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Moveo Ergo Video: Natural Retinal Image Motion and its Effect on Vision

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ABSTRACT
This paper describes highlights in the nearly century and a half long history of continuous research on the role of retinal image motion in limiting or influencing visual acuity. This review is followed by a summary of recent work in which it has been shown that oculomotor compensatory actions leave appreciable retinal image motion that, unexpectedly, has only minor detrimental effects on the capacity to resolve fine details in the visual scene. This paper is based on a talk delivered at an interdisciplinary conference under somewhat unusual conditions — conditions that encouraged adoption of a novel organizing theme to allow description of such a lengthy and voluminous body of work. The coherence of the material in this published version of the talk required preserving and explaining the organizing theme adopted. Participants in the collaborative research described in this paper may have quite different memories of why and how they became involved with the author in the various projects described. The reader is warned that the "motivations" described are, in fact, not fictitious, but they may be entirely true only when seen from the author's viewpoint.

1.1 Prologue

This chapter is based on a talk which was the first time I had been asked to be an after dinner speaker. I only discovered this the night before I spoke. After dinner speaking is usually assigned to someone good at telling jokes. Well, I know only two, neither really good. Surely, I was not asked to speak after dinner for this reason. The organizers of the workshop knew me and my two jokes too well to make this mistake. I also learned the night before my talk that dinner would be accompanied by wine and preceded by a "hosted" reception. Could it be that the organizers gave me the after-dinner slot because they thought that my topic would keep sated listeners ("bombed" in the vernacular) alert despite the hour and their condition? Probably not. Consider, . . .

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I had been asked to talk about the way in which eye movements influence how we see the world. The modern history of this problem goes back 136 years. I was also asked to be sure to include a description of research I, and a number of collaborators (most notably, Han Collewijn, Jack Levinson and Alex Skavenski) had done during the last decade on eye movements and vision when a subject supports or moves his head in a relatively natural manner. Offhand, it isn't obvious that this topic, in itself, guarantees rapt attention. It seems more suitable for a 14 week graduate seminar, or, if not for a seminar, at least for a morning session in front of an alert or, at least, sober audience. In the present circumstances, what was I to do?

For a start, I made a great personal sacrifice, eschewing all alcohol and substituting 6 cups of coffee. In short, I arranged to keep myself awake well past my preferred bedtime. This solved only half of the problem. I was still faced with the inescapable fact that the audience would fall asleep if I didn't do something startling. Sex and violence, the traditional crowd stimulators, were rather tangential to my topic. How could I discuss physiological nystagmus and liven up an audience suffering from physiological nystagmos? I decided to try something unusual in discourse on serious scientific matters. I decided to tell the truth. Here, I describe how our research on natural retinal image motion actually came to be done, what actually motivated our work. We did not self-actualize. We had no theories, no profound thoughts, no important historical precedents, no serendipitous observations, not even sudden insights. We got phone calls — periodic, unlikely, phone calls. I will describe the source and nature of these electronic revelations as we proceed.

1.2 Introduction

Let me begin the substantive portion of this chapter by pointing out that interest in the role of eye movements in vision goes back a long way. Part of the reason for this persistent interest — the reason that most of us working in this area think about today — is rooted in the heterogeneity of the human retina. By way of quick reminder, each of your eyes has about a 100° monocular visual field on the horizontal meridian, and about a 90° visual field on the vertical meridian. Your foveal floor, containing most of the 5 to 6 million cone receptors found in a single human eye, is a densely packed region that only has a diameter of about 90 minutes of visual angle — only a degree and a half — this works out to a "region of best detail and color vision" that occupies something like 1/40th of 1% of the area of the retinal surface. Why did Charles Darwin make our visual detector in this fashion and how do we manage to survive within its limitations?

This question will not be answered in this paper. It will only be mentioned briefly once again when we consider the role of very small eye movements in enhancing contrast. Interest in my topic actually began with a different, and much more fundamental problem, namely, how do we, as perceivers, come to know that the visual world is extended in the 3-dimensional space around us. Modern discussion of this problem starts in 1852 with Lotze, a philosopher-psychologist, who approached it from the position of the Associationist Philosophers, who continued a tradition begun in the 17th C. by John Locke. This tradition in perception emphasizes the important role of learning in constructing a perceptually organized world. Lotze's idea was that you are born with no knowledge of visual extent. You have the capacity to move your eyes and you use your eye movements to construct what he called "local signs" — these are markers that can tell you where things are located in the visual world relative to yourself.

Now, what was the basis for Lotze's model? It was not linear systems or AI symbols; not even neural networks. There were only 2 minor variations of a single model in 1852. You adopted either the St. James version or the Roman version. The central issue, often called the nature-nurture problem, is how much knowledge about His world are you given by the Creator and how much must you learn? Not much is assumed to be given innately in the Locke-Lotze tradition; only sensations of qualities (such mental states as red or sour) and sensations of intensity (such mental states as degree of brightness or sourness). Everything else must be learned. Lotze started his treatment of visual extent by postulating that eye movements were used to learn retinal "local signs" ("place tags" in Koenderink's contemporary usage). Their positions relative to one another were not known a priori. Eye movements established this relationship through a learning process. By the turn of the present century Hering (1899), who preferred a nativistic approach in much of his theorizing about perceptual processing, postulated that retinal "local signs" contained a priori knowledge of the absolute and relative positions of objects in 3-D space that were represented in the visual array (a 2-D representation of the visual field on the retinal surface, i.e., the image plane). Hering used these built-in local signs in seminal ways, as will be shown later, but at the turn of the present century eye movements were still believed by some to play an important role in the perception of relative size. For example, Wundt (1910), the founding father of Structural Psychology, explained the Müller-Lyer illusion by reference to differences in the size of eye movements used to examine each of the figures. His claim was discredited by researchers who measured eye movements while the illusion was viewed. A role for eye movements in perceiving size will not pop up again for more than 60 years when Festinger proposed his "efferent readiness theory", which I will describe after a brief treatment of Hebb's motor theory of form perception.

Hebb (1949) revived the empirical tradition in perception after the Gestalt revolution "died of success" (Boring, 1942). Hebb's model fell out of favor, following the work of Hubel and Wiesel in the 1960s. Hebb required that newly-sighted kittens (as well as human infants) would only perceive what he called "primitive unity", i.e., a shapeless smudge bearing only a crude figure-ground relationship with its surround. It had no contour or shape. Everything beyond this "primitive unity" had to be learned by fixating and making eye movements. First lines and corners or angles were learned. Hebb called these learned features "cell assemblies". Once these features were learned the young animal started to learn eye movement patterns, called "phase sequences", by repeating over and over again the pattern of saccades required to scan from feature to feature in a particular shape. "Engrams" (hypothetical brain correlates of a memory), representing these learned oculomotor patterns, or "phase sequences" provided the neural substrates for perceiving and discriminating shapes. Hubel and Wiesel (1962, 1963) found that the primary cortical monocular receptive field organization of newly-sighted kittens did not differ in fundamental ways from the monocular organization of their parents. Kittens had everything except functional binocular input. This is a fatal problem for Hebb's theory but, interestingly, many contemporaries (including Hubel and Wiesel, 1963) confused Hebb's emphasis on line and corner features with the basis upon which he said that these features were formed. Specifically, for Hebb it was the organism's oculomotor behavior, not pre-existing brain circuitry, that provided the basis on which the perception of shape was learned. Hubel and Wiesel's work with newly-sighted kittens discredited Hebb's claim.

Festinger (1971) revived motor theory of shape and size perception. He explicitly avoided considering the problem of the ontogeny of these capacities and proposed that the oculomotor program that was made ready by the visual representation of a given shape provided the basis of the percept of its shape. How the eye would move to explore a triangle, for example, was the proposed mechanism. This program would be different from the program that would be loaded to explore a round or rectangular form. The question of whether the Creator or the individual infant wrote these programs was ignored. Festinger's approach seemed timely because terminology like "loading programs" had a nice modern ring in the late 1960s and early 70s. Such terms were at least as compelling as "model" or "representation" or "module" are today. None of these terms is quite up to inspiring the glazed looks in both speaker and listener that could be aroused by slowly incanting "massively distributed parallel processing" a few years ago. But talking about "loading programs" did get Festinger's oculomotor theory of shape and size more attention then it deserved on the basis of the long, and clearly fruitless, history of similar, earlier attempts. Festinger's "theory" had the advantage of being almost incapable of falsification because it does not require that any eye movements be made; it was sufficient merely to load the appropriate programs to perceive or discriminate shapes. The one test possible, namely, an examination of spontaneous eye movements that were made in the presence of different forms, did not support the theory (Murphy, Haddad & Steinman, 1974) and it dropped out of sight during the 80s.

