Chapter 13

Eye Movements and Perceived Visual Direction

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With 19 Figures

Contents

I. Introduction

The implicit assumption that visual perception is not susceptible to influences from extraretinal sources[1] has held extremely well in the areas of color vision, contour perception, and intensity discrimination. It has permitted the development of theoretical models of considerable generality for treatment of psychophysical phenomena in these areas that are based essentially on reasonable inferences from present knowledge regarding the neurophysiology, photochemistry, and neuroanatomy of the primary visual projection system. As will be indicated below, where this assumption can be reasonably made in the area of space perception some progress has taken place in a search for physiologically-based theoretical mechanisms for treatment of psychophysical data.

On the other hand, many of the most significant phenomena in space perception suggest a relation between visual perception and retinal stimulation that is susceptible to inputs from sources other than light to the retina, and here there is as yet relatively little physiological information to help with the main problems. Perhaps the clearest simple example of such susceptibility is the visual perception of the vertical, where turning an observer's head and body from an upright position to the horizontal in a frontal plane in complete darkness results in an offset of perceived from physical vertical by no more than 10°—15° (cf., AUBERT, 1861; MÜLLER, 1916; WITKIN and ASCH, 1948; BAUERMEISTER, 1964). Allowing a liberal 10° for uncompensated ocular torsion (cf. WOELLNER and GRAYBIEL, 1958; MILLER, 1962; SCHONE, 1962)[2] leaves a rotation of at least 65° between the orientation of a retinal stimulus and its perceived orientation in a frontal plane consequent to head and body turning. At one time or another it has been suggested that influences on visually perceived orientation, motion, direction, position, size or distance — as well as analogous spatial perceptions regarding the body or parts of the body — derive from afferent signals (from extraocular, neck, or trunk musculature, the intrinsic eye muscles, or the vestibular system), or from signals paralleling those which control the relevant muscles.

Closely intertwined with questions of extraretinal influence on visual space perception are the converse questions regarding the influence of visual stimulation on nonvisual perceptions of the body. In addition problems regarding intermodal discrimination (e.g., perception of the relative spatial locations of a visually presented target and an auditorily presented target), and the influence of visual stimulation on control of bodily movement (e.g., manually pointing to a visually presented target) point us toward questions regarding the genesis and nature of relations between the spatial metrics involved in the different avenues by which communication with the environment is carried out.

Limitations of space prevent a comprehensive treatment of all of these problems. Instead, this chapter will center on a treatment of some aspects of visual

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[1] The terms extraretinal source, signal or influence are intended to refer to any channel in which information is not derived from stimulation of the retina by light.

[2] This is a "worse case" calculation; it is not intended to imply that visually perceived orientation does not involve compensation for ocular torsion. If torsion does not occur or is compensated the disparity between orientation of the retinal stimulus and its perceived orientation consequent to head turning alone would be even greater.

discriminations of spatial relations in the frontal plane. Even here the treatment will not be comprehensive, but rather the focus will be on the relation between perceived visual direction and stimulated retinal locus and on some of the ways in which this relation may be modified.

It will be useful to consider first some material regarding local sign in relation to discriminations that are not susceptible to extraretinal influences, at least to a first approximation.

II. Local Signs — Some Basic Considerations

A. Mean Retinal Local Sign

Perhaps the most elementary fact of visual space perception is that the spatial order of stimulus points in the environment remains correctly preserved in perception. Around this central fact has developed the general viewpoint that the visual perception of direction is mediated in the visual neurosensory pathway by a system of local signs that topographically maps locations of retinal stimuli into values of perceived direction. In essence this viewpoint assumes that a foveally fixated point is perceived as lying in what may be called the principal visual direction; an object whose image strikes any other retinal point is then perceived at a distance to the left, right, above, or below this principal direction in accordance with the retinal signal, i.e., the direction and distance values of the stimulated retinal point relative to the fovea (HERING, 1879; LOTZE, 1886). Quite apart from any considerations regarding the neuroanatomical, genetic or developmental basis of such a mapping or its modifiability we shall refer to the perceived visual direction associated with stimulation of a particular retinal point under any particular set of conditions as its local sign.

HERING's (1879) original suggestion regarding local signs attached the spatial quality to the single photoreceptor. However, on this basis alone sensitivity to position could not be finer than a visual angle corresponding to the separation between two adjacent receptors. Since discrimination of vernier offset of two vertical straight lines (Fig. 1 a) yields thresholds as small as 1″ to 2″ of arc in the central fovea (AVERILL and WEYMOUTH, 1925; BERRY, 1948; BERRY, RIGGS, and DUNCAN, 1950) — a dimension that is less than 1/10 the width of a single foveal cone — some further theoretical developments were called for. It was thus suggested that the vernier discrimination is based on the ability of subjects to detect a difference in the mean retinal positional local sign between the two lines[3] (HERING, 1899; ANDERSEN and WEYMOUTH, 1923; WEYMOUTH, ANDERSEN, and AVERILL,

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[3] HERING's (1899) suggestion regarding a mean local sign basis for vernier acuity presumed a regularity of the mosaic of cones and stability of the retinal image which later work showed did not hold. Nevertheless, the assumption that the local signs associated with particular single receptors can "interact" in determining the perceived location of a stimulus is an important precursor to WEYMOUTH's and to MARSHALL and TALBOT's (1942) later mean local sign "scanning" theory of vernier acuity as well as the theoretical suggestions described below. It is worth emphasizing also that these earlier theories assume that the discrimination underlying the report in the vernier task is one of position. WALLS (1943) has taken a similar point of view: "one does not discriminate the gap or offset between the ends of the line, but the difference in *spatial locations* of the lines" (1943, p. 497).

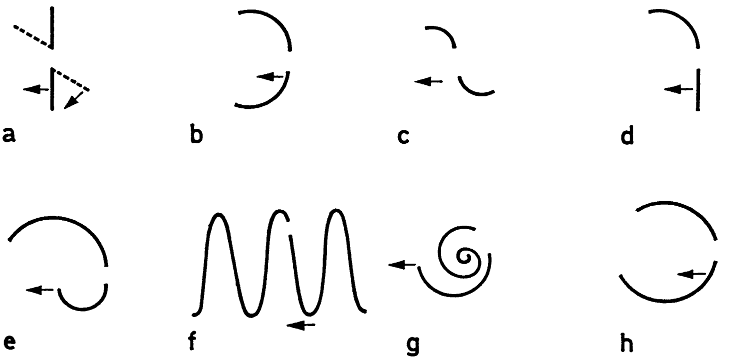

Fig. 1. Some target patterns in which the subject is required to report on alignment of two lines. The arrow in each pattern indicates the dimension along which the experimenter varies the location of the test line during psychophysical experimentation. In (*a*) the solid lines and dashed lines form two separate vernier target patterns. Only one is presented at a time in a given experimental trial; they have been superimposed here for comparison by the reader only (see text). In *a*, *b*, *c*, *d*, and *e* a smooth continuous line can be formed by "filling the gap" with a straight line when the test line is located appropriately. In *h* only a curved line of uniform curvature in the gap will yield a smooth continuous line; in *f* and *g* only a curved line with variable curvature will do so

1923; AVERILL and WEYMOUTH, 1925). This concept assumes that the subject can average over the length of each line the local sign from each cone stimulated at a given moment, and can further average over time the signals from different receptor arrays successively stimulated by the stimulus pattern as a result of the continuous occurrence of involuntary eye movements.

This view of local signs is supported by the fact that vernier acuity improves with increase in line length (AVERILL and WEYMOUTH, 1925; FENDER and NYE, 1962) and increasing exposure duration (AVERILL and WEYMOUTH, 1925; BAKER, 1949; KEESEY, 1960) (Fig. 2). Further, during attempts at steady fixation the median horizontal excursion of the eye in a given time interval grows linearly with interval duration up to at least 1 second, at which point it is about 3′ of arc (RIGGS, ARMINGTON, and RATLIFF, 1954) (Fig. 3). This is roughly six cone diameters, and thus considerable opportunity for temporal averaging over different arrays is possible.

The vernier task is not unique among monocular spatial discriminations in its high precision. For example, thresholds as low as 7″ for the discrimination of width of two narrow rectangles have been reported (VOLKMANN, 1863); [4,5] in addition

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[4] For sufficiently narrow rectangles it is possible that subjects may be making the discrimination on the basis of differences in apparent brightness since stimulus area and luminance have similar influences on apparent brightness.

[5] VOLKMANN (1863, quoted in HELMHOLTZ, 1866) has reported that the average error for discriminating differences in distances between pairs of narrowly spaced parallel vertical lines is proportional to the standard distance over a range from 0.7° to 16.7° $\left(\text{constant of proportionality was between } \frac{1}{80} \text{ and } \frac{1}{100}\right)$; for smaller standard distances (between 2′ and 14′) the average error approaches an asymptote of about 4″. VENIAR (1948) also finds Weber's law to hold for the discrimination of large squares. No information appears to be available on the influence of exposure duration on width discrimination.

when a subject is required to discriminate whether two lines are parallel or not (Fig. 4a) values of Θ (Fig. 4b) as small as 0.1 – 0.2° have been reported for thresholds of relative tilt (Sulzer, 1954; Rochlin, 1955; Andrews, 1967a, b). These reduce to values of differential retinal offset ($W_1 - W_2$, Fig. 4b) as small as 4.5″ (calculated from Andrews' 1967b data) and 7″ (calculated from the data of Sulzer, 1954 and Rochlin, 1955)[6]. Decreased thresholds for the discrimination of parallelness result from increased exposure duration (Andrews, 1967b) and decreased interline separation (Sulzer, 1954; Rochlin, 1955; Andrews, 1967b) as for the vernier task. Increased line length results in a U-shaped function for threshold differential retinal offsets ($W_1 - W_2$) for parallelness (Fig. 5), which is the reverse of the vernier

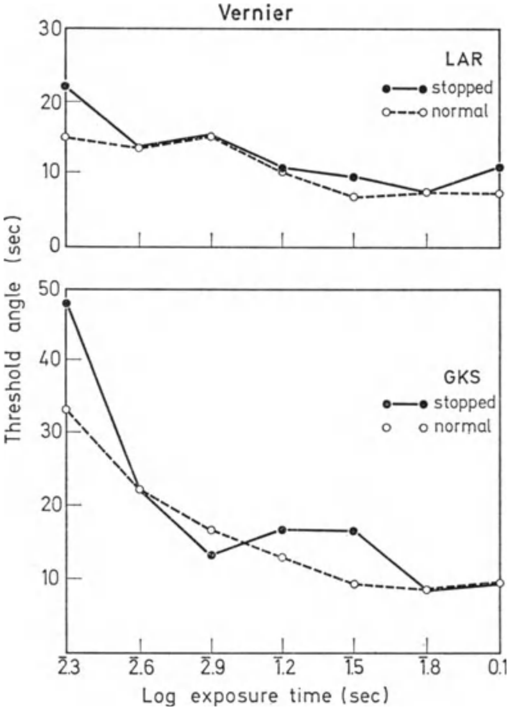

Fig. 2. Threshold curves for vernier discrimination as a function of log exposure time under normal viewing and viewing with a stabilized image for two subjects. (From Keesey, 1960)

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[6] It is worth noting that the stimulus pattern employed for the discrimination of parallelness allows the subject to base his response on a discrimination of length. Thus, for example in the pattern : : the subject may report that the vertical line connecting the two righthand points is tilted counterclockwise relative to the line connecting the two lefthand points when he perceives the horizontal distance between the upper endpoints as smaller than the horizontal distance between the lower endpoints. Similarly, every length discrimination for the horizontal distances with such a pattern could be based on a relative orientation discrimination between the verticals. The point-line and three-point measures of orientation discrimination and partition measurement of length discrimination do not contain this ambiguity.

situation for lines longer than 8′.[7] A reasonable interpretation leaves these results susceptible to a treatment in terms of mean retinal local signs:

The vernier threshold increases approximately linearly with retinal eccentricity of the stimulus (Weymouth, 1958). The major portion of the critical detail for discrimination of vernier offset is in the neighborhood of the gap. For a foveally centered vernier pattern increase in line length leaves the critical detail in the same retinal region — the central fovea — while variability in perceived *angle* of orientation of the two lines decreases. Since variability of perceived orientation of the target lines would be expected to contribute to the variance of vernier discrimination (see below), it would also be expected that the discrimination would improve with line length. On the other hand, since the major portion of the critical detail for the discrimination of parallelness lies at the ends of the lines and increase in line length brings these ends into more eccentric retinal regions where offset discrimination is poorer, the threshold differential retinal offset for parallelness increases with line length.

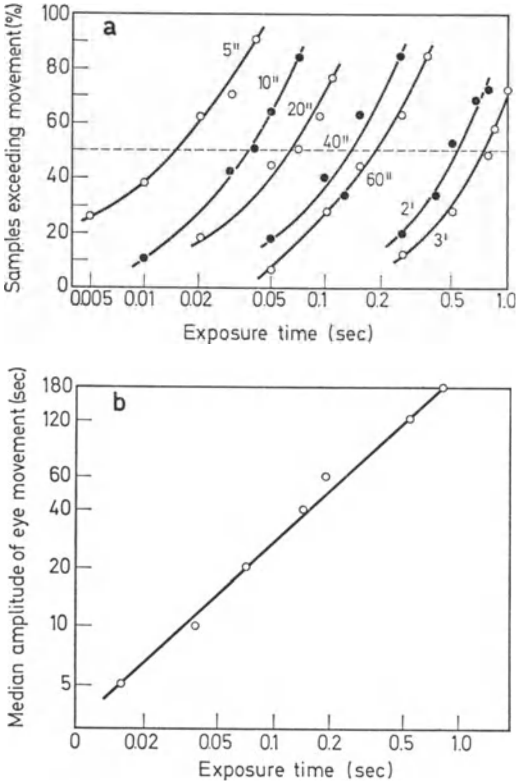

Fig. 3. a) Percentage of eye movement records showing given amounts of motion as a function of the length of the record during attempts at steady fixation. Each experimental point is the result of measuring 50 sample eye-movement records having one particular duration. b) The median extent of motion of the retinal image as a function of exposure time. Medians computed from data in a). (From Riggs, Armington, and Ratliff, 1954)

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[7] Plotted in a different way the same data (Andrews, 1967b) shows a monotonic decrease in threshold Θ with increase in line length. This agrees with previous reports (Sulzer, 1954; Rochlin, 1955).

However, although the concept of a mean local sign for position appears reasonable there are compelling reasons for requiring some further development.

B. Difficulties with the Traditional Version of Mean Retinal Local Sign

Although vernier acuity improves with increased stimulus duration, no differences are obtained between acuities measured under normal and stabilized viewing conditions for stimulus durations up to at least 1.28 seconds[8] (KEESEY, 1960; see Fig. 2), indicating that the improvement consequent on increased exposure duration is *not* due to the fact that from moment to moment *different* receptor arrays look at the image. This result does not comment directly on the assumption of averaging over time or over space, since an average may still be taken, whether over the same spatial array from moment to moment (stabilized viewing) or over different arrays (normal viewing). It is thus not appropriate to conclude from this result either that temporal factors are of lesser importance than spatial ones or that averaging of positional local signs is not involved in the vernier discrimination. The result does however establish that "scanning", which is a central feature of dynamic theories (ANDERSEN and WEYMOUTH, 1923; WEYMOUTH, ANDERSEN, and AVERILL, 1923; AVERILL and WEYMOUTH, 1925; MARSHALL and TALBOT, 1942), is not required for maximizing acuity in the interval from stimulus onset until disappearance sets in.

