatory schemes for the FGMI. We stress that neither is complete, and that both encounter difficulties, currently unresolvable, in the details of the required filtering. The first supposes that the two flashed dots of the FGMI stimulus produce displaced, but overlapping, point images in the cortex. The start and end points of the illusory movement inferred (by the brain) from the edges of this discharging array would correspond closely (after M-scaling) to the dimensions of the point image. The second scheme is sketched in Fig. 4. Here the two-dot stimulus is assumed to fall within the overlapping receptive fields of a number of cortical movement-sensitive cells. The inferred extent of the illusion is determined by the spatial range of cortical cells stimulated, which is again close to the dimensions of the point image. Which, if either, of these two schemes is correct is unlikely to be determined by psychophysical experiments of the present kind. In any event, the established properties of the FGMI reported here and elsewhere (Biederman-Thorson *et al.*, 1971; Foster, 1977) do suggest predictions which might be tested electrophysiologically by recording from central movement-sensitive cells with two-point sequential stimulation of the retina. The critical events underlying the FGMI of course need not occur in striate cortex, but in any homothetically related structure.

Independent of the site of generation of the FGMI, the results of Experiment 1 place specific constraints on any model of movement detection involving cooperative interactions within arrays of sequentially activated neurones. These results may have particular relevance to the problem of extracting global motion signals from sequentially presented random-dot patterns (Braddick, 1974; Morgan and Ward, 1980). In such presentations, each dot in one pattern may be paired with each of several dots in the other pattern: in principle, such pairs can generate differently directed local motion signals. The results illustrated in Figs 1(b)–(l), showing that all FGMI close to each

other interfere destructively unless they are codirectional, suggest that there may be powerful local "disambiguating" effects which elicit a well-defined global-motion percept in response to sequentially presented random-dot patterns.

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