At present, motor theories of shape and size are not prominent in current research on human perception. At least for shape and size perception, the phoenix hatched by Locke has no active support in the contemporary oculomotor community. Robots, however, are beginning to moves their eyes and may, therefore, be learning to discriminate directions, sizes and shapes. At this point I will put aside further discussion of the role of eye movements in higher perceptual processes such as direction, size and shape perception and turn to the role of eye movements at a more fundamental level of visual science, namely, their role in the discrimination of contrast or, using an older, and somewhat broader term, their role in visual acuity.

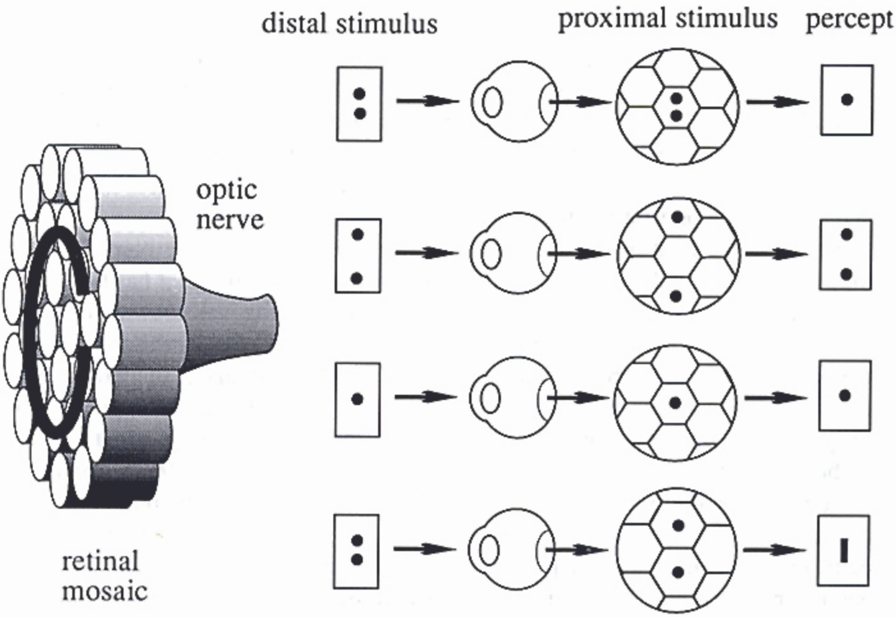


FIGURE 1.1. The retinal mosaic theory of visual acuity. Distinguishing a C from an O requires that one receptor be unstimulated. Distinguishing a point from two points requires at least one unstimulated receptor (redrawn from Hochberg, 1964).

1.3 Relation Between Eye Movement and Visual Acuity Circa 1900

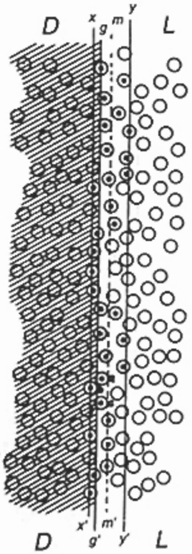
Ideas about this relationship were well-established as the 20th Century began. Here, as well as in many other areas, Helmholtz and Hering adopted alternative views. Helmholtz ignored the role of eye movements entirely and Hering gave them an important role in spatial vision. Helmholtz (1866) is often said to be the author of the "retinal mosaic" theory of visual acuity — an approach that holds that the factor limiting the ability to discriminate spatial details is imposed by the fineness of the receptor grain in the retina. The main idea is illustrated in Fig. 1.1, which illustrates how this idea is presented in introductory treatments of perception.

Fig. 1.1 is largely self-explanatory. It shows, on the left, that the gap in a Landolt C will only be discriminated if the size of the gap allows at least a single receptor in the mosaic to remain unstimulated. On the right it shows that a gap in the retinal mosaic between 2 point stimuli will be necessary for the observer to make out that there are 2, rather than 1, stimuli falling on his receptor surface. Clearly, if the eye were to be in motion, if there were eye movements, the story would become much less straightforward. The receptors near the region of the gap would receive, on average, less light than their neighbors and the students in the introductory perception class would require a prerequisite course in elementary statistics before they would be prepared to deal with how the brain might handle visual acuity by calculating means and standard deviations. Even if the eye was not in motion, there are problems with the "retinal mosaic" theory illustrated in Fig. 1.1 despite its obvious didactic value. First, the source of this theory is controversial. Many authors ascribe it to Helmholtz, but there is reason to question this attribution. Second, it entirely ignores the aberrations of the normal human (or any other) "simple eye". These aberrations (e.g., chromatic aberration, spherical aberration and diffraction) prevent the formation of retinal light distributions even remotely like those illustrated in Fig. 1.1. Sharp edges in the stimulus are blurred when they are imaged on the retinal surface. It seems unlikely to me (as it has to others, e.g., Wilcox & Purdy, 1933, or Walls, 1943) that Helmholtz was unaware of these phenomena in the living eye and their inescapable consequences for the character of the proximal stimulus (the light distribution in the retinal image plane where light is transduced into a neural message).It is hard to believe that Helmholtz actually proposed the theory illustrated in Fig. 1.1 despite the fact that distinguished modern authors have ascribed it to him (e.g., Riggs, 1965, or Le Grand, 1967). There are more plausible alternatives, namely, that Helmholtz implicated the retinal mosaic as an acuity limit for didactic purposes only for the case of hypothetical light distributions of mathematical points or lines and then actually proposed that visual acuity, in real living eyes with real proximal stimuli, is limited by the ability to discriminate differences in light intensity falling on adjacent receptors rather than by the presence of unstimulated retinal elements (see refs. cited just above or Steinman & Levinson, 1990, for a discussion of the controversy surrounding Helmholtz's use of the mosaic concept in his treatment of visual acuity). The idea that visual acuity is limited by the ability to discriminate differences in the intensity of various regions in the retinal light distribution was developed by subsequent investigators who, like Helmholtz, also ignored the potential importance of eye movements. Hartridge (1922) and Hecht (1927, 1928; Hecht & Mintz, 1939) were the most prominent proponents.

Hering's treatment of visual acuity was different. He did not ignore eye movements and introduced the approach that would lay the foundation of what will come to be called "dynamic", as contrasted with "static", theories of visual acuity (Falk, 1956). Hering (1920) distinguished two kinds of spatial vision — "resolving power" as studied in traditional acuity tests (the kind of tasks illustrated in Fig. 1.1) and the "spatial sense" — the remarkably keen capacity to detect minute offsets in vernier and stereo acuity targets, where resolution of offsets was possible of elements differing laterally or in depth by only a few seconds of visual angle, that is, by amounts very much smaller than the grain of the receptor surface (Westheimer, 1981, recently renewed interest in such tasks, calling these capacities "hyperacuity"). It was while considering problems of the spatial sense that Hering introduced his treatment of local signs (mentioned above) that was subsequently picked up in the 1920s by Weymouth and developed into a dynamic theory of visual acuity. Hering's use of local signs to explain the straightness of an edge in a living, moving eye is illustrated in Fig. 1.2.