FENDER and NYE (1962) report no difference in the ratio of magnitudes of horizontal to vertical eye movements between conditions in which vertically and horizontally oriented stabilized vernier targets are being set to alignment. This result adds further evidence against "scanning" theories of acuity by indicating that meridional variations in involuntary eye movements are not produced by variations in line orientation. The result does not comment directly on the converse relation — the influence of meridional variations in eye movements on meridional variations in acuity. In line with these results showing that ocular scanning is not required for localization are GILBERT'S (1969) experiments in which distance comparisons within the frontal plane were made with stabilized and non stabilized viewing. No significant differences in either mean values or variability were found.

Results for stereoscopic acuity are similar to those for vernier acuity: Although stereoscopic acuity is about as fine as vernier acuity (BERRY, 1948) and improves with stimulus duration (OGLE and WEIL, 1958; SHORTESS and KRAUSKOPF, 1961), no significant threshold differences are found between stabilized and normal viewing conditions for durations up to 1.0 second (SHORTESS and KRAUSKOPF, 1961).

To look more closely at the concept of "averaging" over the spatial array of cones stimulated at a given moment, LUDVIGH (1953) required subjects to report on whether a point placed midway between two other vertically oriented points appeared to lie to the left or right of alignment with the two points (Fig. 4e).

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[8] A retinally stabilized image begins to fade and disappear shortly after stimulus onset — generally after at least one or two seconds (RIGGS, RATLIFF, CORNSWEET, and CORNSWEET, 1953; DITCHBURN and GINSBORG, 1952). Since the vernier threshold in both normal and stabilized viewing begins to asymptote at a stimulus duration of about 0.2 seconds, continued stimulation beyond this duration may not influence the report on any given trial (KEESEY, 1960). Thus, even should disappearance take place for the longer stimulations, the report has already been determined by the earlier portion of the stimulation.

Precision in this task is as fine as in vernier discrimination. Ludvigh (1953) points out that since only three bundles of a few cones each are involved in this three-point task, serious questions are raised about whether averaging of positional local signs goes on at all in the vernier task.

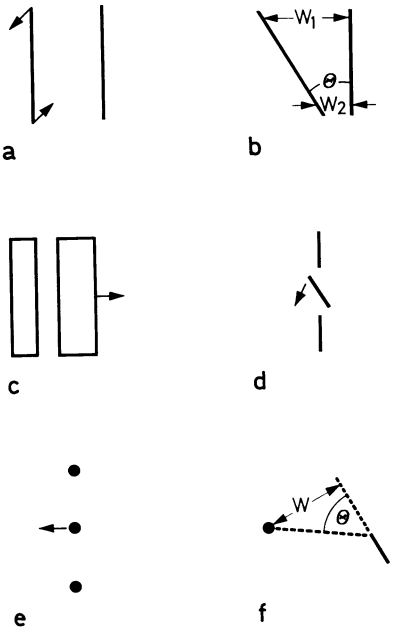

Fig. 4. Some target patterns employed to measure spatial discrimination. a) The discrimination of parallelness can be measured as shown in b) by the angle of tilt between the two lines, Θ, or by W_1—W_2, the visual angle difference between horizontal offsets between the tops of the two lines and between the bottoms of the two lines; c) discrimination of rectangle width; d) a configuration sometimes employed for orientation discrimination; e) the three point task in which the subject is required to report on the offset of the center dot relative to the imaginary straight line connecting the two other dots. Threshold can be given in terms of visual angle offset of dot from this line or in terms of tilt angle Θ between the two lines formed by the three points; other measures are also possible; f) the point/line measure of orientation discrimination

The three-point task, however, differs from the vernier task. It may be viewed as measuring the ability of subjects to discriminate orientations in the frontal plane of the two imaginary lines connecting the three points. Viewed in this way the discrimination in the three-point experiment would appear to be more closely related to the discrimination of parallelness than to the discrimination of vernier offset.

The similarity of the functions shown in Fig. 5 for the three-point and parallelness discriminations supports this view. In addition, some results with the situation in Fig. 4f provide a bridge between the three-point experiment and the parallelness discrimination and make somewhat more feasible the above view that the three-point experiment is primarily concerned with orientation discrimination. Thus Bouma and Andriessen (1968) have found no difference under comparable conditions between thresholds for the discrimination of differences in orientation in this (Fig. 4f) point/line situation and in a situation in which the two endpoints of the line replaced the line itself; the latter is in effect identical to the three-point experiment of Ludvigh with the exception of employing different distances between the center point and the two outer reference points. From his point/line threshold data I calculate 7″ to be the smallest threshold retinal offset of the far end of the line from the projection of the (imaginary) line connecting the point with the near end of the line (W in Fig. 4); this 7″ threshold was obtained for a distance of 5.7° between point and line and a line length of 14′.

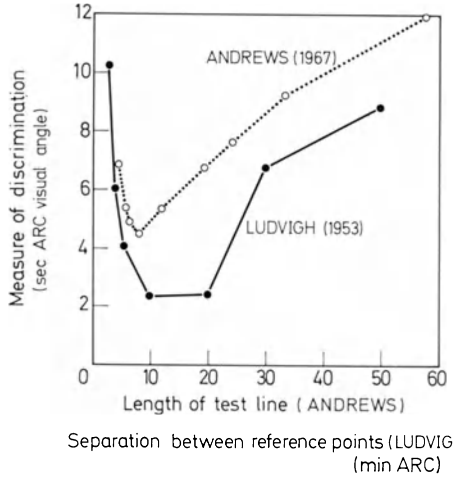

Fig. 5. Ludvigh's (1953) data for three-point discrimination (Fig. 4e) are plotted as offset of center dot needed for 75% correct subject's report (ordinate) as a function of separation between the reference points (abscissa). Andrews' (1967b) data for discrimination of parallelness (Fig. 4a and 4b) plotted as threshold differential retinal offset W_1—W_2 (see Fig. 4b) as a function of line length; values of W_1—W_2 calculated from Andrews' values of threshold Θ by the present author

Although acuity for orientation appears to be involved in the vernier task, the critical detail itself is not orientation. Thus the cogency of Ludvigh's point regarding the need for "averaging" over line length might appear to be somewhat diluted in reference to the vernier task. Bouma and Andriessen's (1968) finding that thresholds for a variant of the three-point task are indistinguishable from the point/line task suggests that two points "define" a linear direction in the frontal plane as well as does an entire line filling the space between the points,[9] and Ludvigh's point might thus at least apply to the discrimination of orientation. In fact, however, the final satisfactory setting of alignment in both orientation (three-point or point/line) and vernier tasks yields an identical appearance — that of a straight line. This would be particularly clear if each task employed two lines. There is thus good reason to expect that vernier acuity would be as good if a pair of points at the extremities of each line were to replace the lines themselves. This would justify Ludvigh's doubt about the need for spatial averaging in vernier discrimination.

However we regard Ludvigh's argument against a concept that involves averaging of positional local signs over the array of photoreceptors stimulated, further difficulties arise from some considerations of discriminations involving curved lines. The thresholds for all four of the configurations in Fig. 1a–1d are

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[9] Constant errors were not the same for point/line and three-point situations in Bouma and Andriessen's data, but this does not influence the above conclusion. Also see Sulzer (1954).

essentially the same as are the PSEs (MATIN, unpublished data). Use of straight lines is thus not necessary for precision in the vernier task. The results further imply that the precision of discrimination cannot be critically dependent on averaging of positional local signs over each of the arrays if photoreceptors stimulated and comparing average horizontal location or any other frontal plane dimension (particularly compare Figs 1 b and 1 c). Instead the subject's setting not only makes use of information regarding visual direction, but also *change* of visual direction between points composing the line (i.e., the derivatives[10] of the line in the viewing plane); at alignment he requires that the relative position of the two lines be such that a continuation across the gap by a straight[11] line would yield a smooth continuous contour[12]. In effect, this implies that in his discrimination the subject is making use of the frontal plane directions of each of the two lines at their adjacent endpoints. This description is reminiscent of the gestalt "principle of good continuation" and suggests that the vernier task, as well as the three-point and point/line tasks, lie very much in the realm of form or contour discrimination.[13]

C. Contours and Cortical Local Sign

MARSHALL and TALBOT's (1942) theory of sensory acuity provided an important advance in our thinking on this problem by moving the locus of HERING's local signs up to the visual cortex. They pointed out that the cortical representation of the fovea was sufficiently fine-grained to deal with the fineness of vernier discrimination. The details of connectivity and interaction in their model of the projection system require considerable revision as a result of more modern work, particularly our increased knowledge regarding the role of peripheral inhibition. But their model yielded the concept that the perceived localization of a point on a contour is correlated with the location of the peak of a spatial distribution of cortical response, in effect, a principle by means of which a mean retinal local sign was obtained as the calculated output of a cortical neuron. The details of the appropriate spread function and the method of its production aside, the general principle appears to be applicable over a broad range of phenomena and across sensory systems (VON BÉKÉSY, 1957, 1960, 1967; RATLIFF, 1965). Incorporated into more complex models of interaction and adaptation in the primary visual projection system, it permits reasonable interpretations (OSGOOD and HEYER, 1952; GANZ, 1966) of figural aftereffect phenomena (KÖHLER and WALLACH, 1944)

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[10] The derivative is the tangent to the curve at the point. Note that in Figs. 1 b and 1 c the subject cannot align the targets by "filling" the gap with a curve with curvature identical to the two shown in each figure.

[11] The "simplest" line which would physically satisfy a requirement of smoothness in Figs. 1 a—e would be the straight line that would be the common tangent to the two curves at their adjacent tips.

[12] In Figs. 1 a—e the curvature of each line is uniform and "requires" a straight line in the gap. It remains to be seen whether thresholds are equally small in alignment tasks such as Fig. 1 h where smoothness requires a curved line of uniform curvature in the gap, and in Figs. 1 f and 1 g where only curved lines of varying curvature will do.

[13] It should be clear that anything we say about the *appearance* of shape of the line "filling" the gap (e.g. "the line appears straight") is a matter of inference on the part of the experimenter and depends at some point on a definition by the experimenter.

based on the assumption that although retinal local sign has been modified cortical local sign has not.

This approach to localization and orientation has now been taken a step further. The presence in cat and monkey of cortical cells selectively sensitive to line stimulation over a restricted range of orientations and locations of the retinal stimulus (HUBEL and WIESEL, 1962, 1968) implies special kinds of selectivity in the determination of connections between retinal ganglion cells and cortical cells as well as between cortical cells themselves. A variety of psychophysical experiments have given evidence of their presence in man (e.g., MCCOLLOUGH, 1965; CAMPBELL and KULIKOWSKI, 1966; SEKULER, RUBIN, and CUSHMAN, 1968; WEISSTEIN, 1969). Most of these experiments involved measuring differential sensitivity to contours differently oriented in the frontal plane following an adaptation period with contours in one orientation. Determinations of either a loss in sensitivity at the orientation employed during adaptation or other orientationally selective aftereffects were generally effected by requiring the subject to report the orientation of a particular aspect of the test stimulus which he could resolve, or the existence of some phenomenal aspect of the stimulus when the latter was presented in different orientations. As such, the tasks were concerned with either resolution or detection acuities rather than with the discriminability of orientation.

ANDREWS (1965, 1967a, b) and BOUMA and ANDRIESSON (1968), however, have attempted to account for data on the discrimination of relative orientation by means of models which employ such "line detectors" as their elements. Here, instead of assuming neural elements with spatial response distributions to point stimuli as in the models discussed above, the assumption is made that each "line detector element" has a gaussian distribution of response magnitude with variation of orientation over a narrow range. ANDREWS assumes that units with peak responses near the horizontal or vertical orientation are more finely tuned than those with response peaks to other orientations, thus accounting for the finding that sensitivity to orientation is greatest near the horizontal and vertical dimensions (ROCHLIN, 1955; ANDREWS, 1967; BOUMA and ANDRIESSEN, 1968). However, BOUMA and ANDRIESSEN point out that this assumption predicts that perceived orientation (PSEs in the point/line situation) will be biased away from the nearest vertical or horizontal in contradiction to the measured variations. They propose instead greater densities of units in the horizontal and vertical dimensions with tuning that is equal in width to those units that have peaks in other meridians. Although the model has not yet been developed in quantitative detail, it predicts the observed variations in both sensitivity and bias for orientation discrimination as a function of orientation.[14]

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[14] The influence of orientation in the frontal plane on threshold is quite similar for vernier discrimination (LEIBOWITZ, 1953; MATIN, POLA, and MCCONCHIE, unpublished data), the discrimination of parallelness (ROCHLIN, 1955), the point/line situation (BOUMA and ANDRIESSEN, 1968), the three line orientation task (ANDREWS, 1967a), and the discrimination of perpendicularity (ONLEY and VOLKMANN, 1958). Threshold is lowest for vertical and horizontal lines and increases symmetrically to reach maxima at tilts of about 45°. Such effects could be due to basic properties of the ocular dioptrics (WEYMOUTH, 1959) or to combinations of astigmatic and accommodative peculiarities. However, a similar effect of orientation on grating (HAMBLIN and WINSOR, 1927; HIGGINS and STULZ, 1950) and fine line (OGILVIE and TAYLOR, 1958; NACHMIAS, 1960) acuities has been obtained. Although changes in the astigmatic

The employment of such hypothetical characteristics and distributions of line detectors for handling psychophysical data has so far involved assuming that their outputs combine in an uncomplicated way, in effect by some averaging process over a selected set of cortical neurons. So again a "mean local sign" is an implied feature of these more recent models, although so far the treatment has been concerned only with "mean cortical local sign for orientation of straight lines." The approach also appears to have some utility in dealing with some of the geometrical illusions of space (BOUMA and ANDRIESSEN, 1970), which are of particular interest in the present context since they are instances of modifications of visual direction induced by simultaneously viewed lines.

Moreover, the results with the three-point experiment do not appear to be at all intractable to such a theoretical approach to orientation since it does not seem unreasonable to assume that a group of units selectively tuned for orientation will be adequately stimulated by three points, leaving units that are inappropriately tuned unstimulated. Since the topographical organization of such cortical "line detectors" preserves the retinal organization by means of selective connectivity of cells between the two layers, an approach that assumes averaging of positional local signs of a subpopulation of cortical cells tuned for orientation also appears to provide a reasonable way of handling the vernier data. In addition, larger numbers of directionally-tuned elements have been observed near the vertical and horizontal in rabbit retina (OYSTER and BARLOW, 1967) and in cat striate cortex (PETTIGREW *et al.*, 1968) — as postulated by BOUMA and ANDRIESSEN in man — although not as yet in monkey. Nevertheless, difficult problems remain for solution for the presently-prevailing view of hierarchically-organized feature detectors: For example, it is clear that the "direction-tagged" outputs of "straight line detectors" cannot be averaged in any simple fashion to deal with dicrimination of offset with curved lines. Neither are "principles" of selectivity available by which curvature could be derived from the output of such detectors.

