

# ROD- AND CONE-MEDIATED INTERACTIONS IN THE FINE-GRAIN MOVEMENT ILLUSION

DAVID H. FOSTER<sup>1</sup>

Optics Section, Department of Physics, Imperial College of Science and Technology,  
London SW7 2BZ, England

(Received 12 March 1976)

**Abstract**—The sequence in which two small, spatially unresolved spots of light are flashed in the periphery of the visual field can be determined by means of a "fine-grain" movement illusion. The illusion can be produced not only by rod-rod and by cone-cone stimulation, but also by rod-cone stimulation. Dynamics of the illusion are obtained by sequence-discrimination experiments for each of these three stimulus conditions.

**Key Words**—rod-cone interaction; movement illusion.

## INTRODUCTION

The rapid sequential flashing of two small, closely spaced spots of light in the periphery of the human visual field can induce an extrapolated illusion—a single spot appears to move in the direction defined by the stimulus sequence (Thorson, Lange and Biederman-Thorson, 1969). It was shown by Thorson *et al.* (1969) and Biederman-Thorson, Thorson and Lange (1971) that the illusion can provide reliable indication of the sequence direction even when the spatial separation of the spots is such that if presented simultaneously they are visually indistinguishable from a single spot. By doing sequence-discrimination experiments, the authors were therefore able to measure objectively the dynamics of the phenomenon. This "fine-grain movement illusion"—shown by Biederman-Thorson *et al.* (1971) to be obtainable in stabilized vision—is phenomenologically distinct from the apparent movement effects usually observed with sequences of widely spaced resolvable stimuli (Kolers, 1972).

It was suggested by Thorson *et al.* that by choosing the spectral compositions and intensities of the stimuli so that each spot is "seen" solely by a particular spectral class of photoreceptor, one could determine whether different receptor systems act independently in the production of the illusion. The present study considers fine-grain interactions within and between the rod and red-sensitive cone systems.

## METHODS

### Stimuli

The fine-grain stimulus was formed by two 20' discs, one above the other, located 16° to the left of a small fixation target. The centre-to-centre separation of the spots was varied from about 4.5' to about 9'. Each spot was either green (499 nm) or red (>660 nm) and each was exposed for 25 msec. The stimuli were presented to the

right eye and in all but one experiment were set at absolute luminance threshold.

### Apparatus

The stimuli were produced by a standard 4-channel Maxwellian-view optical system with a single tungsten-halogen lamp. The system is identical with that used by Foster (1976). Two channels gave rise to the stimulus spots, another to the fixation target, and the fourth to a uniform adapting field. The stimuli were viewed through a 2-mm artificial pupil. Special precautions were taken to minimize instrumental stray light. The exposure times of the spots were controlled by electromagnetic shutters driven by an electronic timer. Rise and fall times of each of the flashes did not exceed 2 msec. The luminance of the stimuli was adjusted with neutral density filters and with a compensated neutral density wedge. The colour temperature of the stimulus fields, without the colour filters in place, was 3000°K. The spectral compositions of the stimuli were controlled by a 499-nm interference filter (Balzers, type B20; peak wavelength 499 nm, half bandwidth 4 nm) and a long pass gelatin filter (Ilford, No. 609; cut-on point 660 nm).

An i.r. eye-position sensor, similar to that described by Stark, Vossius and Young (1962) and Brown (1972), was fitted in the eyepiece. The output signal from the device, indicating the extent of horizontal eye-movement, was displayed on an oscilloscope for inspection by the experimenter.

### Procedure

All observation sessions, except those concerned with the time course of adaptation, were preceded by a half-hour period of dark-adaptation. The subject, using a dental bite-bar, viewed the fixation target with the right eye.

**Recovery curves and directional sensitivity.** To establish the degree of specificity of the green and red spot stimuli for the rod and cone systems respectively, determinations were made of the time course of adaptation for each stimulus and their relative directional efficiency, i.e. the Stiles-Crawford effect. As in a previous investigation (Foster, 1976), the Stiles-Crawford effect was measured by a comparison method. The two spot stimuli were spatially superimposed and presented for 300 msec each, in a 3-sec cycle; the luminance of the green spot was fixed 0.1 log units above absolute threshold, and, for each pupil entry position, the luminance of the red spot adjusted so that the two stimuli matched in brightness.