Hering was concerned with how it was possible to perceive a straight edge when its retinal light distribution would fall on an irregular spaced mosaic of retinal

FIGURE 1.2. Illustrates Weymouth's theory of vernier and stereo-acuity. The diagram shows retinal conditions at the margin of a stimulated area. *D–D* is in darkness, *L–L* is illuminated. The geometrical margin of the image is *g–g′*. The cones are shown as circles. Cones *a*, *b* and *c* (near the bottom of region *g–g′*) have local signs whose "center of gravity" is amidst them, tending to pull b to the right. This action among all of the cones cut by *g–g′*, smoothes the percept of the contour despite the raggedness of the line of cones concerned. Furthermore, normal nystagmus shifts *g–g′* back and forth between the between the extreme positions *x–x′* and *y–y′*, so that *m–m′* represents the center of gravity of all the points stimulated, and is the "local sign" of the percept. The localization of this percept is independent of such factors as the size of one cone (from Walls, 1943).



receptors while the edge moved back and forth through an appreciable distance (the receptor mosaic at the center of best vision in the fovea was believed to be somewhat irregular until quite recently; it is now known that these irregularities were caused primarily by histological artifacts). The edge extending from *x–x′* in Fig. 1.2 moves over to the right to position *y–y′* and back again. The line, *g–g′*, in this figure is the physical edge before it moves and *m–m′* is the average of the positions of the edge, oscillating across the jagged receptors shown as circles. (Fig. 1.2 is taken from Walls' 1943 illustration of how Weymouth's dynamic theory worked. Weymouth, in turn, credited Hering, 1899, with the basic ideas illustrated in this figure.) Hering suggested the idea of averaging local signs to improve the apparent straightness of an edge but did not provide experimental support for the basic idea or for its extension to vernier acuity, omissions Averill and Weymouth (1925) proceeded to correct. The way they did this is illustrated in Figs. 1.3 and 1.4.

The basic idea of their experiments was rather modern. They did a simulation of what should be happening on the retina during a test of vernier acuity. They then had an observer (they called him a "reagent") detect the offset of an edge, which could be stationary or moving in the way they thought the eye would move during maintained fixation. They also varied exposure duration, the length of the edge, and whether the edge was seen with one or with both eyes. These manipulations, like oscillations of the edge, should improve the estimate of the mean positions of features of the edge and thereby facilitate detecting any vernier offset that the experimenters may have introduced. Their apparatus is shown schematically in Fig. 1.3(A). A motor-driven cam, C, carries an edge with a variable offset, V, that could be oscillated in front of a replica of the fovea, R, containing irregularly spaced

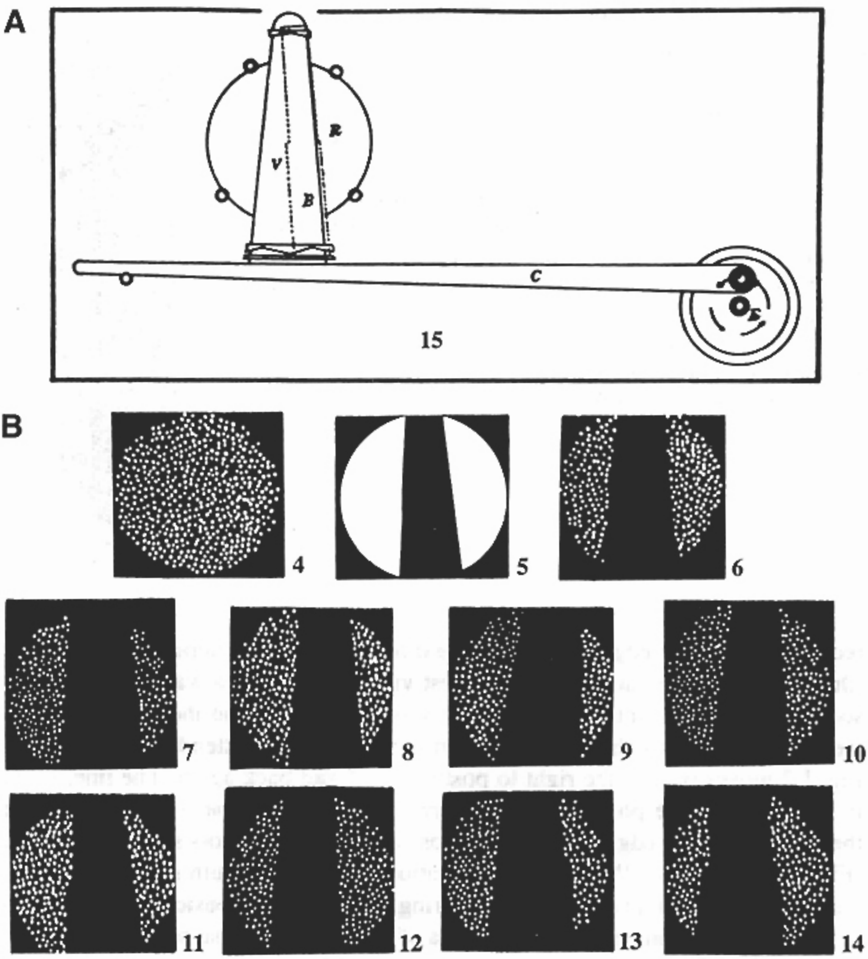


FIGURE 1.3. (A) Diagram of apparatus. R, replica of fovea (Fritsch, 1908) on an aluminum disc, cones being represented by minute perforations (see just below for details). V, inverted V-shaped shield used to produce the image-shadow. B, brass rod with offset (dotted) held in such a position that its broken edge projects just beyond the margin of the shield. C, wooden cross-bar to which the shield is attached. The cross-bar and shield move in an elliptical path whose horizontal diameter is 8 mm (5 cone diameters) and vertical diameter about one-third as great. E, motor-driven eccentric which produces oscillation of the cross-bar and shield in an elliptical path (from Averill & Weymouth, 1925). (B) Stimuli mounted on the apparatus shown in Fig. 1.2. (4) Diagram of retinal mosaic after Fritsch. Note the irregular arrangement of the cones and the great variation in inter-cone distances. This diagram is a replica of the perforated aluminum disc. (5) Appearance of the image shadow with displacement along the left margin and with the wider portion above the offset. (6 to 14) Representations of the retinal field as observed by the subject (reagent) who was required to judge the presence of an offset and its location when an offset was present. For example, in (14) there was a relatively large offset on the left which was wider in the lower part of the retinal field (from Averill & Weymouth, 1925).

perforations that represented the receptors. Fig. 1.3(B) shows the replica of the receptor surface with the receptors shown as minute trans-illuminated holes drilled in a thin sheet of aluminum, 4, and the shadow produced by the edge, 5. Examples of complete test stimuli seen by the reagent are illustrated in Fig. 1.3(B,6-14). The reagent was asked to indicate the position of the offset, and give a confidence judgment, under the conditions of stimulation described above. In Fig. 1.3(B,14), it is easy to see the large offset on the shadow's left edge. The offsets in most of the other test stimuli illustrated in Fig. 1.3(B) are harder to make out.

Averill and Weymouth reported that oscillating targets had lower thresholds than stationary targets, and that longer exposures, longer lines and using two eyes were also better. The first of these findings supports the idea that eye movements favor visual processing, the other results support the general averaging idea but are capable of other interpretations (e.g., probability summation for the binocular case).

Weymouth's dynamic theory remained a curiosity until the Second World War. It was mentioned in textbooks primarily as a minor problem for Hecht's dominant static theory of visual acuity that was built on the retinal intensity discrimination tradition, extending back through Hartridge to Helmholtz (see Steinman & Levinson, 1990, for a more complete review of Hecht's theory). Dynamic theory was presaged by two very influential papers on the electrophysiology of the frog retina published by Hartline (1938, 1940). In these papers, Hartline reported that the most common output of the ganglion cells of this simple eye was "phasic", that is, most neural activity signalled changes in the stimulus. Fifty percent of his units signalled at stimulus onset and offset. Thirty percent signalled only at stimulus offset. The remaining 20% of the units were like those of the ommatidium of the compound eye of the horseshoe crab. They were tonic, that is, they signalled the presence of a stimulus, beginning with a burst when the stimulus came on and continuing to respond as long as it remained, firing all the while at a somewhat reduced rate. Hartline's observations made stimulus transients particularly significant for generating visual neural messages. What better way to produce them then by allowing the eye to move? By 1941 eye movements were beginning to be taken very seriously.