III. Flexible Local Signs

Combinations of eye, head, and bodily movements continually bring about variations in the retinal loci of images corresponding to stationary objects, and questions of how we perceive these objects in stable positions and do not confuse them with moving objects are thus central to any understanding of space perception and sensorimotor coordination. In this section we shall be primarily concerned with modifications of local sign by extraretinal signals normally associated with

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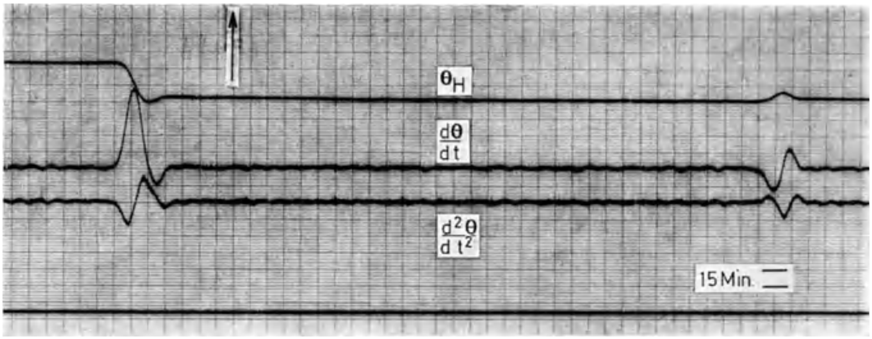
properties of normal eyes with changes in the accommodative stimulus can produce changes in the variation of grating acuity with orientation (ARNULF and DUPUY, 1960; BECK, 1965), the effect on grating resolution remains when a technique of stimulus production is used that bypasses the effects of the ocular dioptrics in forming the retinal image (CAMPBELL, KULIKOWSKI, and LEVINSON, 1966). Thus, for grating acuity at least — and very likely for the other acuities as well — the influence of orientation depends on factors beyond the ocular dioptrics, although the effects can be influenced by the dioptrics. The influence of ocular factors on variation of bias (the point of subjective equality) as a function of target orientation has not yet been determined for any of the alignment tasks (see PEARCE and MATIN, 1969 on this point).

eye movements. These problems will be considered here quite apart from the genesis of the mechanisms in either innate processes or past experience.

Voluntary changes of the direction of gaze are generally thought to be carried out solely by means of saccadic eye movements when the observer views a field of stationary objects (see Fig. 6a); slow voluntary movements on the other hand are generally considered possible only when an observer visually pursues a moving



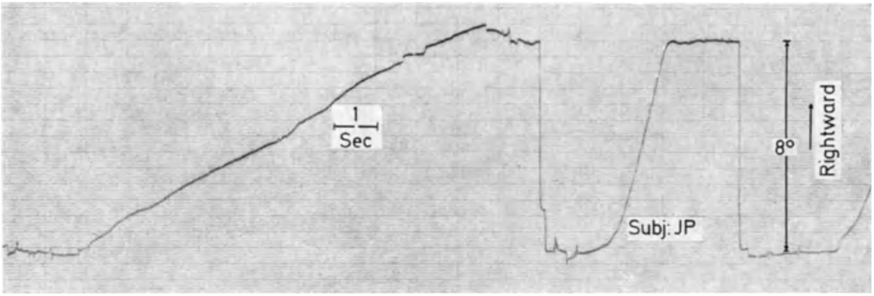


Fig. 6. a) Recording of a voluntary horizontal saccade (near left of figure) made by a subject changing his direction of gaze from one 4′ target to a second one located 39.3′ to the right of the first. Upper trace records change of eye position, middle trace records first derivative of eye position change (velocity), and lower trace records second derivative of eye position change (acceleration). Small oscillations on middle and lower traces (about one per time line) are a measure of velocity and acceleration of involuntary fine ocular tremor. ("grass" on middle and lower traces is amplifier noise). Time lines are separated by 10 msec intervals; major horizontal separations correspond to 15′ of arc for upper trace, 13 deg/sec for middle trace, and 6500 deg/sec^2 for lower trace. The actual saccade length undershot intertarget distance and is about 35′. Saccade velocity normally scales up for increasing saccade lengths; increase is a negatively accelerated function of saccade length (cf., involuntary saccade toward right of figure). (Recording is from Matin and Pearce, 1964). b) Recording of slow horizontal eye movements in the absence of any moving visual stimulus. Two stationary, continuously illuminated circular 3.5′ targets horizontally separated by 8° were the only visual stimuli present. These were employed only to define for the subject the endpoints of the eye movements; essentially identical movements are made by this subject without any visible stimulus. The different velocities of the two slow movements in the figure are under voluntary control of the subject who is able to produce velocities even slower than the one on the left of the figure, and can in a graded series of such movements produce velocities almost up to the speed of saccades. He can, in addition, produce these velocities with the eye moving in either direction, although only slow movement from left to right is shown in the figure with return via saccades. (Unpublished recording is by Pola, Matin, and Matin)

target. Although this does not hold as a generalization (see Fig. 6b), it is undoubtedly true that saccades are usually the means by which voluntary changes of the direction of gaze are achieved when viewing stationary fields.

That slow movements cannot be carried out voluntarily in the absence of a moving stimulus is explicitly stated by numerous authors, and implied equally frequently. Occasional reports of slow movements in the absence of a moving stimulus have appeared. They have perhaps failed to be convincing either because eye movements were not directly measured (GERTZ, 1916), the measuring technique was not sufficiently sensitive to discriminate a smooth movement from a chain of small saccades (DECKART, 1964), or the velocity of the movement does not appear to be sufficiently different from a saccade of equal length (WESTHEIMER and CONOVER, 1954). Recordings obtained with a contact-lens technique leave no further room for doubt (see Fig. 6b).

A. Voluntary Saccades

1. Existence of Saccade-Contingent Extraretinal Signals

During steady fixation a shift of the retinal locus stimulated is normally a sufficient condition for the visual perception of target movement and displacement. If the object giving rise to the shifting retinal stimulation is viewed against a stationary background, relative retinal displacement of object and background is involved. On the other hand, when the observer's eye is turned from one location to another in a stationary visual field, the entire array of retinal images undergoes an essentially undistorted displacement on the retina (in degrees of visual angle) equal to the magnitude of the eye movement (in degrees of ocular rotation) (see Fig. 7). It has therefore been questioned whether an explanation of perceptual stability of visual direction requires extraretinal sources of information at all, and it has been suggested that the spatial relation between objects and "visual frameworks" provide a sufficient basis for an explanation of perceptual stability and visually perceived movement (KOFFKA, 1935). Such contextual influences are of importance in determining where we localize seen objects. However, two well-known observations strongly implicate extraretinal processes, and thus invalidate any explanation which relies on the influence of visual context alone: (1) When the eye is moved by an external object (e.g., pushed by the finger) during an attempt at steady fixation, movement of the visual field is perceived in a direction that would be appropriate to the direction of retinal image shift were the latter generated by physical displacement of the entire visual field with the eye held steady (HELMHOLTZ, 1866). In addition, when the entire visual field is displaced as a unit during an attempt at steady fixation, movement of the field may be perceived. (2) When the eye is immobilized – as a result either of extraocular muscle paralysis or by mechanical restriction of the normal eye – and a voluntary eye movement attempted, motion of the visual field is observed in the direction of the attempted ocular rotation although no motion of the retinal image has occurred (HELMHOLTZ, 1866). Although both situations are "physiologically abnormal" in the sense that the normal linkages between attempted eye movement, actual eye movement, and retinal image shift are severed, the latter observation shows that relative stimulus motion or change of location of objects within the field is not necessary to the perception of movement or change of visual direction. Thus extraretinal influences are effective producers of perceived motion or visual direction change. The observation that a uniform displacement of the entire retinal array need not result in perceptual stability shows that a stable visual framework is not sufficient for perceived stability.

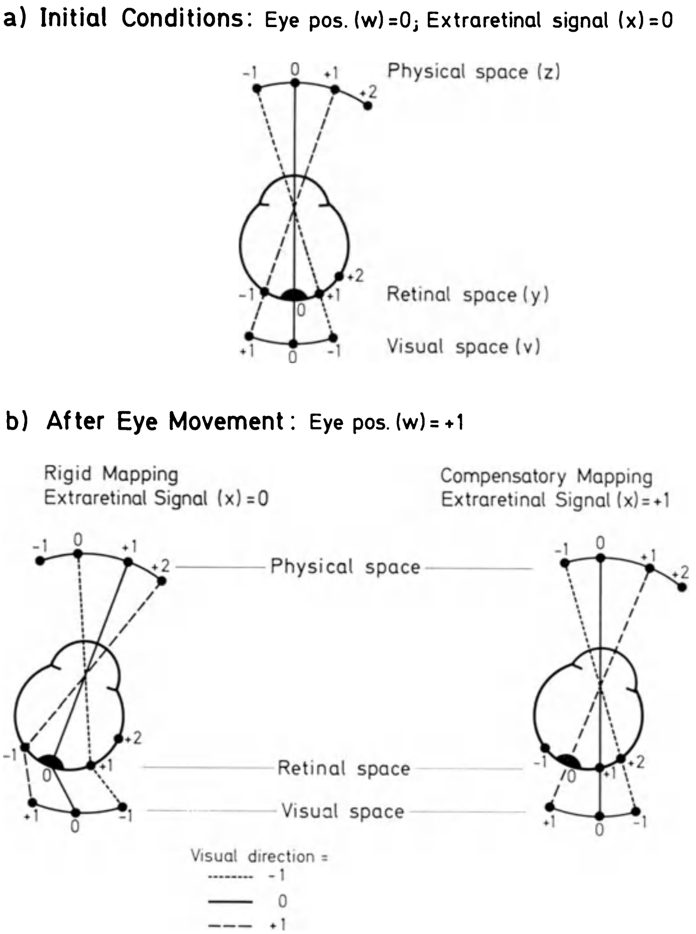


Fig. 7. View of an eye from above (a) while gaze is in some initial direction, and (b) following an eye movement which rotates the direction of gaze 1° to the right. The dark patch at the back of the eye represents the fovea. The figures show the relations between angular distances in the stimulus domain ("physical space"), at the retina ("retinal space") and visually perceived directions psychophysically measured ("visual space") prior to the eye movement (a), and following the eye movement for two cases: no change has occurred in the relation between retinal locus stimulated and perceived visual direction (b, "rigid mapping"); the magnitude of change in the relation between retinal locus stimulated and perceived visual direction exactly compensates the magnitude of the eye movement (b, "compensatory mapping"). The solid, dashed, and dotted lines connecting points in the three spaces are each anchored to a different visual direction and connect to the coordinated points in physical and retinal space. Although angular relations between the three spaces is accurate, angular distances are not drawn to scale

2. Quantitative Properties of Extraretinal Signals Associated with Voluntary Saccades

a) Temporal Development. The extraretinal signal itself, however, although involved in the mechanism underlying the perceived stability of stationary objects when voluntary saccades occur, does not provide a sufficient basis for its explanation. This conclusion derives from a series of experiments in which the influence on visual direction of the saccade-contingent extraretinal signal has been isolated from influences resulting from variations in visual stimulation produced by the saccade (Matin and Pearce, 1965; Matin, 1968; Matin, Matin, Pola, and Pearce, 1968; Matin, Matin and Pearce, 1969; Matin, Matin, and Pola, 1970, also in preparation). In these experiments subjects reported on the visual direction of a brief flash presented at various times either before, during, or after a voluntary saccade relative to the visual direction of a fixation target viewed and extinguished prior to the saccade (see Fig. 8). The stimuli in these experiments were presented in complete darkness; thus the possibility of influences on dis-

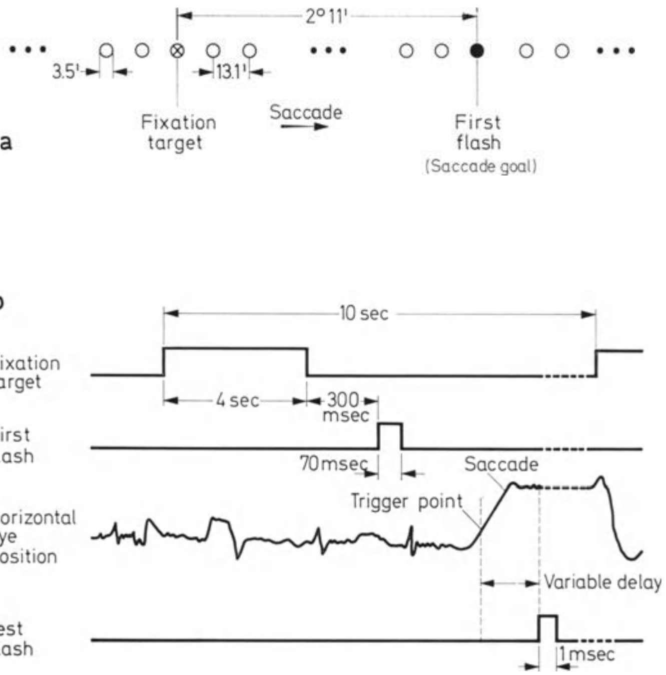


Fig. 8. a) Spatial array of stimuli employed in experiments measuring the relation of visual direction of a flash presented either before, during, or after a voluntary horizontal saccade to that of the previously-viewed fixation target; any target in the array could be used as a test flash. b) Temporal sequence of stimuli. For test flashes produced during the saccade the variable delay was zero; different trigger points within the saccade were employed. Test flashes presented before the saccade were initiated at a fixed duration following first flash onset (350 msec for observer JP and 300 msec for EM); test flash — saccade interval could not be set beforehand as a consequence of the variable reaction time, and was thus measured during each trial. Test flashes during the saccade were 1 msec as shown; test flashes before and after the saccade (when the eye was moving more slowly) were 2 msec

crimination arising from extraneous visual context was completely eliminated. Low intensity but easily visible stimuli were employed and the presentations of the two stimuli whose visual direction were compared were separated by at least 500 msec; thus the influence of afterimages and other similar short-term "visually persistent" consequences of the presentation of the fixation target, which could make the discrimination one of "simultaneously viewed" stimuli, were minimized or eliminated. In addition, the use of a brief flash when the eye was in motion during a saccade essentially eliminated the "smearing" of the retinal image which occurs in continuously illuminated environments.