<sup>1</sup> Present address: Dept. of Communication, University of Keele, Keele, Staffs., ST5 5BG, England.

*Sequence-discrimination performance.* Fine-grain dynamics were measured as follows. The magnitude of the time-lag between the onsets of the two stimulus spots was set at one of eight values between 5 and 1000 msec. For each setting, five "upward" and five "downward" spot pairs were presented in random order to the subject, who indicated his estimate ("forced-choice") of the actual direction of the sequence on each occasion. Subjects based their estimates on the direction of the movement illusion if it occurred. Observations were carried out in blocks of trials, with each time-lag setting occurring once only in each block and the order of selection of the settings randomized within each block. Each block was preceded and followed by a determination of the spatial resolvability of the two simultaneously presented spots. In each such determination, the subject was presented with a randomly ordered sequence of ten stimuli, half of which were the two simultaneously presented spots and half of which were single spots each of luminance twice that of each of the spots in the two-spot case; at each presentation, the subject indicated his estimate of the actual stimulus form.

For each set of experimental conditions (spectral composition of the stimuli, centre-to-centre spacing, etc.) each subject carried out either four or six blocks of trials, with two blocks usually constituting one session. Experimental conditions were not varied within blocks, and, where appropriate, their order of selection within sessions was balanced across sessions.

The subject's fixation was monitored throughout the observation period and stimuli were presented only when fixation was steady. The subject was cued before each stimulus presentation.

#### Subjects

There were two observers: GJB and FMF. Each had normal colour vision and could accommodate the stimuli with the naked eye. Each was familiar with the experimental method. Neither was aware of the purpose of the experiment.

## RESULTS

### Rod- and cone-specificity

Figure 1 (a) shows the time course of adaptation with the green (499 nm) and red (>660 nm) 25-msec spot stimuli, following 2-min white-light adaptation to 6.3 log td at 3000°K. The curve for the green stimulus exhibits the characteristic cone-to-rod transition at about 12 min, and for both subjects the eventual rod-mediated threshold is more than 1.5 log units below the cone plateau. Since the stimuli in the fine-grain experiments are presented at absolute luminance threshold, it is only the rod system that is excited by the green stimulus. The curve for the red stimulus does not depart systematically from flatness after about 6 min. Evidence for the actual cone-preferentiality of the red stimulus, however, comes from the directional-sensitivity data of Fig. 1 (b). The luminous efficiency of the red spot relative to the green spot is plotted against the distance  $r$  of the pupil point of entry of the stimulus rays, with the point  $r = 0$  corresponding to the optimal position. The variation in the relative efficiency  $\eta$  with  $r$  is uniquely associated with the red stimulus, since the green reference stimulus, set 0.1 log units above absolute threshold, is rod-specific. The data for both observers show a clear Stiles-Crawford effect. [The smooth curve is defined by the formula  $\eta = 10^{-0.05r^2}$  (Stiles and Crawford, 1933; Stiles, 1939).] It follows (Flamant and Stiles, 1948) that in the fine-grain exper-

iments the red stimulus is on average below rod threshold by not less than 0.5 log units for GJB and 0.3 log units for FMF. Nevertheless, it is possible that because of variations in individual threshold settings of the red stimulus (S.D. is 0.1 log units for GJB and 0.15 log units for FME) significant rod excitation occurs in a small proportion of the sequence-discrimination experiments involving the red stimulus. It is shown later that if such excitation does take place, it is not an effective factor in determining the fine-grain dynamics.

### Rod-rod and cone-cone fine-grain interaction

Figures 2 (a)-(d) show the results of the fine-grain experiments for the green-green and for the red-red stimulus pairs, with each stimulus spot set at absolute luminance threshold. The proportion of trials in which the direction of the stimulus sequence is correctly estimated is plotted against the delay in onsets of the two flashes, with the vertical bars showing  $\pm 1$  binomial S.E.M. The spatial resolvability of the two spots, when presented simultaneously, is indicated by an arrow against the ordinate. The mean centre-to-centre separation of the two spots is 9', in each case. As expected (Thorson *et al.*, 1969; Biederman-Thorson *et al.*, 1971), the illusion fails at very short and at very long onset delays. There is a range of time-lags, however, usually between 20 and 200 msec, for