1.4 The Marshall-Talbot Dynamic Theory of Visual Acuity

This theory was based primarily on two observations. First, Adler and Fliegelman's (1934) measurements of the miniature eye movements made during carefully maintained fixation, which had shown a high frequency (up to 100 Hz) oscillation of the eye ("physiological nystagmus"), whose average amplitude they reported to be about 2 minutes of visual angle. Second, the report of an anatomical "cortical magnification factor". This factor is based on the fact that 2 minutes of arc of the rhesus monkey's fovea (about 9 micrometers) was found to project to about 1 linear

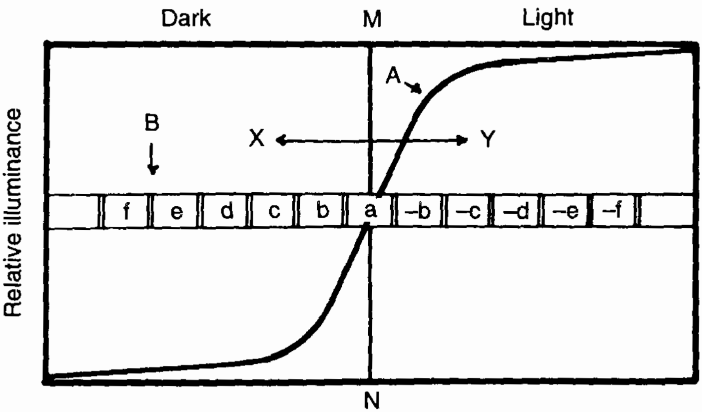


FIGURE 1.4. The distribution of illuminance on the retina across the geometrical boundary (MN) separating Light and Dark halves of a field (from Falk, 1956). See the text for details.

millimeter of its primary visual cortex. This has the consequence of making the effective ratio of cortical visual cells to foveal cone receptors at least 600:1. These observations, taken along with the importance of phasic stimulation demonstrated in frog retina by Hartline, encouraged Talbot and Marshall (1941; Marshall & Talbot, 1942) to develop a theory that made eye movement a necessary condition for acuity. Their basic scheme is illustrated in Fig. 1.4.

This figure shows the proximal stimulus of an edge made by a light and a dark region. The proximal stimulus, curve A, is the intensity distribution on the retina after the edge has been "smeared" by the aberrations of a normal eye (the physical or "distal" stimulus would be an intensity step). The row labeled B is the receptor surface containing foveal cones, having a center to center separation of about 19 seconds of arc (about 1.5 micrometers). These values of cone separation at the center of best vision in the fovea were based on Polyak's (1941) influential studies of primate retina (a somewhat larger value, perhaps about 30 seconds, would probably be preferred today). The arrow labeled "$X \longleftrightarrow Y$" represents the average 2 min arc amplitude of physiological nystagmus suggested by Adler and Fliegelmann. High frequency eye movements of this size would stimulate a row of about 6 cones. The maximum rate of change of stimulation, and hence the maximal firing rate, would be found at cone a, where the slope of the intensity function is maximal. Firing rate would fall off progressively on adjacent cones. The relationship of the firing rate in the maximally stimulated cone, a, to its neighbors, coupled with anatomical "magnification" in the ascending pathway and assumptions about the duration of the neural recovery cycle allowed recovery of the sharpness of the intensity step that was degraded in the proximal stimulus. The size of the cones relative to the size of the high frequency oscillations is critical to this theory, which has sometimes been called a statistical theory of visual acuity, because the physiological process correlating with the critical detail is the average or peak of the distribution of outputs of the neural elements firing in the cortex. (See Steinman & Levinson, 1990, for a detailed critique of this theory.)

1.5 Empirical Tests of the Marshall-Talbot Theory

There were two lines of attack. The first made careful measurements of the miniature eye movements characteristic of steady fixation. The question here was: Does physiological nystagmus have the properties required by the theory? This led to the development of the contact lens-optical lever eye movement recording technique, which was capable of resolution well under one minute of visual angle and was free from translational artifacts. This new method of recording also provided a means for stabilizing the retinal image of a test target — a development that permitted test of the Marshall-Talbot claim that eye movements were necessary for good acuity. Both lines of attack led to clear refutations of the theory.

For example, Ratliff and Riggs (1950) found that physiological nystagmus actually had an average amplitude somewhat less than 20 seconds of visual angle, which meant that it could not stimulate a population of cones. Its frequency was high enough (about 30–80 Hz) but its excursion was so small that the maximum of the oscillating light intensity distribution would be confined to a single receptor. At least part of the problem with Adler and Fliegelman's (1934) eye movement measures, which were used by Marshall-Talbot to devise their theory, was, as Ratliff and Riggs pointed out, an apparent scaling error. Adler and Fliegelman apparently did not realize that an optical lever has an inherent amplification factor of two, that is, a 1° rotation of the eye causes a 2° angular shift of the beam reflected from the mirror mounted on the contact lens.

The work with stabilized images also made trouble for the Marshall-Talbot theory. Riggs, Ratliff, Cornsweet and Cornsweet (1953) found that stabilized and normal viewing both permitted good vision of fine details. It was only when the display remained stabilized for long periods of time and began to fade that natural viewing became better than stabilized viewing. Eye movements were necessary to prevent fading but the discrimination of details was the same with or without eye movements until fading began. These authors also reported that image motion twice "normal" was better for maintaining visibility over prolonged periods than normal image motion. This became a common, and mysterious, finding in subsequent work with stabilized images (see Kowler & Steinman, 1980, for the likely explanation of this mystery).

As I see it, this line of evidence from stabilized image experiments against the Marshall-Talbot theory is less compelling than the measurements of physiological nystagmus (described above) because it has been quite clear since Barlow (1963) examined the quality of the best stabilization obtainable (with the contact lens and Yarbus sucker methods) that excursions of the eye as small as physiological nystagmus had never been stabilized on the retina. I, following Barlow's (1963) lead, am inclined to believe that high contrast targets, confined entirely to the central fovea, probably only lose their sharp edges, but never disappear completely (see Steinman & Levinson, 1990, for a discussion of the vast, and more often than not, controversial literature on stabilized images). But, regardless of the particular reason one prefers for rejecting the Marshall-Talbot theory of visual acuity, it was rather generally agreed about 30 years ago that physiological nystagmus was not a functionally significant eye movement — sufficiently long ago to guarantee that the basic idea will crop up with increasing frequency as the people who know this literature first forget its details and then die off. (The basic findings of Riggs and his coworkers have been replicated many times. See, for example, Ditchburn, 1973, for a review of work he began independently in England in 1953 and Yarbus, also for independent work, done in Russia (Yarbus, 1957a,b, 1967). Krauskopf (1957, 1962, 1963) in this country and Gerrits and Vendrik (1970, 1972, 1974) in the Netherlands added a great deal to our understanding of these phenomena during the heyday of research with images stabilized by means of "invasive" methods. Recent work with noninvasive methods will be described in some detail later.

1.6 The Phone Rang

And I had the pleasure of talking, for the first time, with Fran Volkmann, who was well-known for her work on threshold elevations associated with planning and making saccadic eye movements — "saccadic suppression" in trade jargon (see Volkmann, 1986, for a recent review of this topic and Sperling, 1990, for an alternative point of view). I was flattered to receive this phone call when I heard that Prof. Volkmann wanted me to participate in a workshop to be held at Princeton in April, 1974 that was being organized under the auspices of the prestigious Committee on Vision of the National Research Council of the National Academy.

The proposed plan was to have a number of people sit around and engage in a panel discussion about how we can see clearly as we look and move about in the real world. The panel was to include Ethel Matin, Ulker Tulunay-Keesey, Lorrin Riggs and myself. I was concerned about this topic because, as I pointed out to Fran, all of us worked with contact lens-optical levers, which required that the head be fixed on a biteboard. This might make it difficult, perhaps even dangerous, to extrapolate from this kind of research to the real world — actually I think I said something like "nobody knows anything about this, regardless of what we like to tell people at cocktail parties or claim in grant proposals." My recollection after almost 15 years was that there was agreement, or at least acquiescence, on the other end of the line. I think that Fran said something like: "Yes, but, it would be interesting and valuable to discuss what we do know or at least consider the problems we are facing in answering such a question." Who could disagree with this and I, cheerfully (at least my intent was to be cheerful), agreed to participate in the panel. This phone call probably came sometime in February during an exceptionally busy Spring. There were a number of research projects to get ready for the ARVO meeting in Sarasota at the beginning of May, lots of teaching, and the preparation of a review paper on oculomotor effects on vision I had agreed to deliver at a symposium in Stockholm during June (Steinman, 1975). Planning material for an informal panel discussion was the least of my concerns until the phone rang again sometime late in March. It was Fran Volkmann again. She began by saying: "Hello Bob, I was talking with Lorrin and we agreed that this idea of an informal panel discussion wasn't likely to work so well. We think that it would be better if we each talk about our specialized interests. I'll do a general review of saccadic suppression; Lorrin will talk about some exciting new experiments showing saccadic suppression with electrical phosphenes, rather than light as input; Ulker will talk about acuity with stabilized targets and Ethel will explain how saccadic suppression helps us perceive the direction of objects. We would like you to cover the more general issue of the role of eye movements in maintaining a phenomenally clear and stable world."