The experiments provided measurements of the location of a flash that appeared in the same location as the previously-viewed fixation target (target point of subjective equality or target PSE) as a function of time of test flash presentation measured from the beginning of the saccade. These values are shown in Fig. 9b. From simultaneous measurements of eye position obtained by means

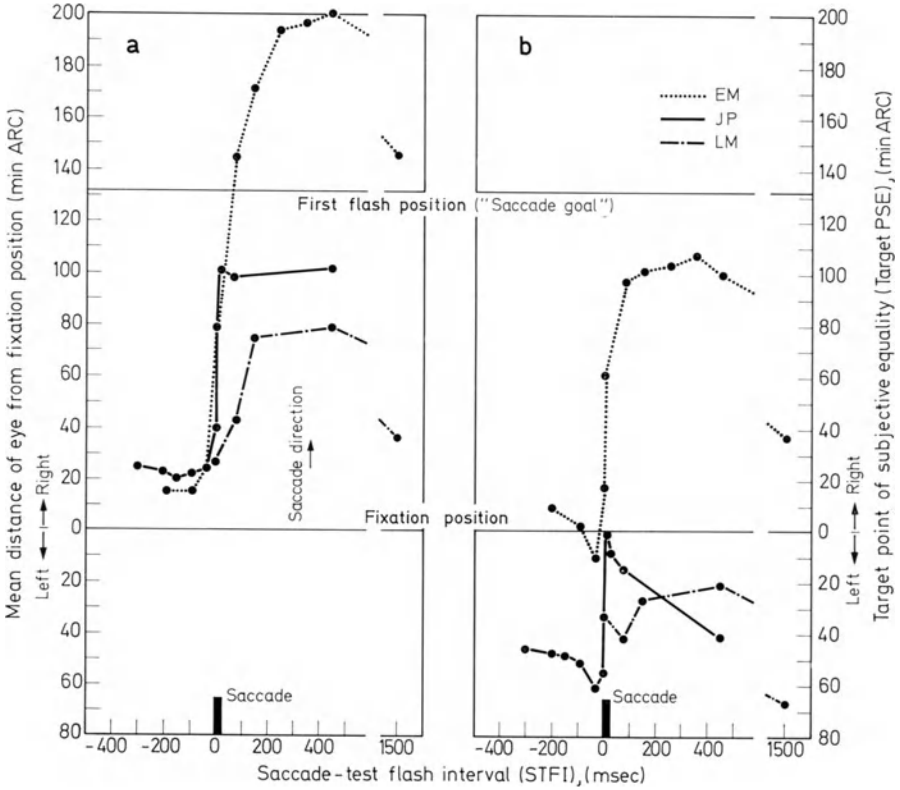


Fig. 9. a) Mean eye position at times before, during and after saccade when test flashes were presented. b) Points of subjective equality at the stimulus array determined from subject's report of horizontal visual direction of test flash relative to previously-viewed fixation target. Negative values of STFI refer to trials in which test flash was presented before the saccade. It was not possible to reproduce on this graph all of the points during the saccade; only one or two are shown here. Presaccadic data for EM are for leftgoing saccades; all the rest are for rightgoing saccades as shown. (Graph compiled from data in MATIN *et al.*, 1969, 1970, also in preparation)

of a contact-lens technique employing invisible (infrared) measuring beams (MATIN, 1964; MATIN and PEARCE, 1964), determinations were made of the variations of retinal locus at which the target PSEs were imaged (see Fig. 7). These values (retinal PSEs) are shown in Fig. 10.

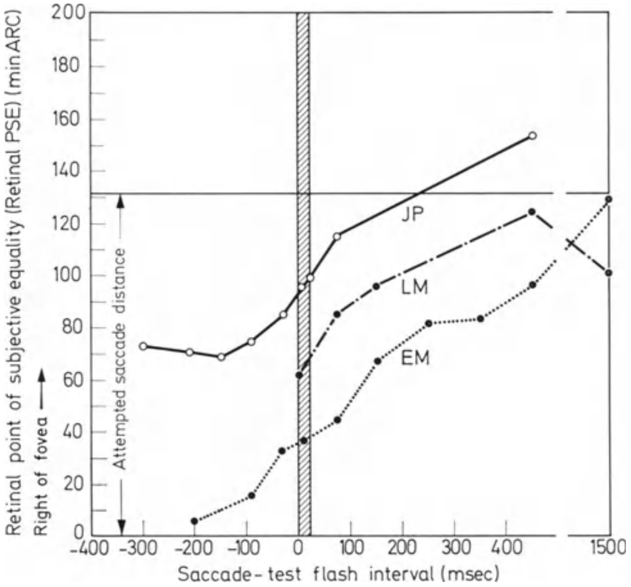


Fig. 10. Points of subjective equality for the fixation target measured as horizontal distances at the retina. These are plotted as a function of time relative to saccade onset. The data are from the same experiments as Fig. 9. Although there is a close correspondence between the retinal PSEs and the differences between mean eye position and target PSEs at corresponding values of STFI, it is not exact; this is mainly a result of the fact that distributions of eye positions at fixed values of STFI were frequently skewed. Each retinal PSE was calculated directly from the distribution of retinal distances and psychophysical responses over trials at a given value of STFI

It is apparent from Fig. 10 that the mapping of visual direction into retinal locus changes in the time period associated with the saccade (i.e., there is a saccade-contingent shift in retinal local signs). Since this shift in local signs occurred in the absence of ongoing visual stimulation, it may be attributed to the growth of an extraretinal signal whose magnitude is monotonically related to the magnitude of local sign shift. However, it is also apparent from Fig. 10 that the growth of extraretinal signal is very much slower and more prolonged than the saccade itself, beginning to grow considerably before the saccade begins, changing only slightly when measured with flashes presented during the saccade, and showing considerable growth both before the saccade and for some time after the saccade is completed. In these experiments the peripherally presented target was 2° 11′ from the fixation target. Essentially similar results have been obtained with separations of 4° 22′ for flashes presented during the saccade (MATIN, MATIN, and

PEARCE, 1969), and with separations of 5° and 8° for flashes presented during and after the saccade (POLA, 1971).

The comparison of the time courses of extraretinal signal growth and of the saccade itself shows that a saccade-contingent extraretinal signal cannot be the sole factor responsible for the production of perceived stability when saccades occur. Quite apart from the specific details of any theory regarding the nature of the extraretinal signal or the mechanism by which it influences perceived visual direction, if its operation were to be the sole means by which stability of perceived visual direction is produced, the shift of local signs could follow only one time course. It would have to parallel the eye movement exactly; if it did not, variations of the perceived visual direction of stationary targets would result. Clearly such a time course was not followed.

b) Determination of Extraretinal Signal Magnitude by Time, Eye Position, Saccade Length, and Distance of the Saccade's Goal. Since eye position changed systematically with time in the saccadic period (Fig. 9), it follows that the variation in local signs with time shown in Fig. 10 implies a variation with eye position. But this is not an incidental relation; even at a specific time the local sign shift is a function of eye position. This was determined by making use of the considerable trial-to-trial variability in saccade length and in eye position at a given time[15]. Sensitivity of this shift was about 0.5 minute of arc shift in local signs per minute of arc change in eye position at 75 msec following the saccade (MATIN, MATIN, and POLA, in preparation). Since saccade length and eye position at a given time after the saccade are highly correlated it is not yet known which is the more significant.

In further work, POLA (1971) has extended these findings to 8° saccades. In addition, by preconditioning a reduction in saccade length he has been able to extend the range of positions assumed by the eye on different trials at particular times during and following the saccade.

The preconditioning was carried out by a technique based on a finding by McLAUGHLIN (1967). During a saccade to a target 10° removed from a fixation target, McLAUGHLIN displaced the distant target 1° toward the original point of fixation. This resulted in an overshoot of the saccade with respect to the new target position. When this was repeated several times, the saccade's length was reduced to nearly 9°. By a variant of this procedure the saccades of POLA's subjects were reduced from 8° to nearly 5° in preconditioning over 100 trials. Sessions in which reduction in saccade length was preconditioned were mixed with those in which saccade length reduction was not preconditioned, thus extending the total range of saccade lengths obtained.

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[15] Repeated saccades between two given points in a continuously-illuminated environment are extremely uniform. Hence the eye reaches a given point in every saccade at virtually the same interval after saccade initiation. In the experiments referred to above the peripheral target toward which the saccade was aimed was presented as a 70 msec flash. Since the subject did not turn his eye to look at the peripheral flash until it appeared, it was extinguished before the saccade had begun. This mode of presentation precisely localized the retinal location of the peripheral flash and prevented its image from being dispersed over the retina at successive moments during an eye movement as it would were the stimulus presented for a longer duration. It also permitted the employment of a stimulus sequence in which no two stimuli were simultaneously presented. However, when the eye saccades to a target that is no longer present in a dark field, as in the above experiments, there results considerable inaccuracy and variability in saccade length, more frequent occurrences of multiple saccades on a single trial (most frequently two), and particularly for the longer saccades some variability in saccade shape and duration. (See also BECKER and FUCHS, 1969).

POLA reports that at a given duration not only is the local sign shift linear with eye position but that sensitivity is the same when saccade length is experimentally reduced and when it is not. In addition, he finds that the distance of the peripheral target eliciting the saccade may be a less potent variable in determining visual direction than is the actual distance that the eye travels. Thus, although the temporal development of the local sign shift consequent to saccade elicitation by a target 5° in the periphery is roughly a scaled down version of the 8° function, a substantial portion of this difference is due to the fact that a 5° target typically elicited a smaller saccade than a target 8° in the periphery.

c) Summary of Characteristics of Growth of the Saccade-Contingent Extraretinal Signal. The change in retinal locus associated with a given visual direction prior to, during, and following a voluntary saccade is much slower and more extended in time than the saccade itself, beginning at least 100 msec before the saccade and growing monotonically until at least 300 msec following saccade completion. Although the shift is in a direction that is compensatory for the actual saccade, and reaches a magnitude that is close to the distance between the peripheral target calling out the saccade and the prior fixation target, considerable inaccuracy is manifested in reporting the visual direction of flashes before, during, or after the saccade relative to a previously-viewed fixation target. Three variables are connected with the growth of extraretinal signal guiding the shift of local signs: (1) time relative to saccade beginning, (2) either saccade length or position of the eye at the moment the test flash is presented, (3) either distance of the peripheral target eliciting the saccade or the "attempted saccade magnitude." The two alternatives for each of variables (2) and (3) have not yet been separated.

The experiments on which these conclusions are based were carried out under conditions of visual stimulation that differ from normal viewing: (1) the fixation target, the standard target in the comparison, was removed before the saccade had begun; (2) the comparison target was presented as a brief flash; (3) a stable visual background was absent; (4) the target toward which the saccade was aimed was extinguished before the saccade had begun. If the influence of the extraretinal signal on perceived visual direction were to be sufficient to account for perceptual stability, however, its operation should be tied to either the position of the eye or the subject's intention to move it, and independent of the details of the visual stimulation per se. Hence these conclusions regarding extraretinal signal influence should be applicable to more normal viewing situations. Since, then, the growth of extraretinal signal does not parallel the change in eye position, it cannot by itself be sufficient to explain the stability of visual direction in the presence of voluntary saccades. The following section will also indicate some restrictions placed on the operation of the extraretinal signal by conditions of visual stimulation.

3. Influence of Visual Stimulation on Visual Direction in the Presence of Voluntary Saccades

Two aspects of the spatiotemporal pattern of visual stimulation have been shown to have substantial influences on the relation of visual direction and retinal locus when voluntary saccades occur. These are: (1) the time interval between stimulations whose visual directions are being compared and (2) factors related to visual masking.

a) Failure of the Extraretinal Signal to Mediate Relative Visual Direction during Brief Time Intervals. In the experiments described above there was a minimum time interval of about 500 msec between stimulations from the two targets whose visual directions were compared (see Fig. 8). Quite different results were obtained with shorter time intervals (Matin and Pearce, 1965; Matin, Matin, Pola, and Bowen, 1971), although the dependence of visual direction on this temporal variable has not yet been determined in detail for short intervals. In an experiment in which a flash was presented when the eye was at each of two different positions during a single 8° horizontal saccade (approximately 30 msec between presentation of the two flashes), it was necessary for the two successive flashes to strike very nearly the same horizontal retinal coordinate in order for the flashes to appear in the same visual direction (Fig. 11). This result could not be predicted from an extraretinal signal function for 8° saccades obtained for this subject in a way similar to the one in Fig. 10. Thus, although the target PSE for the previously-viewed fixation target was 3° to the left of the fixation target when the test flash was delivered with the eye 1° into the saccade, and 1/3° to the right of the fixation target when the eye was 6° into the saccade (Fig. 11), there was a failure of transitivity between the outcome of these comparisons and the direct comparison to each other of the directions of flashes from the two targets corresponding to the target PSEs (Fig. 11). The difference between the target PSEs for the fixation target determined when the eye is at the two different points in the saccade corresponds to a difference of 1−2/3° at the retina. But when the visual direction of a flash presented as the eye crosses the 6° point was compared to a flash presented when the eye crossed the 1° point the required retinal distance was reduced to near zero.

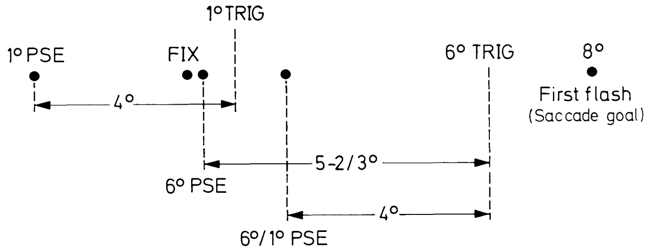

Fig. 11. Points of subjective equality (PSEs) were measured for the fixation target under two conditions: (1) Test flashes were presented when the eye crossed a point (1° trig) 1° from the fixation target (measured value indicated at 1° PSE); (2) On other trials test flashes were presented when the eye crossed a point (6° trig) 6° from the fixation target (measured value indicated at 6° PSE). On each of another set of trials a first flash was presented from the target at "1° PSE" when the eye crossed 1° trig, and a second flash was presented when the eye crossed 6° trig from a target whose location was randomly varied. The subject reported the location of the second flash relative to the first; the PSE is indicated at "6°/1° PSE." (From Matin, Matin, Pola, and Bowen, 1971)

Further indication of the failure of saccade-contingent extraretinal signals to differentially influence the visually perceived directions associated with visual events that are sufficiently close to each other in time may be derived from the following: When an entire visual scene is presented as a brief flash during a saccade, spatial relations within the scene appear undistorted. Yet, it is well known that dimmer stimulus intensities result in visual responses with longer latencies, and that a substantial portion of these differences are already present at the level of the optic nerve and thus presumably prior to influence by extraretinal signals. Influence on visual direction by a saccade-contingent extraretinal signal whose magnitude grows with time (such as in Fig. 10) would then be expected to yield distortions in the briefly-flashed visual scene that are related to local intensity variations in the scene.[16] Failure to observe distortion in brief flashes has been confirmed in a formal experiment in which detection of horizontal vernier offset was measured for two vertical lines differing by 2 log units in stimulus intensity that were simultaneously presented in a 1 msec flash during a horizontal saccade (MATIN, MATIN, POLA, and BOWEN, 1971).

It has been possible to measure distortion when parts of a "scene" were sequentially presented. In an experiment which employed the stimulus configuration and temporal sequencing shown in Fig. 8, the subject was required to report whether the randomly-located test flash (presented when the eye was at a point near the middle of the saccade) lay to the left of the fixation target, between the fixation target and the flash target defining the goal of the saccade, or to the right of the latter target (MATIN and PEARCE, 1965). PSEs for each of the comparison targets are illustrated in Fig. 12.[17] In this case the test flash was presented more than 500 msec following fixation target extinction (300 msec + reaction time to the flash from the target which constituted the "saccade's goal"), but only about 200 msec (the subject's reaction time alone) following onset of the flash from the saccade's goal. The results indicate that the comparison of visual direction of the test flash to that of the fixation target was influenced by an extraretinal signal of substantial magnitude, but that the comparison of the test flash to the flash

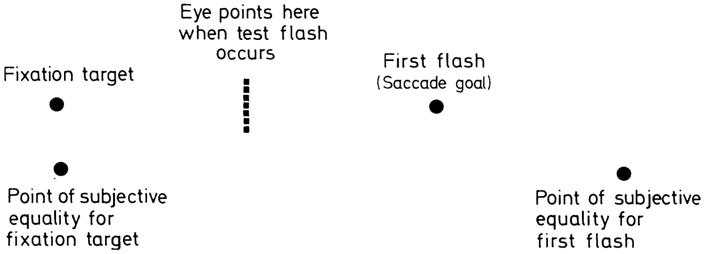

Fig. 12. An experiment in which Points of Subjective Equality (PSEs) for two targets viewed before the saccade were simultaneously determined by use of test flashes presented during the saccade (see text). PSEs were actually on same horizontal line as targets and are vertically displaced in the figure only for clarity. (From MATIN and PEARCE, 1965)

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[16] The consideration that variation of latency with intensity might be sufficient to generate distortion is in fact much too simplistic; for example, it neglects the fact that more intense stimuli also generate longer lasting discharges in the optic nerve.