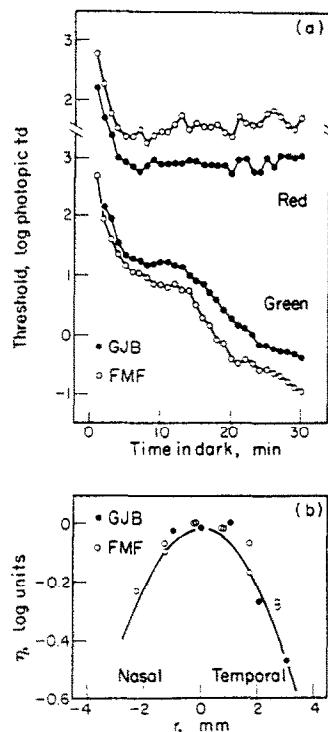


Fig. 1. (a) Dark-adaptation curves for the red (>660 nm) and green (499 nm) 25-msec spot stimuli. Each point represents a single threshold measurement obtained by the method of adjustment. (b) Relative luminous efficiency  $\eta$  of the red spot stimulus as a function of distance  $r$  of the pupil point of entry from the optimal position. Each point represents the mean of four measurements, each obtained by the method of adjustment. The smooth curve is defined by the formula  $\eta = 10^{-0.05r^2}$ . Observers: FMF and GJB.

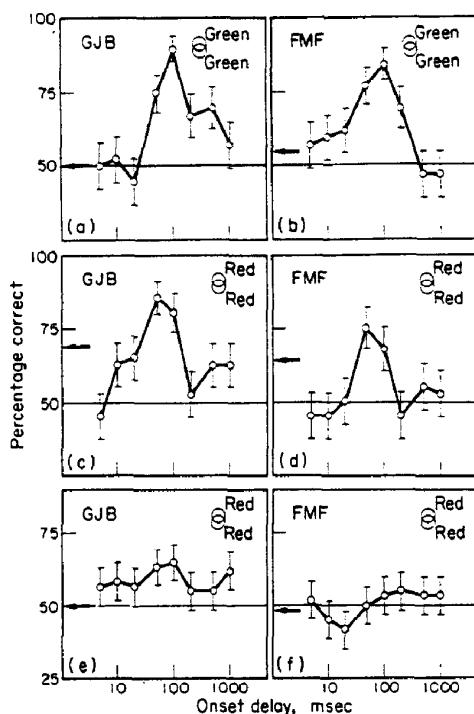


Fig. 2. Sequence-discrimination performance as a function of stimulus onset delay, for (a) and (b) both spots green (499 nm), and (c) to (f) both spots red (>660 nm). Each point represents the mean percentage of correct estimates of sequence direction ("upward" or "downward") at a fixed time-lag between onsets, for either four or six sets of 10 randomly ordered trials consisting of 5 "upward" and 5 "downward" spot-pair presentations. Total number of sequence estimates per point is 40 in (a)-(d), and 60 in (e) and (f). The vertical bars correspond to  $\pm 1$  binomial S.E.M. The mean centre-to-centre separation of the two spots is 9' in (a)-(d), and 4.5' in (e) and (f). In each case, the spatial resolvability of the two simultaneously presented spots is indicated by the arrow against the ordinate. Each resolvability score is the mean percentage of correct estimates of stimulus form ("one spot" or "two spots") for either eight or 12 sets of 10 randomly ordered trials consisting of 5 two-spot stimuli and 5 one-spot stimuli. Total number of resolution estimates is 80 in (a)-(d) and 120 in (e) and (f). Spatial resolvability is not significant ( $P > 0.1$ ) in (a), (b), (e) and (f), and is significant ( $P < 0.01$ ) in (c) and (d). Observers: GJB and FMF.

which the illusion can occur and can give rise to reliable sequence-discrimination performance. Consider first the green-green stimulus data [Figs. 2 (a) and (b)]. These reflect rod function only. In spatial resolution tests, the two spots can be distinguished from the one by GJB on about 50% of occasions and by FMF on about 55% of occasions. Neither score is significantly different from chance level ( $P > 0.1$ ). In the sequence-discrimination tests, however, the proportion of trials in which stimulus direction is correctly estimated reaches about 90% at 100 msec for GJB and about 85% at 100 msec for FMF. Both results are highly significant ( $P < 0.001$ ).