In short, I was expected to give a lecture on a topic I believed to be a complete mystery. What was I to do in these circumstances? I did what everyone I know does in such circumstances. I agreed to do the talk, knowing full well that I could begin with a disclaimer about actually being able to answer the big question and then move quickly to talk about what I actually was doing and could say something about. This lecture was not going to end there. It was to be published along with any discussion it engendered. This fact made it imperative that it included some new material. I was compulsive about this when I was young professionally (I know better now) probably because my doctoral mentor and role model (Jack Nachmias) had not been enthusiastic when confronted with rehashes of old stuff at meetings. What was I to do? Less than a month was available for generating some new and, at least superficially, relevant data. After discussion with my colleagues we decided that the best that could be done in the circumstances would be to find out the scope of the problem facing the oculomotor system. Specifically, when a human being sits still with the head free from artificial supports, the head was sure to move. These irreducible head movements would have to be compensated by the oculomotor system if the person is to be able to maintain gaze steadily on some stationary feature in the visual environment. Put differently, how much additional work did the oculomotor system have to do when the head was not supported by a biteboard? Fig. 1.5 shows how we tried to find this out.

Fig. 1.5(A) shows the late Brian Murphy (Steinman, 1976, p. 136) sitting in David Robinson's magnetic field eye movement recording apparatus at Johns Hopkins in Baltimore. He looks a little scrunched-in because this set-up is usually used to measure the eye movements of young rhesus monkeys, whose heads are held near the center of the wooden framework by means of a metal ring and bolts screwed into their skulls. Brian is more or less centered within 2 pairs of Helmholtz magnetic field coils, one pair above his head and below his elbows and the other pair to his left and right. These field coils were driven by sinusoidal A.C. signals in quadrature mode (orthogonal in space and time). In this type of instrument, the amplitude (voltage) of the signal induced in a sensor coil located within this magnetic field is proportional to the sine of the angle of the sensor coil with respect to the direction of the magnetic field. The induced signal is zero when the sensor coil's windings are parallel and maximal when the windings are perpendicular to the direction of the magnetic field. The horizontal and vertical components of the magnetic field are 90° out of phase and independent measurement of the sensor coil's orientation along each meridian can be measured by using a phase-lock amplifier tuned to the orthogonal phases of the induced signal. In Fig. 1.5(A), the sensor coil can be seen just in front of Brian's mouth where it was held by attaching it to a biteboard

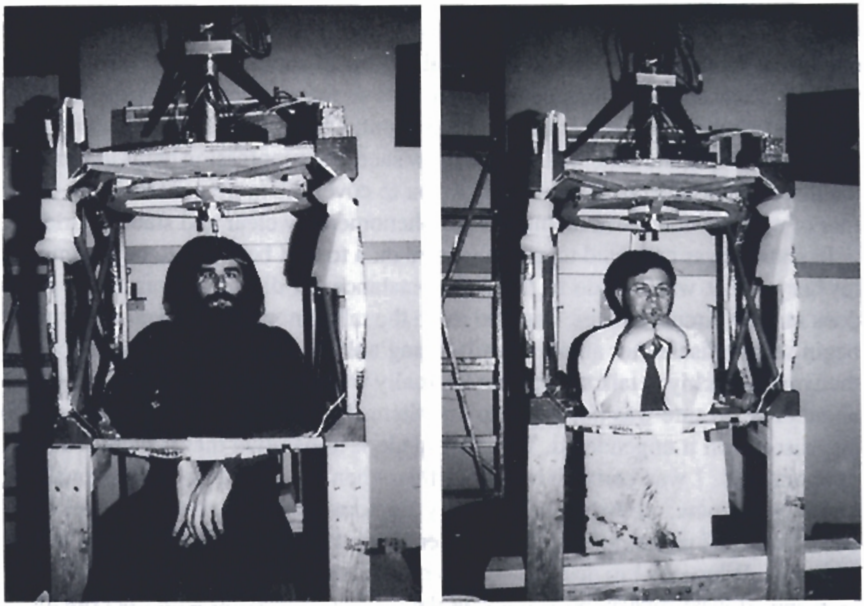

A B

FIGURE 1.5. (A) Brian Murphy sitting in Robinson's magnetic field instrument having movements of his head measured by means of a sensor coil mounted on a biteboard (from Steinman, 1976). (B) David Robinson sitting in his magnetic field instrument having movements of his head measured by means of a sensor coil mounted on a biteboard (from Steinman, 1976).

(a silicone dental impression made on a sheet of plastic) clenched between the teeth. The lead from the sensor coil can be seen passing near the left side of his head to a connector located just above his hair. Brian's task was to sit as still as possible, breathing normally and also while holding his breath, using only natural supports to help him remain still. In this posture, Brian had only neck muscles to steady his head on his torso. His torso could be stabilized by resting his arms on the framework of the apparatus — a posture much like the one used while sitting still in an armchair. Fig. 1.5(B) shows another subject and another natural posture studied. The subject in Fig. 1.5(B) is David A. Robinson, the bioengineer, who developed the magnetic field-sensor coil technique that has proven to be so valuable in contemporary oculomotor research. He is shown using another commonly employed natural posture for supporting the head while sitting still and examining objects in the real world.

We found that the head rotated quite a bit even when the subject tried to sit as still as possible. This "fact" was published in the book covering the proceedings of the workshop (Steinman, 1976). I won't say anything further about these measurements because they were not what we thought them to be at the time, namely, they were not actually head rotations. We got this wrong because Robinson did not appreciate, or more likely had forgotten, that his, and similar instruments, were not suited for making such measurements. This became apparent only when I decided

FIGURE 1.6. Alex Skavenski sitting in his magnetic field instrument having movements of his head and right eye measured by means of the amplitude-detecting technique (from Steinman, 1975).

to go one step further and show some free-headed compensatory eye movements in Stockholm. This decision began a period of jet-set science between College Park, Boston and Rotterdam. The first series of flights were to Alex Skavenski's lab in Boston where attempts to measure free-headed eye movements began in earnest. Fig. 1.6 shows Alex sitting in his version of the Robinson amplitude-detecting magnetic field-sensor coil apparatus. His set-up was a bit larger than Robinson's because Alex routinely records eye movements in human, as well as in monkey, subjects. The Helmholtz coils have an outer wrapping of black vinyl electrical tape that covers the aluminum foil Faraday shields that are visible in Fig. 1.5.

Skavenski is wearing a tight-fitting scleral contact lens that is held in place on his right eye by means of suction. Suction is established with a syringe filled with contact lens fluid and applied to the contact lens by means of the thin plastic tube visible as it passes across his nose near the patch over his left eye. A sensor coil is embedded in the surface of the contact lens. Its lead (a very thin twisted pair) can be seen near the right side of his nose as it passes directly upwards to a connector overhead. The white round object just below his nose is the sensor coil used to measure head rotations. It is mounted on a biteboard — the same placement used in Baltimore. Fig. 1.7(A) shows the author in the same apparatus. I am wearing a motorcycle helmet with a very tight chin-strap. Its purpose can be seen in Fig. 1.7(B). This figure shows that a loudspeaker was mounted at the back of the helmet with a mass of bolts stuck to its voice-coil. This rig was used to oscillate the head passively at frequencies up to 30 Hz with very small amplitudes (up to about 5 minutes of arc). These arrangements were used to study oculomotor compensation for head rotations beyond the range of head movements that could be induced naturally.

I reported the initial observations made with this instrumentation in Stockholm (Steinman, 1975) but was very careful to limit comment to saying that it was obvious that the oculomotor system had a lot to do and that a lot was going on. More was not said because it was becoming very clear when we started analyzing our records quantitatively that something did not make sense. The nature of the problem, as well as its solution is illustrated in Fig. 1.8.