[17] Exact PSE values could not be meaningfully calculated since the eye position during the saccade at the moment of test flash presentation was not held constant over trials. The error in estimating the PSEs due to this factor would not have exceeded 5′, however.

from the target constituting the saccade's goal was not — thus requiring rough identity of retinal locus in order to be seen in the same visual direction.

The phenomena described in this section suggests that the influence of a saccade-contingent extraretinal signal on relative visual direction of different stimuli is severely restricted unless a "sufficiently" long time interval separates their presentations. Relative visual directions of successive stimulations presented at shorter time intervals appear to be essentially judged on the basis of relative retinal location alone as in the steadily fixating eye. The short interval effects evidently depend on whether the neural consequences of the earlier stimulation can persist into the time period during which the second stimulus is being processed. This peristence will undoubtedly depend on variables such as state of light adaptation and stimulus intensity.

The general picture that emerges so far suggests that we may conceive of two storage "registers": a "short-term" memory storage and a "long-term" storage. When a saccade occurs, the extraretinal signal associated with it may influence the relation of visual directions of two targets only if the neural process corresponding to one of them exists in the long-term storage when the other one is seen. It is not likely that the movement of a memory from short to long term storage is abrupt. Rather it is more likely that the memory of direction of a given target will have one foot in short term and the second in long term memory for some time and that as more of it moves into the long-term memory the susceptibility to extraretinal influence of a discrimination of this target against a more recently presented one increases.

b) Suppression. When voluntary saccades are carried out in a normally illuminated environment we generally do not perceive stimulation available to the eye during the movement. Dodge (1900, 1905) originally suggested that the effect was a consequence of the close temporal adjacency of different images at a given retinal region resulting from the sweep of the retina across the image plane of the eye, and that the observer had learned to disregard the resulting blur. Holt (1903) suggested that a "central anesthesia" accompanied voluntary saccades. The latter suggestion has received support from several studies in which a diminished sensitivity to very brief flashes has been shown to have a time course synchronized to the saccade (Volkmann, 1962; Latour, 1962; Volkmann, Schick, and Riggs, 1968; Zuber and Stark, 1966; Richards, 1969; Pearce and Porter, 1970). Since this increase in threshold is only about 0.5 log unit it is not sufficient by itself to account for the fact that in normally illuminated environments we generally do not perceive stimulation during the saccade. However in a recent report (Matin, Matin, Pola, and Kowal, 1969) evidence was presented for a suppression mechanism which would be sufficient. That mechanism is backward lateral inhibition or metacontrast. The experiment that led to this suggestion was the following:

When a small target is presented for 0.5 msec against a background of complete darkness shortly after the onset of a horizontal saccade, it is seen as a small spot. If on subsequent trials the flash onset again follows the onset of the saccade but the flash duration is extended so that it is present during more of the saccade, the appearance is of a horizontally extended "smear" whose length increases with stimulus duration. Maximum smear length appears to be reached when the flash is extinguished at about the time the saccade terminates. Further increases in flash duration result in *decreasing* length of the "smear" and finally, if the stimulus is left on for a sufficiently long period of time, no smear is seen and the appearance of the target reverts to that of a small spot. This phenomenon has now been studied as a function of flash luminance and duration against a dark background with 4° horizontal saccades (Fig. 13, MATIN, CLYMER, and MATIN, in preparation). Similar observations were made at other values of luminance, contrast, and saccade length.

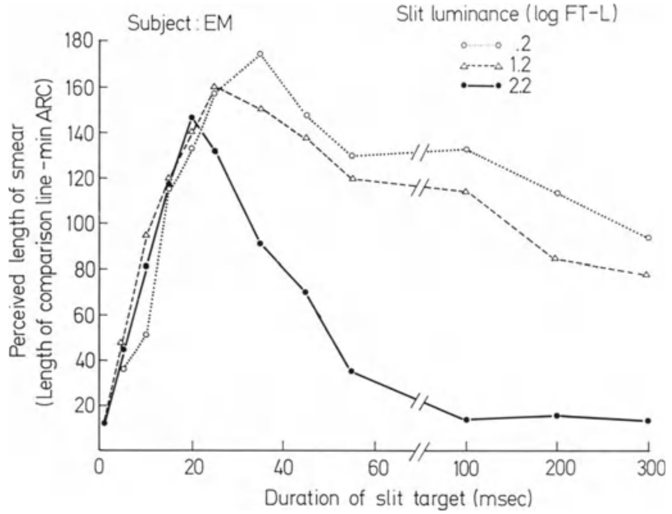

Fig. 13. Perceived length of a 2′ wide slit illuminated when the eye had traveled 1° into a 4° horizontal saccade. The slit remained illuminated for the duration indicated on the abscissa. Saccade duration was approximately 36 msec. A variable length 3.2 ft. L. comparison line was presented for 2 msec 350 msec following onset of the slit and was located 1.5° above the slit; since this presentation was in the postsaccadic period the eye was virtually steady. (MATIN, E., MATIN, L., CLYMER, A., in preparation)

The increase in perceived smear length with stimulus duration until length reaches a maximum correlates well with the retinal energy distribution.[18] However, the diminution in perceived smear length for increasing stimulus durations after the maximum length is reached strongly suggests inhibitory interactions like those generally classified as metacontrast i.e., masking produced by subsequent

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[18] SMITH (1969a, b) has determined relations for the dark-adapted steadily-fixated eye among luminance, velocity, wavelength, target diameter, eccentricity, and arc length for a target moving with constant angular velocity in a circle around a fixation point in order for a stimulus to appear as a continuous fused arc (to appear as an evenly illuminated band in all parts of the field at once). She finds that for parametric values similar to those employed in dealing with smears during saccades (above), a target traveling over 1.7° of visual angle will appear as a fused arc if it remains in the field as long as about 75 msec (traveling at a velocity of about 22.7° of visual angle per second). Targets traveling for shorter duration (higher velocities) over the same arc length all appear fused. Thus increasing smear length with increasing stimulus duration up to duration of the saccade (36 msec) might be expected for a stationary eye and identical spatiotemporal energy distribution across the retina [However, note the nonuniformity of ocular velocity during the saccade (see Fig. 6a) and consequent nonuniform spatial energy distribution over the retina].

stimulation to retinal areas adjacent to those whose threshold is being measured (cf., Stigler, 1910; Werner, 1935; Alpern, 1953; Kolers and Rosner, 1960; Kolers, 1962; Raab, 1963; Kahneman, 1968; see Weisstein, chapter 10, this volume). This interpretation is particularly suggested by the fact that the diminution in length begins at about the time the saccade ends and subsequent stimulus energy all "piles up" on a restricted retinal locus. Threshold increase for a test flash in a metacontrast situation also is an increasing function of energy with a fixed duration masking flash. The detailed relation to parametrically measured influences in metacontrast phenomena has not yet been worked out although the characteristics of smear shortening do appear consistent with them.

Thus, for example, it has generally been found (Kolers, 1962) that threshold increase produced at any given temporal interval between test and masking flashes is maximum when the two share a common border and that the effect decreases monotonically with angular separation. In the present case with increasing stimulus duration the smear begins to disappear first at its tail, i.e., the portion that is further away from the retinal region at which the increased energy accruing from increased stimulus duration piles up. But the retinal region at which the tail of the smear would exist was also the first to be stimulated by the prolonged flash, and so the tail would have preceded the beginning of "energy pileup" by the longest time. Therefore, the decrease in smear length could be caused by a type B temporal metacontrast function (Kolers, 1962), in which the threshold decrease produced by a subsequent fixed duration flash at a given angular separation increases with increased temporal separation of test and masking flashes up to intervals of 20—100 msec. The disappearance of the tail of the smear first is thus consistent with presently available data on metacontrast.

In the present context it is worth noting that MacKay (1970) has reported decreased sensitivity with a steadily-fixating eye when a uniformly-illuminated, circular 10° background was horizontally-displaced by 3.06° at various times relative to the presentation of a 100 ms test flash (background displacement was completed in 10 ms after displacement onset); the retinal area under test was homogeneously stimulated by the background throughout; the moving contour was never less than 1.8° away from the retinal area tested.

Whatever the details of the mechanism underlying the decrease in smear length with increased stimulus duration beyond that corresponding to the saccade, its significance for spatial localization is clear. If we neglect for the moment the existence of visual stimulation from a stationary scene present before the saccade begins, the perception of the smear produced by the saccade that corresponds to each point in the scene will have been masked by stimulation from that same point after the eye "comes to rest" at the end of the saccade, and the entire "blur" will thus not be seen. Of course stimulation of a given retinal locus by many points in the scene complicates this point-by-point analogy to the observations on smear length and remains to be worked out. If postsaccadic stimulation from a stationary scene also has masking effects on presaccadic stimulation as well as on stimulation during the saccade, it should hasten the removal of the persistent effects of prior stimulation. As noted above these persisting effects tend to pull discriminations of visual direction toward one based on retinal identity alone; operation of the extraretinal signal requires removal of these persisting effects.

B. Pursuit Eye Movements

1. Existence of Extraretinal Signals Related to Pursuit Eye Movements

When a subject visually tracks a target moving sufficiently slowly with uniform linear motion the target appears to move. Such movement is perceived whether the target moves in complete darkness or against a visible background. If tracking were perfectly accurate so that the retinal locus of the tracked target was stabilized the appearance of movement of the target in complete darkness would imply an extraretinal basis for the perceived movement.

But if tracking were perfectly accurate what basis would the oculomotor system have for tracking at all? Some "retinal error signal" appears to be necessary if ocular velocity is to have any relation at all to stimulus velocity. This is even more obvious in the tracking of a target oscillating in one dimension of the frontal plane with sinusoidal motion; here not only are target position and eye position changing with time but velocity and acceleration as well. Reports of the characteristics of pursuit eye movements have tended to emphasize that a brief time after the target begins to move, the eye catches up to the target with a brief saccade and then for target velocities up to 20°/sec — 40°/sec, ocular velocity matches target velocity (WESTHEIMER, 1954; RASHBASS, 1961; DODGE, TRAVIS, and FOX, 1930; STARK, VOSSIUS, and YOUNG, 1962; ROBINSON, 1965). BARMACK (1970) has also reported accurate velocity matching up to 90°/sec for brief periods. Some authors, however, report that the eye continues to lag the target even at very low velocities (FENDER and NYE, 1961; ST-CYR and FENDER, 1969; PUCKETT and STEINMAN, 1969). What aspects of the motion of the stimulus are significant in controlling the pursuit velocity of the eye is not yet clear but it seems clear *a priori* that some characteristic of the deviation of the target's image at the *retina* must be involved. Whether this "retinal slip" is primarily or secondarily involved in the perception of motion during target pursuit is not yet known.

Some information is derived from viewing afterimages (which are of necessity retinally stabilized). Afterimages viewed in a completely dark background appear to move in the direction of the eye movement when voluntary eye movements are made (HELMHOLTZ, 1866). These apparent movements consist of a series of jerks that suggests synchronization with the voluntary saccades (GREGORY, 1958) although no direct evidence exists on the matter. The apparent movement of the afterimage appears to be converted to smooth motion when the observer attempts to visually track the "proprioceptive locus" of his own moving hand in complete darkness (GREGORY, 1958). When a subject turns his eye slowly in darkness (Fig. 6b) while viewing an afterimage it also appears to move slowly (POLA and MATIN, unpublished observations). Attempts at fixating an afterimage of a small target eccentrically located on the retina also result in a series of jerky apparent movements in the direction of the "fixation movements" if the eccentricity is large; if eccentricity is of the order of 0.5°, however, attempts at fixation may result in smooth apparent motion (CRONE and LUNEL, 1969). Attempts at fixating a well-centered stabilized image may reduce apparent motion (MATIN and MACKINNON, 1964). Although more work is needed here, these observations suggest that an extraretinal signal influential in determination of visual motion and direction is associated with slow pursuit-type eye movements. The latter observation also suggests that the "error signal" guiding the slow motion may be a retinal *positional* error and the prior two observations suggest that the error signal need not simply be a retinal signal (see however RASHBASS, 1961).

2. Some Relations between Perceived Motion and Pursuit Eye Movements

Although experiments have not yet been reported in which pursuit eye movements and perceived visual direction or motion have been measured simultaneously so that direct determinations of the retinal stimulus could be obtained, absolute velocity thresholds for motion of a luminous target moving in darkness have been found to be 10–20 min/sec when the subject attempts to maintain fixation on the moving target (AUBERT, 1886; BOURDON, 1902). In attempting to maintain fixation during actual target movement, pursuit movement would necessarily have been engendered. Both of these workers noted the unavoidable occurrence of autokinetic movement and its possible disturbing influences on their measurements. PEARCE and MATIN (1966) have measured velocity thresholds for the detection of target motion in complete darkness in a direction opposite to the direction of ongoing autokinetic movement during attempted steady fixation. Immediately following the subject's initial directional report of autokinetic movement while viewing a spatially fixed oscilloscope spot, a step of uniform linear motion in a direction opposite to the reported autokinetic movement was imposed on the target for 3 seconds followed by target extinction. The velocity of target movement was varied between trials, and reports of reversal or no-reversal of motion were obtained. Threshold velocities for reversal of 20′/sec were obtained with fixation in the primary position (involving displacements of 1° during the three second period of target movement) and 40′/sec with fixation in extreme secondary or tertiary fixation positions. These reversal thresholds may be considered objective measures of the speed of autokinetic movement as well as absolute motion thresholds, and thus are in agreement with previous reports of increased speed and unidirectionality of autokinetic movement for extreme fixation positions (CARR, 1910; ADAMS, 1912; MATIN, PEARCE and MACKINNON, 1963).[19] These absolute thresholds are an order of magnitude higher than minimum thresholds obtained for a moving target against a visible background (AUBERT, 1886; BOURDON, 1902; GRAHAM, 1968; HENDERSON, 1971). But since involuntary fixation patterns show standard deviations of 3′–5′ of ocular motion (see Fig. 3), such thresholds for visual motion of a target must be considered very fine indeed. Whether they are simply a result of "retinal slip" during pursuit or of an extraretinal signal or of some combination of these influences remains to be determined.

Such involuntary movements would constitute a noisy background of displacements of the retinal image against which real target movement would have to be discriminated in darkness. Since these movements produce correlated shifts of the retinal image of test target and visible background, they should be of less significance when a visible background is employed.