With the red-red stimulus pair [Figs. 2 (c) and (d)], the two simultaneously presented spots can be distinguished from the one by GJB on about 70% of occasions and by FMF on about 65% of occasions.

Although resolvability of the spots is for both subjects significant ( $P < 0.01$ ), correct estimation of sequence direction is, at best, no better than with the green-green stimulus pair. For FMF, the peak performance score is, in fact, about 10% lower [compare Fig. 2 (d) with (b)]. Note that with the change in stimulus composition from green-green to red-red, there is, for both observers, a shift in the performance curve towards shorter onset delays. From the dark-adaptation and directional sensitivity data, it is evident that the average level of rod excitation with the red-red pair is lower than that with the green-green pair. But Biederman-Thorson *et al.* (1971) have shown that a reduction in stimulus luminance is associated with a shift in the dynamics of the illusion towards longer onset delays. The notion that there is an effective rod involvement in the production of the illusion with the red-red stimulus pair may thus be rejected.

The cone-mediated performance does not improve with a reduction in the spatial separation of the spots [see Figs. 2 (e) and (f)]. With a mean centre-to-centre spacing of 4.5', where spatial resolvability of the red spots is for both observers not significant ( $P > 0.1$ ), sequence-discrimination scores approach chance level ( $0.1 > P > 0.01$ ).

#### *Effect of background luminance on fine-grain characteristics*

Under light-adapted conditions, the cone-mediated performance at sequence discrimination can increase greatly, without any corresponding improvement in visual acuity. Figure 3 shows performance at estimating sequence direction with the red-red stimulus pair superimposed on a bright blue conditioning field. The mean centre-to-centre spacing of the spots is 9'. The illumination of the conditioning field (3.4 log td) and spectral composition (determined by an interference filter: Balzers type B40, peak wavelength 465 nm, half bandwidth 8 nm) were such that the stimuli, presented at increment threshold, excited only red-sensitive cones (Wyzecki and Stiles, 1967). The equivalent data for the zero-background situation are reproduced on the same figure for comparison. Data are for one observer only (FMF). The proportion of trials in which direction is correctly estimated in the bright background case reaches the highly significant level ( $P < 0.001$ ) of 95% at 20 and 50 msec onset delays; under dark-adapted conditions, scores fail to exceed 75%. The spatial resolvability of the two simultaneously presented spots in the bright background case remains not significant ( $P > 0.1$ ).

#### *Rod-cone fine-grain interaction*

That the rod and cone systems can interact with each other in the production of the illusion is evident from the data of Figs. 4 (a) and (b). The stimuli consisting of one red spot and one green spot were presented at absolute luminance threshold to the dark-adapted eye. With a mean centre-to-centre separation of 9', the spatial resolvability of the spots is for both observers not significant ( $P > 0.1$ ). Sequence-discrimination performance, however, reaches highly significant levels ( $P < 0.001$ ) at onset delays of 100 msec for GJB [Fig. 4 (a)] and 50 msec for FMF [Fig. 4 (b)]. The temporal dependencies of the interaction for the two observers are quite different, and for GJB

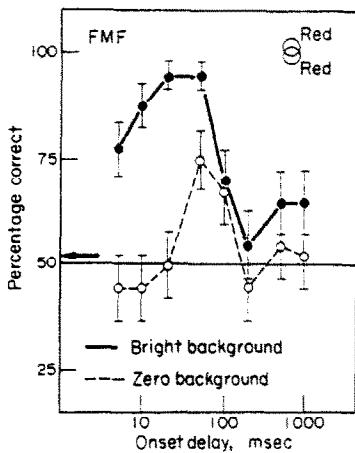


Fig. 3. Effect of background luminance on the variation of sequence-discrimination performance with stimulus onset delay. The continuous line shows data obtained with a bright blue (465 nm) conditioning field and both spots red ( $> 660$  nm), each at increment threshold. Corresponding data obtained with no background [from Fig. 2 (d)] are shown by the broken line. In both cases, the number of sequence estimates per point is 40; the vertical bars correspond to  $\pm 1$  binomial S.E.M. The mean centre-to-centre separation of the two spots is  $9'$ . The spatial resolvability of the two simultaneously presented spots in the bright background case is indicated by the arrow and is not significant ( $P > 0.1$ ). Observer: FMF.