Fig. 1.8(A) shows Skavenski sitting in his new, large Helmholtz field coils. His head was free as he maintained fixation on a small point of light located at optical infinity in an otherwise dark room. One of two sighting tubes (at left center) that were used to position Alex's experimental eye in a precalibrated portion of the magnetic field, and a wooden framework around, but not touching his head, can also be seen in this photo. Fig. 1.8(B) shows a close-up of Alex rigged and ready for recording. The wooden framework around his head permitted 3-D movements of about 1 cm in any direction. He was careful to avoid touching any part of the wooden framework with his head while recordings were made. A white surgical stocking cap was worn to allow some room between his curls and the wooden framework (men wore hair long in the 1970s, see the author in Fig. 1.7(A)). The head sensor coil was still supported by means of a biteboard, but the round, white sensor coil was now attached to a plastic extension that located the head coil at the bridge of the nose where it was near the experimental eye. This arrangement placed the eye and head coils about the same distance from the head's center of rotation and also placed them near each other in the magnetic field. The scleral contact lens is very prominent in this photo because it was necessary to increase the number of turns of wire in its sensor coil in order to maintain a reasonable S/N ratio with the relatively weak magnetic field that could be generated with the large field coil arrangement and the field-driving amplifiers available. Alex covered the new multi-turn sensor coil with a white, dental plastic tooth-filling compound, which made the appearance of his eye rather dramatic.

Why all these changes in instrumentation (Steinman, 1986a)? Simply because the Helmholtz coil arrangement only provides a minuscule region near its center where the magnetic flux is homogeneous, that is, the magnetic vectors are parallel within each of the orthogonal directions. If the head is free in a small Helmholtz field coil arrangement of the kind used in all primate research prior to Skavenski's new set-up, translations, as well as rotations, of the head will cause changes in the amplitude of signals induced in the sensor coil. If the translations are large relative to the rotations, it's a real mess. It was the use of small Helmholtz field coils that made interpretation of our initial free-headed eye movements impossible (Steinman, 1975) and the initial report of head "rotations" artifactual (Steinman, 1976). The large field coils used by Skavenski, Hansen, Steinman and Winterson

A

B

FIGURE 1.7. (A) Steinman sitting in Skavenski's apparatus having his head and right eye movements recorded. See the text for an explanation of the purpose of the helmet. (B) Skavenski sitting in his apparatus having his head and right eye movements recorded. See the text for an explanation of the purpose of the helmet.

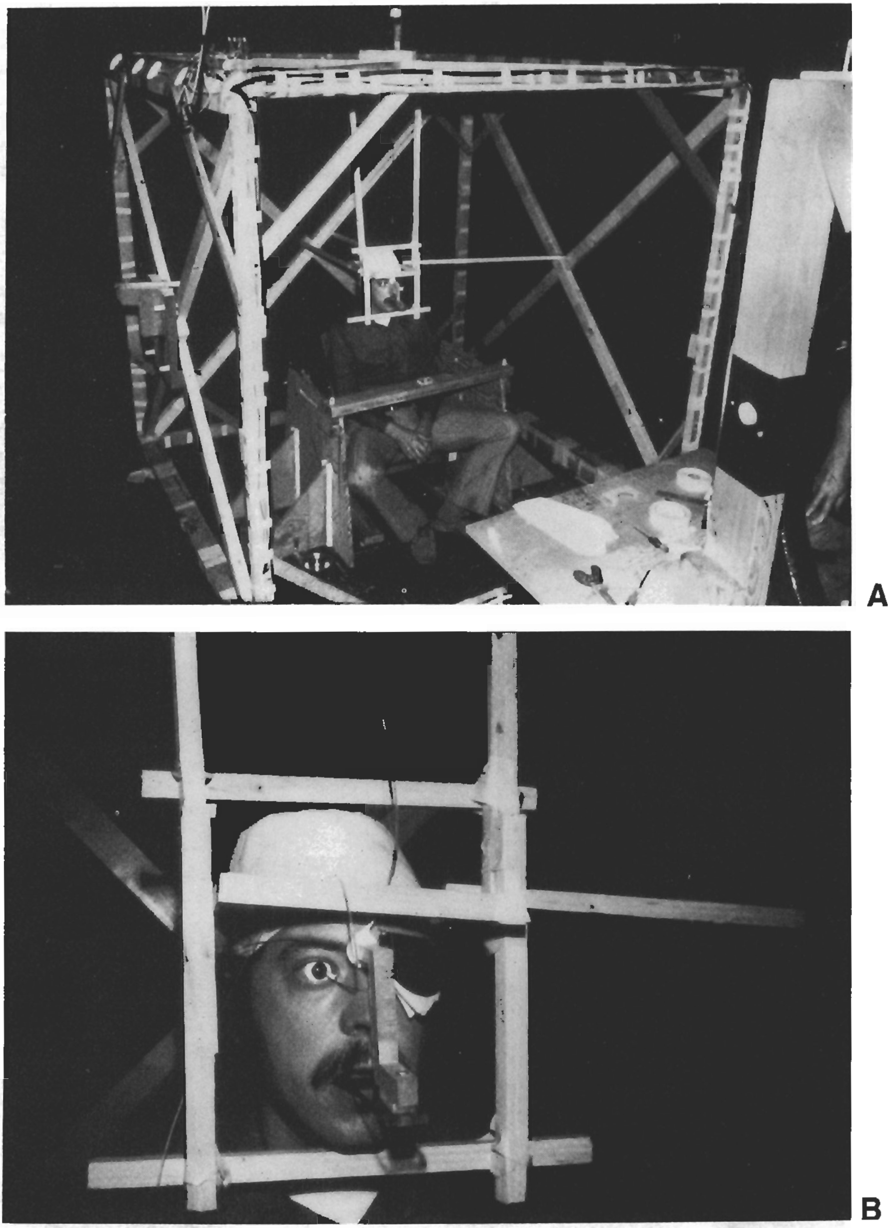


FIGURE 1.8. (A) Skavenski sitting in his large, new Helmholtz field coils having movements of his head and right eye recorded while he sat as still as possible without artificial supports. (B) Close-up of Skavenski's head in the apparatus shown in (A).

(1979) only provided a small, but practicable, homogeneous region in the sense that translations of the head did not produce artifacts equivalent to rotations of the eye larger than 1 minute of arc. (N.B., the standard deviation of a fixating eye, when the head is supported on a biteboard, is only about 2–3 minutes of arc; see Steinman, Haddad, Skavenski & Wyman, 1973). This means that very good instrumentation is required to study human fixation with accuracy and precision better than the oculomotor system itself. Pretty good bandwidth, as well as accuracy and precision, is needed because saccades (the eye movements used to shift gaze rapidly), which achieve maximal average peak speeds of about 525°/sec in human beings, can cover distances approaching 80° of visual angle in a single step with pretty fair accuracy (see Collewijn, Erkelens & Steinman, 1988a,b, for measurements of binocular saccades over their entire range of operation on both vertical and horizontal meridians with bandwidth = 244 Hz; accuracy and precision = 1'; and linearity > 0.01% and Erkelens, van der Steen, Steinman & Collewijn, 1989a and Erkelens, Steinman & Collewijn, 1989b, for equally accurate measurements of "vergence" eye movements).

Fig. 1.9 illustrates the results obtained with Skavenski's elaboration of Robinson's method (Skavenski et al., 1979). These records show that the unsupported head during sitting, as well as during standing, provided an unsteady platform (our head spectrum measurements showed considerable power in a range extending from D.C. to 7 Hz). These head movements were only partially compensated by eye movements, meaning that there was considerable retinal image motion of the fixation target when the head depended entirely on natural supports. Specifically, the retinal image velocity of the fixation target increased by a factor of 2–4 over velocities observed with the head on a biteboard and the standard deviation of fixation on a single meridian increased from about 2–3' to about 30'. Perfect oculomotor compensation during steady fixation would produce horizontal straight lines in the traces reproduced in Fig. 1.9 because these records show the angular orientations of the eyes and head with respect to an earth-fixed coordinate system. If the line of sight of the eye stayed exactly on-target, the trace shown in the record would not move. It would be a horizontal straight line even when the head trace indicated that the head was oscillating. All subsequent eye and head movement records will use this earth-fixed coordinate system so all of the traces have the same significance, that is, perfect oculomotor compensation for oscillations of the head will produce a horizontal straight line in the eye traces in all records shown.