It has been noted that during pursuit of a moving target against a textured background the latter tends to move very much more slowly in a direction opposite to the target (FILHENE, 1922; GREGORY, 1958). It has not yet been determined how this relates to functioning of the extraretinal signal, to background conditions, or to differential sensitivities of the central and peripheral retinas to movement.

3. Variation of Visual Direction during Pursuit Eye Movements

STOPER (1968) has carried out psychophysical experiments which provide measures of relative visual direction during pursuit movements. Although the method employed was based on the one described above for saccades, direct

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[19] The small values of target velocity required for nulling and producing reversal of the autokinetic motion in these extreme viewing positions provide some interesting questions when juxtaposed with subjective estimates of autokinetic velocity. Values as large as 60°/sec are frequently reported.

determinations of eye position were not made. Instead, two types of controls were employed; in one case the control gave some assurance that deviations of the eye from the moving fixation target were not greater than ± 2°, and in a second case that ocular velocity was between 6°/sec and 12°/sec when tracking a target moving at 9°/sec. In one experiment, STOPER's subjects tracked a small fixation target moving (rightward) horizontally in darkness over a 27° distance at a velocity of either 0°/sec, 9°/sec, 13.5°/sec or 27°/sec. When this target reached the midpoint of its traverse a vertical line was flashed 0.36° to the right of the fixation target's momentary location. At some later time (102, 204, or 306 msec) a second vertical line was flashed at a location that varied from trial to trial. The subject reported whether the second target appeared to the left or right of the first target. In a second experiment interflash intervals ranged from 306 to 1734 msec with the fixation target traveling at 9°/sec and the first flash presented 7° to the left of the moving fixation target at the moment that the latter crossed the midline of the field. PSEs for two subjects in the second experiment are shown in Fig. 14.

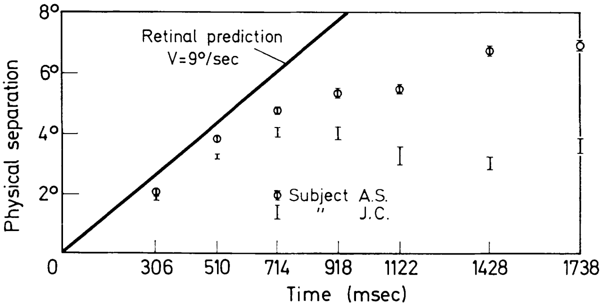

Fig. 14. Physical separation of two flashed lines reported to lie in the same visual direction, whose presentations were separated by the time interval shown on the abscissa. The eye pursued a fixation target at the velocity indicated. The diagonal line in the figure is the locus of points for which the two lines would strike the same horizontal retinal locus if ocular pursuit was accurate. Data would fall along abscissa if report was accurate with regard to physical location. Data for first experiment (not shown) lie close to diagonal. (Data from second experiment by STOPER, 1968)

If we assume accurate tracking by STOPER's subjects we must conclude that up to interflash intervals of 300—700 msec there is only a slight indication of extraretinal signal involvement in the discrimination. Up to then the judgments do not depart substantially from those that would be made were the subjects to have required that the two targets strike the same vertical retinal meridian; whatever apparent deviation does occur from such a requirement might be due to failure of the eye to keep up with the target. However, for interflash intervals beyond 700 msec deviations from a "retinal identity" basis cannot reasonably be attributed to such failure; the deviations here are too large. Since the target (and presumably the eye also) had already traveled 13.5° when the first flash occurred (for the 9°/sec velocity, the moving fixation target and eye had then been traveling for 1.5 sec), we may infer from STOPER's data that departure from a discrimination based on identity of horizontal retinal locus during pursuit (i.e., where a shift of retinal local sign is first manifested) does not depend on time from onset of the target movement or ocular movement, but simply on the delay between presentations of the first and second flashes. This result is similar to the one described above in relation to saccades, and suggests some common aspects between the mechanisms for judgments of visual direction in the presence of voluntary saccades and pursuit eye movements. There are not yet enough data for the two types of situations, however, to permit any evaluation of the degree of commonality.

It has generally been assumed that stability of visual direction in the presence of voluntary saccades and the appearance of visual movement of the moving fixation target during ocular pursuit are manifestations of the same mechanism. For the former it has been presumed that the extraretinal signal regarding ocular movement "compensates" visual direction for the shift in location of the retinal images of stationary objects; for the latter it has been presumed that the extraretinal signal operates in a similar fashion but is "unopposed" by a shift in location of the retinal image. No direct evidence exists on this question, however.

C. Involuntary Eye Movements

1. Visual Direction during Fixation of a Visible Target

During fixation of a visible target (see Fig. 3) the probability that an involuntary saccade will return the eye toward a mean or "optimum" position increases monotonically and approaches 1.0 as the deviation of the eye from this position approaches 7′ (CORNSWEET, 1956). Some correction of ocular position is also carried out by means of slow drifts (NACHMIAS, 1959). Since there is a considerable increase in amplitude and rate of the involuntary eye movements when the fixation target is removed and the subject attempts to maintain a steady eye position in the dark (DITCHBURN, 1955; CORNSWEET, 1956; NACHMIAS, 1960; MATIN *et al.*, 1966; MATIN, MATIN, and PEARCE, 1970; SKAVENSKI and STEINMAN, 1970), it is clear that this correction is controlled mainly by information arising from the displacement of the image on the retina from some preferred position[20] and at most in only a minor way by information regarding deviation of the eye itself from a preferred position. Furthermore, since subjects do not "perceive the retinal locus stimulated," but rather perceive targets in particular visual directions, it is clear that the retinal displacement of the image of the fixation target could provide an effective signal regarding error in eye position only if the involuntary ocular displacement is not perfectly compensated by an extraretinal signal involved in the stabilization of visual direction. A similar conclusion follows if we assume that the useful information in eye position correction is direction of retinal image travel rather than a specific retinal offset (or set of offsets). The conclusions drawn in an earlier section regarding failure of the extraretinal signal to maintain stability of visual direction for successive stimulations separated by short durations, along with data regarding typical drift durations (0.5 sec) during attempts

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[20] It has on occasion been suggested that the central 15′ or so in the "fovea" constitutes a "dead zone" within which detection of target displacement is not possible. Clearly this is not so. CORNSWEET'S (1956) results and also those of BEELER (1967) quite conclusively rule out the possibility of such a dead zone.

at steady fixation, and the values of thresholds for detection of direction of real target movement, all have a sufficient correspondence to support the conclusion drawn here that visual direction of a stationary target is not stabilized by an extraretinal signal at least during movement away from the optimum position.

Further evidence on this point stems from some binocular observations. With continuous binocular central fixation on a stereoscopically-presented target adjusted for zero fixation disparity, small brief flashes to eccentrically-located corresponding points of the two eyes will sometimes appear spatially separate ("binocular flash diplopia"). The frequency of this report increases with increase in delay between flashes to the two eyes and with decrease in the area of the flashed targets (Matin, 1962). If accurate compensation of visual direction were associated with the involuntary eye movements, spatial doubling ought not to increase with delay.

Standard deviations of fluctuation in convergence between the two eyes are about 2′—3′ during attempts at steady fixation (Krauskopf *et al.*, 1960). The sizeable correlation between the positions of the two eyes is almost wholly due to the synchrony and correlation in magnitude and direction of the involuntary saccades; drift components show no significant relationship. Although the relative size of synchronous saccades in the two eyes tend to correct for vergence errors, Krauskopf *et al* (1960) have provided evidence that monocular errors in fixation rather than vergence errors provide the stimulus for saccades. The eye that is further from its optimum position generally triggers the saccade and its saccade magnitude is generally larger.

The magnitude of these fluctuations in convergence are roughly the same as Palmer (1961) finds in subjects' reports regarding whether the upper of two 1.5′ targets is to the left or right of the lower when the targets are presented simultaneously for 10 msec, one to each eye. The extent of Panum's area measured with a similar pair of targets with no vertical disparity was about 15′ in the central fovea (Palmer, 1961). Palmer determined this from reports of "singleness" or "doubleness." The ability to report on spatial doubling is thus in part limited by processes of summation and fusion between stimulations to the two eyes. Ogle (1963) has found that reliable reports of depth in response to flashes presented successively to regions of the two eyes which vary in disparity from 0 to 2.5′ extend up to interstimulus intervals between 60 and 100 msec.

2. Visual Direction in Darkness

As indicated above, the increase in magnitude of the involuntary eye movements which occur in total darkness implies that accuracy of fixation of a visible target is controlled mainly, or perhaps wholly, by the displacement of the image on the retina from some preferred position. Typically, these movements contain very many fewer involuntary saccades than do movements in the presence of a visible target (Fig. 15). Available data indicate that the mean (unsigned) deviation of the eye from the prior fixation position increases with time in the dark, reaching about 25′ in 3 seconds (Matin, Matin and Pearce, 1970) and 2° in 2 minutes (Skavenski and Steinman, 1970). In addition, the eye irregularly changes mean position with time in the dark although the eye movement pattern deviates from a random walk (Matin, Matin, and Pearce, 1970).

The increase in variablity in control of ocular position is accompanied by sizeable errors in the report of visual direction of a brief flash presented after fixation target removal to that of the previously-viewed fixation target (Matin and Kibler, 1966; Matin, Pearce, Matin, and Kibler, 1966). With a three second dark interval the proportion of correct reports increased monotonically with physical separation of the flash and fixation target with standard deviations of the response distributions that ranged from 17.4′ to 46.3′ with viewing in primary position; these increased systematically in secondary viewing positions. PSEs systematically shifted leftward and upward as viewing position was moved rightward and downward respectively, changing within a single subject by as much as 1°11′ in the horizontal dimension for a 69° change in viewing position, and 42′ in the vertical dimension for a 67–1/2° change in viewing position (Matin and Kibler, 1966).

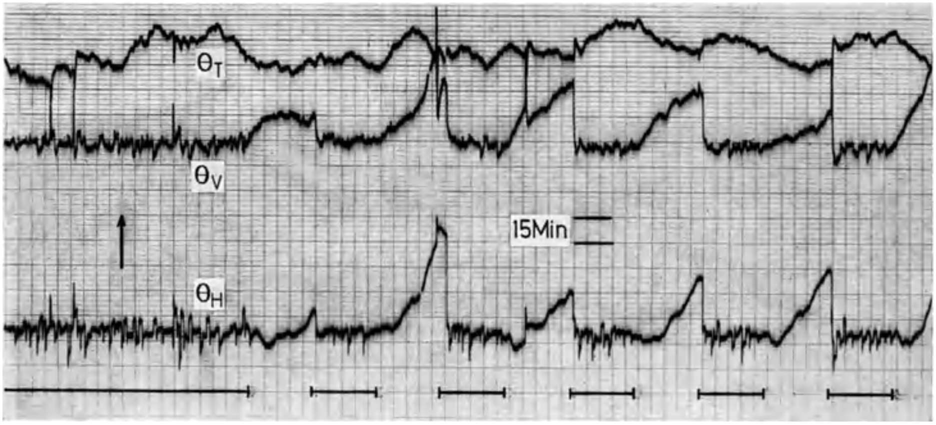

Fig. 15. Involuntary horizontal (Θ_H), vertical (Θ_V), and torsional (Θ_T) eye movements of left eye during periods in which fixation target was alternately visible and extinguished in an otherwise dark environment. The dark horizontal line at the bottom indicates periods during which target was visible; gaps indicate periods of total darkness. Subject attempted to maintain a steady fixation position. The 15′ calibration applies to all three traces. Arrow indicates ocular rotation to right in Θ_H, downward in Θ_V, and top of eye nasalward in Θ_T. Time lines separated by 1 sec. (From Matin and Pearce, 1964)

Between 2/3 and 3/4 of the variance of the response distribution for the horizontal discrimination in primary position was accounted for by making use of simultaneous measurements of eye position (Matin, Pearce, Matin, and Kibler, 1966). Independently of where the eye was located at the moment of flash presentation, the proportion of reports that the flash was to the right of the fixation target increased monotonically as the retinal location of the test flash lay further to the right. Since the psychophysical report for any particular retinal locus of flash stimulation was independent of eye position it was concluded that systematic participation of extraretinal signals containing accurate information regarding eye position was not involved in the report of flash direction relative to the previously-viewed fixation target. Offset of PSE at the retina of as much as 12′ from the central fovea (the mean retinal locus that had been occupied by the image of the fixation target), however, indicated that systematic distortions in local sign had taken place. Similar conclusions were reached by Fiorentini and Ercoles (1968) for similar kinds of experiments employing stabilized images.

In further experiments (Matin, Matin, and Pola, 1968), two vertical lines, one above and the other below a fixation target, were sequentially flashed in darkness each for 2 msec 400 msec after the removal of the fixation target and a report of horizontal vernier offset was obtained. Trial-to-trial variability of the response distribution increased with the interstimulus temporal interval through 800 msec along a negatively accelerated curve (Fig. 16). As in the experiments described above in which the visual direction of a subsequently-presented flash was compared to that of a previously-viewed fixation target, a portion of the response variability was predictable simply from the offset at the retina of the two flashes.

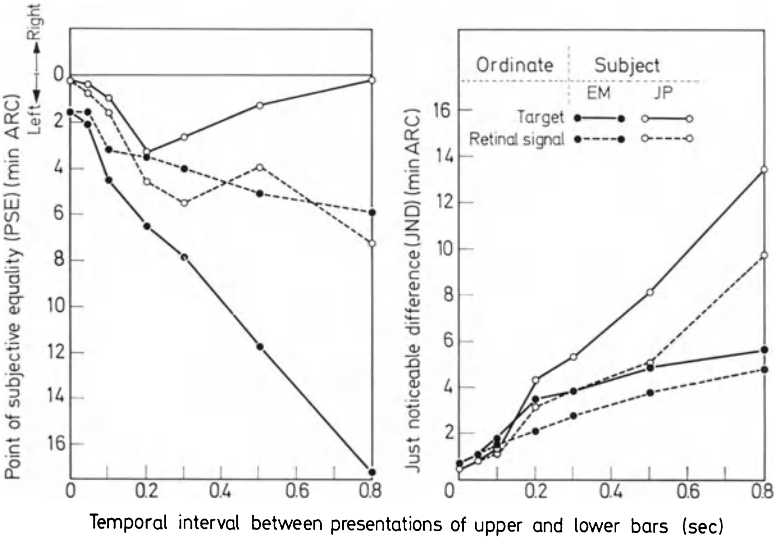

Fig. 16. Points of subjective equality (PSEs) and just noticeable differences (JNDs) for detection of horizontal vernier offset as a function of time between flashed presentations of two vertical lines. "Target" values refer to visual angle distances at the stimulus array. "Retinal Signal" values refer to visual distances at the retina; these were calculated from horizontal offset of the two flashed targets and eye positions at the moments that the two targets were flashed. (From Matin, Matin, and Pola, 1968)

Thus, for example Fig. 17 shows the response distribution over trials for one subject when the two lines had a fixed spatial relation to each other on all trials and were sequentially presented with a 100 msec interflash interval. The horizontal retinal offset (abscissa) between the two lines is thus a result of the 21″ of target offset fixed over all trials represented in Fig. 17 *plus* the offset resulting from the eye movement between the flashed presentation of the two lines (variable from trial). Not only did response variability increase with interflash interval when target offset at the stimulus array was considered without considerations of eye movement, but an increase also was obtained with horizontal *retinal* offset treated as the stimulus (as in Fig. 17); this is also shown in Fig. 16. By employing distributions such as Fig. 17 for different target offsets at any given interstimulus interval, it was possible to compare the response to a given retinal offset under conditions in which the eye had moved different distances in the interflash interval. Since no systematic differences in response were obtained it was possible to conclude that systematic participation of extraretinal signals containing accurate information about the eye movement that had occurred in the interflash interval was not involved in the report of relative visual direction. The latter conclusion held at all interflash intervals and was in agreement with the conclusions reached in the experiments described above in which the previously-viewed fixation target was compared to a subsequent flash.