there is a sharp fall in discrimination ability at 50 msec. Both subjects reported that at some onset delays the illusion was stronger in one direction than in the other, consistent with the response due to the green stimulus lagging behind that due to the red stimulus. This difference in response latencies, characteristic of the rod and cone systems (McDougall, 1904; Arden and Weale, 1954; Frumkes, Sekuler, Barris, Reiss and Chalupa, 1973), was estimated by the apparent-movement method (Exner, 1875; Arden and Weale, 1954; Roufs, 1974). The red and green spots were separated until they were spatially resolvable and then presented at absolute luminance threshold with systematically increasing or decreasing onset delays. The retinal location of the stimuli was the same as that for the fine-grain experiments. Classical apparent movement was elicited at sufficiently long positive and negative time-lags and the relative rod latency was taken as the mean of the "null" values<sup>2</sup>. The relative rod latency for GJB was thus evaluated as 60 msec and for FMF as 70 msec (S.D.  $< 10$  msec for each). The original fine-grain sequence-discrimination experiment was then repeated with the red member of the red-green pair given a fixed additional delay equal to the estimated relative rod latency. Figures 4 (c) and (d) show the results. For both subjects, there is a general improvement in sequence-discrimination ability, with, in particular, performance at 50 msec by GJB [Fig. 4 (c)] increasing from chance level to about 80% and performance at 100 msec by FMF [Fig. 4 (d)] increasing from chance level to about 75%. The spatial resolvability of the two simul-

taneously presented spots remains not significant ( $P > 0.1$ ). The temporal dependencies of the interaction for the two subjects are fairly similar; the differences found in the uncompensated situation [Figs. 4 (a) and (b)] may reflect different strategies employed by the subjects in responding to the asymmetric fine-grain illusions.

#### DISCUSSION

The main finding of the present investigation is that the fine-grain movement illusion can be induced not only by cone-cone and by rod-rod excitation, but also by rod-cone excitation. The after-flash effect (Stigler, 1910; Alpern, 1953), in which the brightness of a flash of light is reduced when it is followed by a second flash presented to an adjacent region of the retina, occurs in a similar range of interflash intervals and spatial separations; it also has similar dichoptic and peripheral vs central (position on the retina) properties. For these reasons, Thorson *et al.* (1969) hypothesized that the two phenomena may have a common basis. They suggested that the hypothesis could be tested by the experiments presented here, since Alpern (1965) and Alpern and Rushton (1965) had shown in their experiments on the after-flash effect that each of the  $\pi$  mechanisms acted independently. Nevertheless, the present results do not disprove the hypothesis since it has been demonstrated (Foster, 1976) that under suitable conditions interaction between rod and cone systems in the after-flash effect can in fact be obtained. Rod-cone interaction has also been shown to occur in the production of some colour-contrast effects (Willmer, 1949; McCann

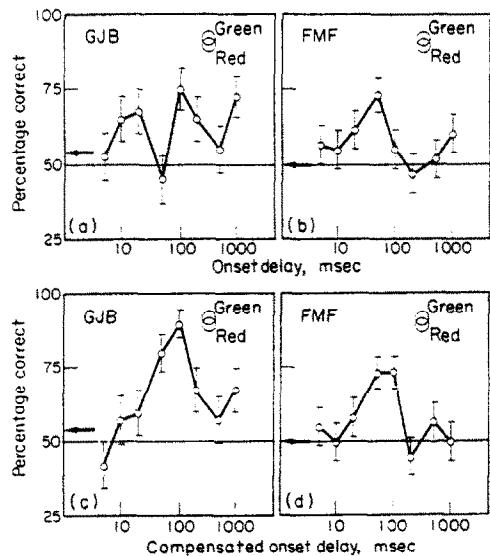


Fig. 4. Sequence-discrimination performance as a function of stimulus onset delay with one spot red ( $> 660$  nm) and one spot green (499 nm). Data in (a) and (b) are obtained without compensation for relative rod latency. Data in (c) and (d) are obtained with compensation; the additional delay given to the red stimulus is 60 msec for GJB and 70 msec for FMF. Number of sequence estimates per point is 40 in (a) and (c), and 60 in (b) and (d). The vertical bars correspond to  $\pm 1$  binomial S.E.M. The mean centre-to-centre separation of the spots is  $9'$ . The spatial resolvability of the two simultaneously presented spots is indicated by the arrow and in each case is not significant ( $P > 0.1$ ). Observers: GJB and FMF.