Furthermore, when movement is apparent in the eye trace when the head moves, the degree and source of such departures from perfect oculomotor compensation can be inferred from the amount of motion of the eye and its direction relative to the head. Namely, if the eye moves in the same direction as the head in the record, the eye, trying to maintain fixation on a distant, stationary object, is under-compensating for the head movement (gain is too low). This allows the fixation target to move on the retina. When the eye moves opposite to the direction of the head in the record, the eye is over-compensating (gain is too high), and the fixation target image will also move on the retina. Keeping these features in mind will help the reader interpret the recordings reproduced from here on.

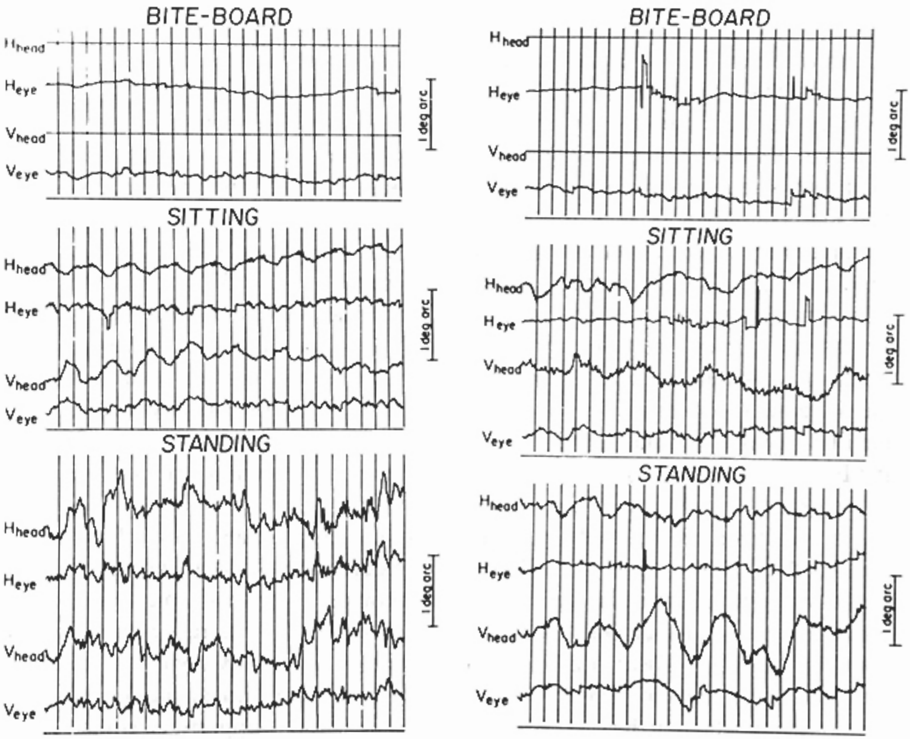


FIGURE 1.9. Representative horizontal (H) and vertical (V) head position and gaze (retinal image position) of subject Skavenski (left) and Steinman (right) while they fixated a target at optical infinity with their heads supported on a bite-board, or while they were sitting or standing as still as possible. Records begin on the left. The vertical time-lines show 1 sec intervals and the vertical scales on the right side of each record show 1 degree of visual angle. Upward changes in these position traces signify rightward or upward rotations (from Skavenski et al., 1979).

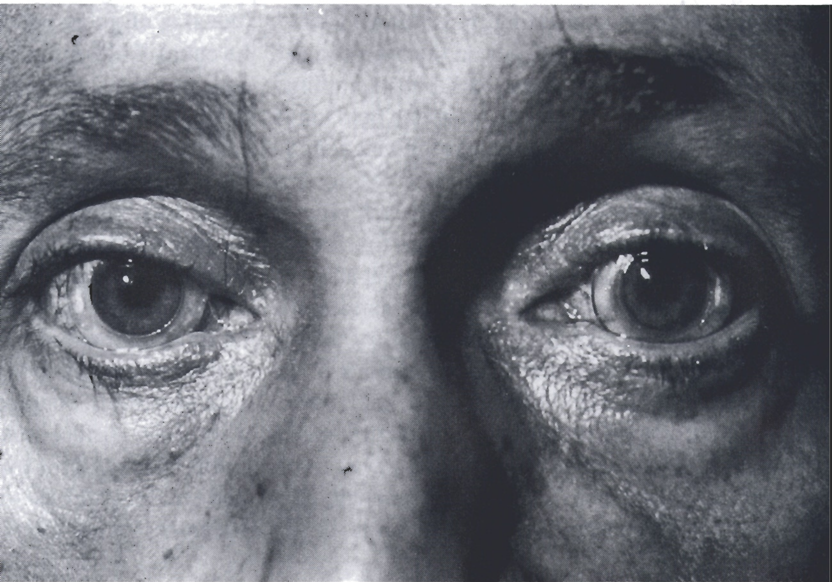
We also found that a larger proportion of rotational head movement was compensated when head oscillations increased in vigor over those observed when the subject sat or stood as still as possible. This result encouraged us to conclude that the goal of oculomotor compensation is not the reduction of retinal image motion to some minimum, near zero, value but, rather, the goal was to keep retinal image motion at some higher level that was optimal for visual processing because this goal would prevent fading whenever the observer wished to see well while sitting still. This idea, which will eventually have good direct support, will be described later (Collewijn, Martins & Steinman, 1981, 1983). Other important developments intervened and the next step in this story took place in Rotterdam when Han Collewijn (1977) measured the eye and head movements of freely-moving rabbits — an undertaking that required major improvements in existing recording methodology. I will first describe the controversy that led to the beginning of what has become a long and stimulating collaboration and then say a few words about Collewijn's new methods. These methods have made it possible to record eye and head movements under increasingly natural conditions and to examine the role of natural retinal image motion in visual processing.

Collewijn (1977) reported that the eye movements of his rabbits compensated, virtually perfectly, for movements of their heads as they moved about. We, on the other hand, reported that human beings failed to compensate anywhere near perfectly once their heads were free to move (Skavenski et al., 1979). Were humans less competent than rabbits in oculomotor as well as in reproductive skills? This seemed unlikely. Perhaps humans would do better if they were allowed to move their heads actively, rather than to sit quietly or have their heads oscillated passively through small amplitudes: the way we had done our work. There was also the fact that Collewijn had observed the eye movements of his rabbits on a rather coarse scale because the dynamic range of his recording instrument was limited and the animals tended to move their heads (and/or bodies) through large angles. It's not easy to explain to a rabbit that it should always face north and only oscillate its head through amplitudes rarely exceeding 20° peak to peak. Human beings can be instructed to do this quite easily. Han was as curious about our disagreement as I and we arranged for me to visit his lab in Rotterdam where his new instrument would be used with ourselves and his colleagues as subjects in a replication of his experiment with rabbits. The visit was planned for early June of 1978, just after I had returned from the annual ARVO meeting in Sarasota. As I was packing my bags for my trip to the Netherlands, . . .

1.7 The Phone Rang Again

It was Jarus Quinn, the Executive Secretary of the Optical Society, who called to thank me for agreeing to participate in a Symposium on Binocular Vision at the annual meeting of the Society in San Francisco in October. He assured me that I wouldn't have to pay to register at the meeting because I was an invited speaker, but that there were no funds for my expenses. This came as somewhat of a surprise. Not the business about expenses, I knew that physicists were tight with money. I was surprised because this was the first I had heard of the symposium, much less agreed to participate. I told Jarus that it must be some kind of mistake, but he insisted that Prof. Gerald Westheimer had made these arrangements and that I was expected to participate. Jarus apologized for the mixup and explained by saying that Prof. Westheimer probably had expected him to contact me and that he had thought that Prof. Westheimer would contact me. He suggested that I should phone Prof. Westheimer and discuss my participation with him. I stopped packing my bag and phoned Dr. Gerald (he calls me Dr. Bob) and pointed out that I was somewhat at a loss because I really didn't know much about binocular eye movements, had never measured them, and, in fact, didn't even have an instrument that could be used for the purpose. Dr. Gerald was unperturbed and suggested that I do something appropriate (or some such thing). Then I knew! Quinn had been chosen to make one of those unlikely phone calls. Suddenly, it came to me. I realized that I could make binocular recordings easily in the Netherlands with Collewijn's technique and said goodbye to Dr. Gerald, assuring him that I would come up with something by October. That's how Collewijn and I got into the human binocular eye movement business. We were assigned the task — no questions asked. How we began to do this is shown in Fig. 1.10.