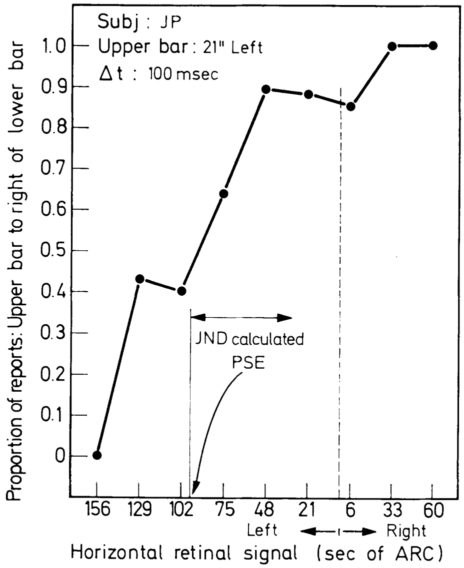

Fig. 17. Proportion of trials in which subject JP reported that the upper vertical bar appeared to the right of the lower vertical bar when one was flashed 100 msec after the other. At the target array the upper bar was 21″ to the left of the lower bar. The abscissa is the horizontal offset between the retinal loci of the two flashes; trial-to-trial variation in this retinal distance is wholly due to trial-to-trial variation in the eye movement between the two flashes. (From Matin, Matin, and Pola, 1968)

However, as in the previous experiments, the PSEs showed substantial offsets from physical colinearity of the targets (Fig. 16). Considered in terms of *retinal* offset, PSEs increased monotonically from values of 20″ when the lines were simultaneously presented through interflash intervals of 800 msec at which point values of about 6′ were obtained (Fig. 16).

It was suggested that the increase in variability of retinal offset for the discrimination of visual direction as well as the systematically increased mean "error" as time elapses between viewing of the two targets whose visual directions are being compared are both indications of a "gradual loss of memory" for the location of the target viewed first (Matin, Pearce, Matin, and Kibler, 1966; Matin, Matin, and Pola, 1968). It was also suggested that the lack of a systematic influence of eye position in these experiments (apart from its effect on the retinal locus stimulated by a flash from a target at a particular location) might be a consequence of a stochastic accumulation of errors in the relation between magnitudes of actual eye position change and the associated extraretinal signals, and that such "noise" might in part underlie the loss of memory (Matin, Pearce, Matin, and Kibler, 1966).

This "loss of memory" would not be easy to reconcile with KOFFKA'S (1935) related view that no stable localization is possible without a stable visual framework. For KOFFKA the apparent vertical and horizontal are determined by the main lines of organization of the visual field, and localization is made relative to them. Since no visual field is present during the experimental session, KOFFKA'S formulation predicts that memory loss should progress throughout a session in spite of periodic presentation of the fixation target-test flash sequence. Such a progressive increase in errors was not found.

A deeper analysis than we can provide here would consider the question of whether a memory loss involves a change in remembered direction (e.g. a target striking a retinal locus which originally signaled "straight ahead" is remembered as lying "to the left" when recall or recognition is tested X seconds later) or such remembered directions remain stable and subsequent inputs to the same retinal locus are seen in different directions than previous ones. Similar questions need to be raised regarding the shifts in local signs related to saccades and pursuit movements.

3. Ocular Torsion in Relation to Visual Direction and Orientation

When a subject assumes a particular direction of gaze, rotation of the eye about the visual axis relative to the orbit may be defined as a torsional rotation. Production of torsional movement is not under voluntary control. However, it has been suggested that torsional responses are stimulated by (a) viewing several different kinds of visual stimuli, and (b) rotation of the head in the frontal plane. In both cases the existence and quantitative properties of such movements need to be considered, and if they exist the question arises as to whether or not they are accompanied by extraretinal signals which influence visual direction. Torsion also accompanies rotations of the globe to tertiary positions of gaze (this has often been called "false torsion"). The discussion below will be limited to (a).

a) Tilt Adaptation. If a line tilted from the vertical within a frontal plane is viewed monocularly for a period of time it appears less tilted. Immediately after viewing the tilted line, the subject reports that a vertical line appears tilted from the vertical (GIBSON and RADNER, 1937; GIBSON, 1937). The change is of the order of 1.5° after viewing a line tilted by 5° for 20 seconds. GIBSON (1937) considered the effect in the context of successive contrast and adaptation to norms. KÖHLER and WALLACH (1944) suggested that it could be treated simply as a figural aftereffect whose general characteristic was an apparent displacement of the test figure away from the location of the inspection figure. The existence of a factor other than or in addition to figural aftereffect displacement is indicated by the fact that after viewing a line tilted from the vertical, a horizontal line appears tilted in the same direction as does a vertical line. The horizontal line appears tilted toward the previously-viewed line which is contrary to the displacement principle of figural aftereffects. In fact, tilt aftereffects of several kinds have been distinguished (MIKELIAN and HELD, 1964; MORANT and BELLER, 1965; EBENHOLTZ, 1968; MORANT and MISTOVICH, 1970).

The apparent tilts of both vertical and horizontal lines are compatible with the occurrence of a torsional eye movement in the same direction as the tilt of the line turned from vertical. Nevertheless, although HOWARD and TEMPLETON'S (1964) subjects displayed a 2° tilt aftereffect to viewing a line tilted 10° from vertical for 10 seconds, they were unable to measure any mean change of torsional eye position by means of a technique capable of 0.2° resolution.

b) Cyclofusion and Torsion. Hofmann and Bielschowsky (1900) used cards of identical print on the two sides of a haploscope. A horizontal line was above center on one card and below center on the other. The fused view is of a single card of print with two horizontal parallel lines. When the two cards are slowly rotated in opposite directions about their centers, fusion is maintained and the lines continue to appear parallel until rotations of 5° to 8° are reached at which point the lines gradually begin to deviate from parallelism and with further rotation fusion breaks. From this it has been concluded that as long as the lines remain parallel, in both eyes ocular torsion has occurred of a magnitude equal to the card rotation (Ogle, 1946).

A sizeable number of other phenomena suggest a similar conclusion. For example: When a binocularly fixated vertical line is tilted around its center in the median plane it no longer can strike the same retinal meridians on the two retinas that it did when it was vertical unless torsional movements occur in opposite directions in the two eyes. Yet such a tilted line has been reported to continue to appear vertical without the onset of diplopia (Ogle, 1946).

By means of meridional afocal magnification lenses, Ogle and Ellerbrock (1946) simultaneously introduced binocular retinal disparities of equal magnitudes in a vertical and horizontal line, but in directions such that, if the binocular disparity for the vertical line were to be eliminated by ocular torsion, the disparity for the horizontal line would be simultaneously doubled, and vice versa (Fig. 18).

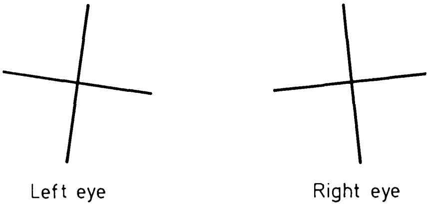

Fig. 18. Stimuli presented to the left and right eyes by Ogle and Ellerbrook (1946). The fused image of the lines nearer the vertical appears like a line in the median plane with the top tilted toward the observer. By rotating the near-vertical lines alone (in effect, this rotation was by equal angles to the two eyes, but in opposite directions in the frontal plane) a setting was determined at which the line no longer appeared tilted

If such targets produce stimuli for torsion, then the stimuli from the two lines were for torsion in opposite directions. Under these conditions the vertical line does appear tilted out of the frontal plane in the direction of the physical tilt predictable from its disparity. Ogle and Ellerbrock then had their subjects adjust the line tilted from vertical until it appeared vertical. This was done over an 80° range of induced tilts and yielded settings which suggested that torsion of a magnitude sufficient to remove the binocular disparity for the horizontal line had occurred (see Fig. 19).

A substantial number of related phenomena have been subsumed under the name "binocular depth contrast" (Werner, 1937; Ogle, 1946). Werner (1937) suggested that these phenomena involved a change in retinal correspondence between the two eyes. Ogle (1946) later suggested that these phenomena and the ones described above indicate that torsion takes place in the interest of maintaining fusion. However, he also reports that when one or more vertical lines are placed on each side of a line tilted within the median plane, the tilted line appears tilted in the direction appropriate to the physical tilt within the median plane and the vertical lines appear tilted in the opposite direction. In this case, while torsion can succeed in placing the retinal images of either the vertical or tilted lines on corresponding meridians, it cannot accomplish both simultaneously. Yet all lines continue to appear single, which indicates, like the examples described above, that torsion is not necessary for fusion to take place.

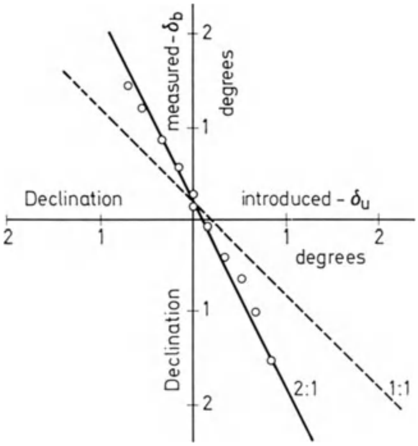

Fig. 19. Data for the configuration in Fig. 18. Declination introduced — δ_u (abscissa) is the deviation of the near-horizontal lines from horizontal. Declination measured — δ_b (ordinate) is the deviation of each of the retinal images of the near-vertical lines from the physical vertical when the fused image appears vertical. (A value of about 1.9° for δ_b would be produced under normal conditions when both eyes view a line tilted in the median plane by 50° at 2 meter viewing distance). That the data follow the 2 : 1 ratio is ascribed by Ogle and Ellerbrook (1946) to the eyes' torting so as to eliminate declination at the retinas for the near-horizontal lines; the subject's setting eliminates declination at the retinas for the near vertical lines

Some of the binocular depth contrast phenomena were later independently treated in the context of three dimensional figural aftereffects (Köhler and Emery, 1947). That something other than figural aftereffect displacement is probably involved, however, is indicated by the fact that such aftereffects are not predicted when the same single tilted line serves both as inspection and test figure; but as indicated above, the latter is an important case in point.

In 1936 Beasley and Peckham looked at the eye through a telescope and reported in a brief note that they could observe no torsion under conditions in which vertical stimuli were rotated by ± 10° (or horizontal stimuli rotated by ± 3°) in stereoviewing while fusion was maintained. Recently, Kertesz and Jones (1970) have reported the maintenance of fusion for rotations by ± 5° in each eye of stereoscopically-presented horizontal lines (as in Fig. 18). But measurement of torsion by a contact-lens technique and by observation of a radial conjunctival blood vessel did not reveal any change in torsional position of the eye while fusion was so maintained. (They report a resolution of 0.5 and 0.25° for the two methods respectively). Further, by comparing the magnitude of binocular vertical retinal disparity introduced by the rotation of the horizontal lines to MITCHELL'S (1966) values for the sizes of Panum's area, KERTESZ and JONES (1970) conclude that fusion could have been maintained within Panum's area entirely without the occurrence of torsion.

Although the fact that fusion does not require torsion in the situations described above was clear in the older data, KERTESZ and JONES' failure to find torsion suggests the possibility of local sign flexibility in some of the phenomena described above and the need for new explanations. Thus, the facts that a line tilted in the median plane appears vertical when viewed alone, and appears appropriately tilted when viewed along with a fused horizontal line with equal sized but "oppositely-directed" disparity (Fig. 18) are left unexplained. The former may be a manifestation of simultaneous tilt adaptation in the two eyes. The latter phenomenon and some of the binocular depth contrast phenomena can be similarly interpreted.

A simplified statement of one such interpretation is: Simultaneous viewing of the two lines in Fig. 18 by each eye alone would induce opposite tendencies for tilt adaptation; hence no net adaptation would occur in each eye. Thus when the targets in Fig. 18 are viewed, the fused image arising from the lines tilted from vertical in the frontal plane should continue to yield the appearance of a line tilted in the median plane. However, the basis of tilt adaptation itself is not understood. In addition, in the original demonstration by HOFMANN and BIELSCHOWSKY, the two horizontal lines (one to each eye) would have changed their relative retinal orientations by 10° to 16° if no torsion had taken place. More work is needed on these problems.

D. Convergence

Within some limits objects do not normally appear to undergo substantial changes in size when viewing distance is changed despite size changes in the retinal image. When fixation is shifted from a distant point to a near point the triple response of convergence, accommodation, and pupillary contraction occurs. Whether extraretinal signals associated with any of these oculomotor adjustments are involved in the mechanisms underlying size constancy is a question that has proved difficult to analyze. No clear information is presently available with regard to either accommodation or pupillary size changes. However, HEINEMANN, TULVING, and NACHMIAS (1959) have quite convincingly shown that variation in convergence does result in changes of apparent size in a direction appropriate to assist in the production of size constancy.

In their experiments subjects were required to compare the sizes of two discs sequentially presented at different distances under conditions in which contextual cues were eliminated. Use of 0.5 mm artificial pupils eliminated changes in accommodative adjustment in response to a change in viewing distance, and under one condition variations of accommodation were eliminated with drugs. When the subjects carried out a monocular comparison of a variable disc presented at a distance of 400 cm with a 1° standard disc presented at 25, 33.3, 50, 100, or 300 cm, the size equation (with the artificial pupil in place) resulted in settings that were essentially retinal size matches. However, when a binocularly-viewed fixation point was fused under different degrees of convergence (with artificial pupils) the size comparison of the discs (again monocularly-viewed) changed with viewing distance in a way that did not result in an equation of the retinal images of the two discs. The retinal image of the more distant disc (at 400 cm, viewed monocularly with convergence appropriate to the distance) had to be made smaller than that of the nearer disc (at variable distance but always subtending 1°, and viewed monocularly with convergence appropriate to its distance) in order to appear equal to it. This decrease in size changed systematically with viewing distance of the nearer disc (in the direction of a tendency towards size constancy). The total effect of convergence itself, however, is only a small part of size constancy. Identical effects were obtained with and without paralysis of accommodation. The latter condition eliminated changes in accommodation consequent to changed convergence and the resultant possibility of an extraretinal involvement due to accommodative change itself. Essentially similar results have been obtained by BIERSDORF, OHWAKI, and KOZIL (1963).