<sup>2</sup> Classical apparent movement can also be obtained by interactions between the different cone systems  $\pi_1$ ,  $\pi_4$  and  $\pi_5$  (Foster and Idris, 1974).

and Benton, 1969; Stabell and Stabell, 1975). in the cancellation of flicker induced by a mesopic time-varying stimulus (MacLeod, 1972), and in the modification of test-flash thresholds measured against various spatially superimposed conditioning fields (Frumkes *et al.*, 1973; Makous and Boothe, 1974). Certain grating threshold measurements (Sternheim and Glass, 1975) and the "fluttering-heart" illusion (Von Grünau, 1976) are also suggestive of rod-cone interaction. Retinal processes that might subserve such interactions have been described by Gouras and Link (1966), Barlow and Levick (1968), Steinberg (1969), Ruddock and Svaetichin (1973), Fain (1975), and Rodieck and Rushton (1976). [See Ronchi (1975) for additional references.]

Biederman-Thorson *et al.* have indicated that the fine-grain experiment is analogous to the experiments of Barlow and Levick (1965) on the two-spot stimulation of directionally selective movement-detecting ganglion cells in the rabbit retina. If the fine-grain illusion is interpreted as the result of the two-spot stimulation of movement-detecting mechanisms in the human visual system, and Biederman-Thorson *et al.* have given data supporting this notion, then the results of the present study imply that these mechanisms can give reliable information even at extremely low luminance levels. A general scheme capable of relating the illusion to patterns of neural activity has been put forward by von Seelen (1973), who considered the excitation of a linear homogeneous nerve net with facilitatory and inhibitory components. A model for real-movement detection that may also be relevant has been described by Foster (1971a,b).

*Acknowledgements*—I thank Dr. W. S. Stiles for valuable advice and Drs. J. Thorson and M. Biederman-Thorson for many helpful discussions and for critical reading of the manuscript.