E. Basis for Extraretinal Signals Related to Eye Movements

HELMHOLTZ (1866) concluded from the appearance of visual movement consequent on attempts at turning the paralyzed eye and consequent to passive ocular movement that an extraretinal signal derived from the "effort of will" was responsible for maintaining the normal appearance of stability when the direction of gaze was changed ("outflow theory"). Unopposed by the normal displacement of the image at the retina in the paralyzed eye, this signal was presumed to give rise to the visual appearance of movement. Unopposed by the "effort of will", the retinal image displacement caused by passive eye movement was also presumed to give rise to visual movement. On the other hand, JAMES (1906) and SHERRINGTON (1918) argued that muscle spindles in the extraocular musculature provided the source for the extraretinal signal resulting in perceptual stability when eye movements occur ("inflow theory"). The evidence presented in earlier sections above makes it clear that the extraretinal signal, regardless of its source, is not sufficient to account for the normal stability of perception of stationary objects. Nevertheless, the basis for the extraretinal signal remains a problem.

The results with the immobilized (MACH, 1906) or paralyzed eye have weighed most heavily in the considerable number of subsequent evaluations of the problem, and KORNMULLER'S (1930) work, in which the subject reported visual apparent movement when he attempted to turn his eyes following novacaine injection into his extraocular muscles, is generally considered to provide the clearest support for the older observations. This is also generally considered decisive in favor of outflow theory. Since the paralyzed eye does not move it has been presumed that change in muscle spindle discharge could not be involved when an attempt is made to turn the eye. Furthermore, the observation that an afterimage viewed in darkness does not appear to move as a consequence of passive eye movement (HELMHOLTZ, 1866) has also been cited in support of outflow theory, as has the finding that involuntary movements during attempts at steady fixation in darkness do not systematically influence fluctuations in local sign (MATIN *et al.*, 1966. See above).

These results are less than critical, however, and further considerations are in order. (These considerations are taken here not to affirm the validity of the hybrid mechanism described below, but to point out that the "paralyzed-eye" experiments cannot, without further kinds of manipulations, rule out the utility of an inflow signal in determining visual perception of direction.) KORNMÜLLER (1930) did not believe that the novacaine which he injected into the extraocular muscles in the region of the insertion in the globe produced paralysis, but that instead the large mass of injected fluid produced an exophthalmic condition which in effect immobilized the eye. Further, if muscle spindles continue to be active in such immobilization, or in experimental or clinical paralysis, apparent movement on attempts to turn the eye does not at all rule on whether the extraretinal signal is inflowing or outflowing. It is now well-known that two sources can modify the afferent signal from muscle spindles: (1) Modification occurs when the extrafusal muscle is stretched or contracted. (2) Modification occurs when motor innervation to the intrafusal muscle fiber that is part of the spindle is changed (GRANIT, 1955). The latter innervation is via the gamma efferent motor fibers, some of whose sources of control are central and do not appear to lie within direct reflex paths such as might be expected to produce stretch reflexes. It is thus possible that when the extrafusal muscle of extraocular musculature was paralyzed, intrafusal fibers remained active. Certainly this would be so in experiments which involve immobilization without paralysis. One possible consequence of a subject attempting to turn his eye then is a centrally-arising increase in excitation of the gamma-efferents leading to spindles in the agonist muscle and a reduction of excitation or an inhibition of the gamma efferents leading to spindles in the antagonist. These changes would result in an increase in tension in the associated intrafusal muscle of the spindles in the agonist and a decrease in tension in the associated intrafusal muscle of spindles in the antagonist. Such a consequence would produce oppositely-directed modifications in the afferent signals from muscle spindles in the two muscles and thus could give rise to a directionally-biased extraretinal signal which produces a change in the relation between perceived visual direction and retinal locus when the subject attempts to change his direction of gaze. Such a result does not depend at all then on whether the eye position, and so muscle length, actually changes or not. If the attempt does not yield an eye movement, as in the paralyzed or immobilized eye, the extraretinal signal would produce an appearance of visual movement; if the attempt yields an eye movement, as in the normal eye, visual movement would not result (MATIN and MATIN, in preparation).

Since the location of most spindles is at the other end of the muscle from the site of KORNMÜLLER'S novacaine injection, and since the anesthetic did not appear to diffuse rapidly, continued spindle activity is not unlikely. Whether spindles remain active in fresh cases of clinical paralysis, when visual apparent movement occurs with attempts to turn the eye by the paralyzed muscle(s), is also unclear. Still further, SIEBECK (1954) reports that curare injections into extraocular muscle resulted in apparent movement only during the prodromal period when attempts were made to turn the eye. He reports that when paralysis was complete such attempts did not result in apparent movement, and ascribes this to the subject's awareness of his limitation of change of the direction of gaze. Since transmission in extrafusal neuromuscular junctions is more sensitive to curare than transmission at intrafusal myoneural junctions (MATTHEWS, 1964) it would also be expected that the gamma control of spindle afference would be eliminated later during the developing paralysis. SIEBECK'S results are thus easily interpretable in terms of the hybrid mechanism pointed to in the previous paragraph. This hybrid mechanism could also serve to explain some aspects of the information presented above. For one thing the sizeable shifts in local sign for stimulation presented as early as 240 msec before the saccade (MATIN, MATIN, and POLA, 1970; see also Fig. 10) are not reasonably treated in terms of SHERRINGTON'S inflow theory which requires the occurrence of the eye movement before extraretinal signal generation can occur. In addition, the influence of either eye position or saccade length on the shift of local sign for test flashes following the saccade (Fig. 10) requires that outflow theory become somewhat more complicated. It can be handled directly, however, by the hybrid mechanism. A more detailed analysis of the psychophysical and pharmacological aspects of the "paralyzed eye" could do much to clarify the mechanism. Among other things, it would be worth knowing whether the elimination of apparent movement after the prodromal period in SIEBECK'S experiments could be caused by the effects of learning during that period.

Although the dual control of spindle output, and the consequent possibility of a hybrid mechanism, make the available "paralyzed eye" data less crucial for support of the outflow theory (indeed SIEBECK'S report provides negative evidence), a variety of related considerations have led a number of workers to conclude that muscle spindles play no role in our sense of position – for the eye or for limbs – or in determining perceived visual direction (IRVINE and LUDVIGH, 1936; LUDVIGH, 1952a, b; ROSE and MOUNTCASTLE, 1959; BRINDLEY and MERTON, 1960; MERTON, 1961, 1964). Noting that afferent signals from muscle spindles are not uniquely related to muscle length (and so, in limbs, to joint angle and limb position), due to modulation of these signals by the gamma efferent fibers which control the tension of the intrafusal muscle fibers of the spindle, ROSE and MOUNTCASTLE (1959) conclude that signals from the spindles cannot reliably inform on limb position. In addition, they question previous reports that spindle signals arrive at somatosensory cortex, considering such arrival necessary if spindles are to subserve a sense of limb position. The necessity for such arrival if spindles are to mediate a position sense may be questioned. In any case, the presence of spindle signals from forelimb muscle arriving at the cortex has been established in cat (OSCARSSON and ROSEN, 1966), and the possibility of further instances cannot be ruled out.

Perhaps most damaging to the possibility that signals from muscle spindles inform on position sense or influence visual direction is the attractiveness of the interpretation which treats them as "misalignment detectors" (MERTON, 1951, 1964; ELDRED, GRANIT, and MERTON, 1953). This interpretation assumes (a) that such detectors serve to maintain muscle length constant under varying load, and (b) that voluntary attempts at movement result in gamma barrage which produces an increased spindle output preceding the contraction of extrafusal muscle, and that extrafusal muscle contracts only so far as is necessary in order to return the signals from spindles back to the level they had before the command to move was given. If this is the case, then spindle signals could hardly serve to signal muscle length. Too little is known about single units during voluntary movements to consider it as more than an interesting hypothesis at the moment. MATTHEWS (1964) states "the idea that movements are ever normally initiated solely by means of the γ route is not yet established." Although GRANIT (1966) contests this, his argument does not refer to voluntary movements in the intact preparation. In fact the results of TAUB *et al.* (1966) on monkeys with spinal deafferentation raise serious questions for the misalignment hypothesis as fundamental in voluntary movement.

For jointed limbs it is clear that position sense for passive movements is subserved in a major way by receptors in the joints since anesthetization of a joint either considerably reduces or completely eliminates the ability of a subject to report on passive movement of the attached limb (see ROSE and MOUNTCASTLE, 1959, and MERTON, 1964 for summaries). Further, MERTON reports that when a pneumatic tourniquet is placed on the wrist, making the joint and skin of the thumb anesthetic without any effect on the muscles, the subject becomes insensitive to passive movements of the top joint of the thumb. Active movements (without visual stimulation) are made with the same accuracy as without ischemia, and if movement is restrained by holding the thumb while the subject attempts to move it he believes that he has succeeded in moving it. In MERTON's subject stretch reflexes remained, as indicated by increased electromyographically recorded discharge from the flexor when the upper joint of the thumb was forcibly extended while the subject was attempting to maintain steady flexion. MERTON reports that the subject could generally detect the forced extension but attributes it to slight consequent movements of the forearm causing slight changes in pressure to the skin rather than to changes in spindle output.

In jointed limbs a given limb position may be associated with a large range of loads on the associated muscle. It is not known for the case of voluntary movement whether such variations in muscle tonus at fixed limb positions are associated with variation of afferent signals from muscle spindles, although this appears to be likely. If this is so, the likelihood of spindle signals as useful sources for informing on limb position is reduced. However, for the extraocular muscles under normal conditions, muscle load and length (and thus eye position) are in an essentially invariant relation. Nor do the muscles serve an antigravity function. Stretch reflexes do not seem to be present. Something approaching an invariant steady state relation between gamma input, spindle output, and muscle length is thus a more likely possibility for extraocular muscle.

In experiments partially analogous to those MERTON (1964) reports for the anesthetized thumb, BRINDLEY and MERTON (1960) have found that when the eyes of subjects in total darkness are passively rotated (by pulling with forceps on the anesthetized conjunctiva), the subject is not able to report a change in eye position even for rotations as large as 30°. Since the muscle spindles present in human extraocular muscle (COOPER and DANIEL, 1949) must have been stimulated, it was concluded that whatever information is available for verbal communication regarding eye position or change in eye position does not arise from spindles. On the other hand, when the eyes were prevented from rotating (again in total darkness) while the subjects attempted to turn them, they reported that the eyes did turn (BRINDLEY and MERTON, 1960). The authors interpret these results as supporting an outflow mechanism for the position sense, as does MERTON (1964) for the experiments on the thumb. However, the latter result could be a consequence of a hybrid mechanism at work with gamma motor input changing during the attempt at turning the eyes and producing a change in spindle output which is treated as change in eye position by the subject. In addition, SKAVENSKI (1970) has recently reported that when a subject's eye is pulled from a resting position in darkness while he attempts to maintain a prior fixation position during maintained application of the force, his subsequent movements return the eye toward the prior position. The subject is able to correctly report the direction of pull when a force of at least 10 gm is imposed (1.25 gm/deg. is the normal relation between applied force and ocular rotation: ROBINSON, 1964; SKAVENSKI, 1970). The basis for the disagreement between the results of BRINDLEY and MERTON (1960) and of SKAVENSKI (1970) is as yet unclear. Although it is not altogether likely in view of the large rotations to which BRINDLEY and MERTON subjected the eyes of their subjects, the possibility exists that the passivity of their subjects (they were not attempting to hold their eyes in a given position) played some role in their inability to report that their eyes were turned by unloading the spindles via the gamma motor fibers. Some support for this possibility, and for this version of a hybrid approach to the ocular position sense, can be found in WHITTERIDGE'S (1959) report that increased input to the gamma motor fibers subserving spindles in the extraocular muscle of the goat resulted in an increased sensitivity of the spindle to stretch (i.e., an increased slope of the function relating spindle firing rate to applied stretch). If this were the case in humans it would provide a basis for interpretation by the hybrid mechanism for both of BRINDLEY and MERTON'S key observations and for both of SKAVENSKI'S.

Selective elimination of spindle output from extraocular muscle has not yet been feasible although it would clearly be a desirable means of separating inflow and outflow signals. Monkeys with complete spinal deafferentation can reach accurately for seen objects without viewing the hand (TAUB *et al.*, 1966; TAUB and BERMAN, 1968), thus demonstrating the presence of an outflow signal involved in position sense for the arm and the lack of necessity for signals from muscle spindles. The possibility of inflow involvement, however, is indicated by the finding that adaptation to horizontal displacement of the visual field induced by wearing wedge prisms, normal monkeys showed only a 39 % initial aftereffect on prism removal, whereas for deafferented animals the initial aftereffect was 100 % (TAUB *et al.*, 1966; TAUB and BERMAN, 1968). Whether the inflow involvement is spindle-mediated, or mediated by cutaneous and joint receptors cannot yet be decided, however, since spinal deafferentation was complete.

In effect, then, for the visual system we are left with no clear picture as yet whether an inflowing signal (via a hybrid mechanism) or an outflowing signal, or both, are involved in the ocular position sense or in the visual perception of direction. This ambiguity of outcome is perhaps mirrored in uncertainty about the neural locus of such an extraretinal signal. Although not entirely ruled out, the primary visual projection system through striate cortex is unlikely. The frontal eye fields have sometimes been considered as a prime possibility for such a locus. However, this possibility has not yet been sufficiently explored. BIZZI (1968) and BIZZI and SCHILLER (1970) report two types of cells related to eye movements in the frontal eye fields. Units of Type 1 discharged during (but not before) saccades in a given direction and during the fast phase of optokinetic or vestibularly-induced nystagmus, but were silent during slow eye movements and during steady fixation. Units of Type II responded during steady fixation, during slow movements, and during the slow phase of nystagmus with discharge frequency monotonically related to eye position. These show quiescence during saccades. Neither type appears to be influenced by visual stimulation. The authors mention some indirect evidence against the relation of their results to an inflowing mechanism, but the interpretation is by no means certain as yet. Some single cells in the superior colliculus have visual receptive fields (SCHAEFER, 1966; MCILWAIN and BUSER, 1968; STERLING and WICKELGREN, 1969), others receive vestibular (SCHAEFER, 1967) or proprioceptive inputs (COOPER *et al.*, 1953), while others without apparent direct sensory control fire before eye movements (WURTZ and GOLDBERG, 1971). This has suggested the superior colliculus as a focus at which extraretinal signals may influence the perception of space. Of course, it is entirely possible that transformations of local signs by extraretinal inputs involves activity at more than one central neural locus.

It is reasonable to think that a subject's difficulty or inability to verbally report eye position and to control eye position in darkness, and his ability to counteract and report the direction of an imposed rotational force applied to the eye bear on the question of the basis of the extraretinal signal involved in visual direction. In this discussion, these effects have been considered separately as well as together. The connection, however, is not a necessary one. Although it is frequently presumed that the extraretinal signal involved in visual direction should be identical to the one used for reporting on eye position and for controlling it, it has not been conclusively shown that information on eye position influences the perception of direction of visual stimuli. There are, however, a number of studies in which subjects were required to report on the direction of visually-presented targets and the data are interpreted as measures of an ocular position sense. Clearly the question of where a subject feels his eye to be and where he sees a visual target are separable questions. How the two are related is an additional question. Although some basis for a relation is evident in experiments involving modification by experience, this issue takes us beyond the scope of the present chapter. (See HELD and FREEDMAN, 1963; HARRIS, 1965; ROCK, 1966; HOWARD and TEMPLETON, 1966, for related considerations.)

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