#### REFERENCES

- Alpern M. (1953) Metacontrast. *J. opt. Soc. Am.* **43**, 648–657.
- Alpern M. (1965) Rod-cone independence in the after-flash effect. *J. Physiol., Lond.* **176**, 462–472.
- Alpern M. and Rushton W. A. H. (1965) The specificity of the cone interaction in the after-flash effect. *J. Physiol., Lond.* **176**, 473–483.
- Arden G. B. and Weale R. A. (1954) Variations of the latent period of vision. *Proc. R. Soc., Lond.* **B142**, 258–267.
- Barlow H. B. and Levick W. R. (1965) The mechanism of directionally selective units in rabbit's retina. *J. Physiol., Lond.* **178**, 477–504.
- Barlow H. B. and Levick W. R. (1968) The Purkinje Shift in the cat retina. *J. Physiol., Lond.* **196**, 2P–3P.
- Biederman-Thorson M., Thorson J. and Lange G. D. (1971) Apparent movement due to closely spaced sequentially flashed dots in the human peripheral field of vision. *Vision Res.* **11**, 889–903.
- Brown B. (1972) Dynamic visual acuity, eye movements and peripheral acuity for moving targets. *Vision Res.* **12**, 305–321.
- Exner S. (1875) Experimentelle Untersuchung der einfachsten psychischen Prozesse. *Pflügers Arch. ges. Physiol.* **11**, 403–432.
- Fain G. L. (1975) Interactions of rod and cone signals in the mudpuppy retina. *J. Physiol., Lond.* **252**, 735–769.
- Flamant F. and Stiles W. S. (1948) The directional and spectral sensitivities of the retinal rods to adapting fields of different wave-lengths. *J. Physiol., Lond.* **107**, 187–202.
- Foster D. H. (1971a) The response of the human visual system to moving spatially periodic patterns: further analysis. *Vision Res.* **11**, 57–81.
- Foster D. H. (1971b) A model of the human visual system in its response to certain classes of moving stimuli. *Kybernetik* **8**, 69–84.
- Foster D. H. and Idris I. I. M. (1974) Spatio-temporal interaction between visual colour mechanisms. *Vision Res.* **14**, 35–39.
- Foster D. H. (1976) Rod-cone interaction in the after-flash effect. *Vision Res.* **16**, 393–396.
- Frumkes T. E., Sekuler M. D., Barris M. C., Reiss E. H. and Chalupa L. M. (1973) Rod-cone interaction in human scotopic vision—I. Temporal analysis. *Vision Res.* **13**, 1269–1282.
- Gouras P. and Link K. (1966) Rod and cone interaction in dark-adapted monkey ganglion cells. *J. Physiol., Lond.* **184**, 499–510.
- Kolers P. A. (1972) *Aspects of Motion Perception*. Pergamon Press, Oxford.
- MacLeod D. I. A. (1972) Rods cancel cones in flicker. *Nature, Lond.* **235**, 173–174.
- Makous W. and Boothe R. (1974) Cones block signals from rods. *Vision Res.* **14**, 285–294.
- McCann J. J. and Benton J. L. (1969) Interaction of the long-wave cones and the rods to produce color sensations. *J. opt. Soc. Am.* **59**, 103–107.
- McDougall W. (1904) The sensations excited by a single momentary stimulation of the eye. *Br. J. Psychol.* **1**, 78–113.
- Rodieck R. W. and Rushton W. A. H. (1976) Cancellation of rod signals by cones, and cone signals by rods in the cat retina. *J. Physiol., Lond.* **254**, 775–785.
- Ronchi L. (1975) *150 Years of Rods and Cones. An Annotated Bibliography*. Fondazione "Giorgio Ronchi", Florence.
- Roufs J. A. J. (1974) Dynamic properties of vision—V. Perception lag and reaction time in relation to flicker and flash thresholds. *Vision Res.* **14**, 853–869.
- Ruddock K. H. and Svaetichin G. (1973) Fast and slow components of intracellularly-recorded responses from retinal units of a teleost fish (*Eugerres plumieri*). *Vision Res.* **13**, 1785–1788.
- Seelen W. von (1973) On the interpretation of optical illusions. *Kybernetik* **12**, 111–115.
- Stabell U. and Stabell B. (1975) Scotopic contrast hues triggered by rod activity. *Vision Res.* **15**, 1115–1118.
- Stark L., Vossius G. and Young L. R. (1962) Predictive control of eye tracking movements. *IRE Trans. hum. Factors Electron.* **3**, 52–57.
- Steinberg R. H. (1969) Rod-cone interaction in S-potentials from the cat retina. *Vision Res.* **9**, 1331–1344.
- Sternheim C. E. and Glass R. A. (1975) Evidence for cone and rod contributions to common "adaptation pools". *Vision Res.* **15**, 277–281.
- Stigler R. (1910) Chronophotische Studien über den Umgebungskontrast. *Pflügers Arch. ges. Physiol.* **134**, 365–475.
- Stiles W. S. (1939) The directional sensitivity of the retina and the spatial sensitivities of the rods and cones. *Proc. R. Soc., Lond.* **B127**, 64–105.
- Stiles W. S. and Crawford B. H. (1933) The luminous efficiency of rays entering the eye pupil at different points. *Proc. R. Soc., Lond.* **B112**, 428–450.
- Thorson J., Lange G. D. and Biederman-Thorson M. (1969) Objective measure of the dynamics of a visual movement illusion. *Science, N.Y.* **164**, 1087–1088.
- Von Grünau M. W. (1976) The "Fluttering Heart" and spatio-temporal characteristics of color processing—III. Interactions between the systems of the rods and the long-wavelength cones. *Vision Res.* **16**, 397–401.
- Willmer E. N. (1949) Low threshold rods and the perception of blue. *J. Physiol., Lond.* **111**, 17P.
- Wyszecki G. and Stiles W. S. (1967) *Colour Science*. Wiley, New York.