Fig. 1.10(A) shows the author (tan after a week in Sarasota) looking off into the distance with something taped to his forehead and a suggestion that he may be wearing something on his eyes. Connectors overhead and parts of a couple of magnetic field coils can also be seen. Fig. 1.10(B) shows a close-up of the eyes, which can now be seen to be wearing silicone annulus sensor coils. Collewijn, van der Mark and Jansen (1975) developed these ingenious devices as substitutes for custom-fitted scleral contact lenses in oculomotor research. One size fits all (annuli for research are available from SKALAR in Delft). Tight-fitting scleral research contact lenses, even when held to the eye with as much as 100 mm of mercury suction, move around when large ($> 10^\circ$) eye movements are made. Collewijn's silicone annulus, on the other hand, has been shown to adhere to the eye during even the largest eye and head movements (see, for example, Collewijn et al., 1981; de Bie, 1985; in addition to the original description of the new device by Collewijn et al., 1975). Each annulus contains a 9-turn coil of very fine copper magnet wire (approx. 47 AWG). The coils and their very delicate twisted-pair leads can be seen in this photo. The easiest lead to see in this photo is coming from the subject's right eye near the inner canthus and goes in front of the eyebrow on its way to one of the connectors overhead. The 9-turn sensor coil can be seen best in the other eye on the right side of the photo. A similar annulus was taped to the forehead above the eyes (see Fig. 1.10(A)). The eyes are anesthetized with drops before the annulus is inserted. Annuli can be worn for periods up to 40 minutes, individual subjects experiencing very different degrees of discomfort. Their effects on vision are minor in most subjects, who have been tested in concurrent visual psychophysical experiments, but wearing these annuli is not likely to catch on as a popular pastime, all things considered. They do, however, make it possible to study eye movements over their entire range of rotation and place no constraints on the vigor or speed of oculomotor responses. Ferocious blinks or clumsy experimenters can break leads, but the leads are relatively robust and it is not unusual to be able to sterilize an annulus and use it for 10, and often more, recording sessions. They can even be used to measure eye movements accurately during blinks and also when the eyes move under eyelids that are kept closed (Collewijn, van der Steen & Steinman, 1985). In short, the development of these annuli was a very large advance in human oculomotor research. In the author's opinion, it was larger than the introduction of the tight-fitting scleral contact lens, which got the modern eye movement recording era going 40 years ago. These annuli fit almost all adult human eyes. They adhere to the eye during large eye movements and, when used with the phase-detecting method introduced by Collewijn (1977), are capable of absolute calibration — a very convenient feature in the basic science oculomotor laboratory,



and a necessity in the clinic where one cannot count on a patient understanding instructions or being able functionally of following instructions to shift gaze or to track.

The silicone annulus sensor coil was only one of three major improvements in the technology for measuring eye movements that were introduced during the late 1970s by Collewijn's group in Rotterdam. Another is illustrated in Fig. 1.11(A), which shows the author sitting with his head near the center of the apparatus Collewijn had used to measure the eye and head movements of unrestrained rabbits. It looks like I am sitting in jail, surrounded by coils of wire. Actually, I was at the center of a pair of cube-surface field coils. The cube-surface field coil configuration was developed during World War II as a practical way to degauss ships to protect them from magnetic mines. The optimal coil-arrangement (i.e., a good approximation to a true solenoid) was described theoretically just after the war by Rubens (1945) and introduced into eye movement research by Collewijn in his rabbit paper (1977). The cube-surface field coil arrangement makes it possible to achieve a relatively large homogeneous central region of magnetic flux by using 5 coils on a meridian, rather than the Helmholtz pair of coils traditionally used (see Rubens, 1945, or Collewijn, 1977, for the required ratios of windings in each of the 5 coils). The cube-surface field coil arrangement permits the subject to move his head through appreciable distances (about 20 cm in the apparatus in Fig. 1.11(A)) without introducing disconcerting translational artifacts (the area of good, i.e., 1 part in 1000, homogeneity depends on the overall size of the cube). Collewijn also developed the technique of phase- rather than amplitude-detecting the signal produced in a sensor coil by a rotating magnetic field (an idea suggested by Hartmann & Klinke, 1976). A homogeneous rotating magnetic field can be made by having 2 cube-surface coil arrangements oriented 90° to each other (in spatial quadrature) and driving them out of phase with each other (in phase quadrature). This arrangement will generate a magnetic vector that rotates through 360° during every period of the frequency of the a.c. currents that are driving each cube-surface field coil. The phase-detecting technique has a number of advantages over amplitude detection; namely, it gives linear indications of the orientation of the sensor coil throughout 360°, it is insensitive to fluctuations in the strength of the revolving magnetic field and it is capable of absolute calibration. These properties, coupled with the solution of the translational artifact by means of the cube-surface field coil arrangement just described, opened the way for beginning to study how eye movements allow us to maintain a phenomenally clear and stable world as we move about — the question Prof. Volkmann raised 3 years earlier in her fateful phone call.

The visual stimuli we used are shown in Fig. 1.11(B). This is the view to the North-West from the window just outside the rabbit phase-detecting, cube-surface field coil apparatus on the of 15th floor of the Medical Faculty in Rotterdam. Our fixation stimulus was the control tower at the Rotterdam airport (indicated by an arrow). It was 5000 m from where the subject was seated. On particularly clear days we used a building near the horizon in the suburbs of Den Haag (35000 m away). The subject's task was to fixate either of these far targets and to oscillate

his head about its vertical axis through peak to peak amplitudes not exceeding 20°, increasing frequency and simultaneously reducing amplitude until the limits of active head oscillations had been reached. The subject was also asked to note the appearance of the visual scene as he moved his head throughout this entire range of head frequencies and amplitudes. The photo reproduced in Fig. 1.11(B) illustrates the most remarkable aspect of this body of collaborative research done in Rotterdam. We needed fixation targets that were far away because maintaining steady fixation when the head translates with a near target requires that the eye makes compensatory rotations. Said differently, with a nearby target gaze must shift in space in order to keep the image of the target in the same position on the retina. This comes about because the angles between the target and the eyes change a lot when the head translates relative to a nearby target. This does not happen when the target is far away. It is impossible to assess the steadiness of fixation, that is, the amount of motion of the retinal image of the target, if the target is near and the amount of head and eye translation is not known. We had no way to measure this at the time with the accuracy required to interpret eye movement records (10 years of additional instrumentation development were required before this could be done; see Collewijn et al., 1990; Kowler et al., 1990, for the first reports of accurate measurements of eye and head translations and rotations while fixating nearby targets and Epelboim et al., 1993, 1994a,b, for more up-to-date reports).

The view from the window reproduced in Fig. 1.11(B) was the only convenient way we had of getting far targets because an optical collimator that was suitable for use with large head movements required a very large diameter, short focal length lens. We did not have one and even if we had had one, the configuration of the experimental set-up would have made it difficult to set it up properly. The view from the window was the way to go, but who goes to the Netherlands, expecting to be able to see farther than 10 or 20 m through the fog, rain and/or haze more than an hour or two, once or twice each month. June of 1978 was unusual in Rotterdam. The weather remained as clear as is shown in Fig. 1.11(B) day after day after day. Readers familiar with the climate of the Netherlands will appreciate that this was a supernatural event. Based on the author's prior and subsequent visits to Rotterdam, such weather was almost as miraculous and every bit as helpful as Moses' parting of the Red Sea in biblical times. The head and eye movements of 4 subjects recorded under these conditions are illustrated in Fig. 1.12.

Each recording began with low frequency, large amplitude head movements (the panel on the left) and continued through intermediate frequencies and reduced amplitudes (the middle panels) and ended with the subject oscillating his head as fast as possible (the panels at the right). These very high frequency, small amplitude oscillations were accomplished by clenching the teeth and tensing the platysmas muscles. The separation of what were, in fact, continuous recording runs in Fig. 1.12 was done for convenience during plotting. The head trace at the top of each subject's record shows head position divided by 10, the right eye trace is below the head trace, the left eye below it and the "vergence", that is, the difference between the gaze directions of each eye is shown in the lowest trace.

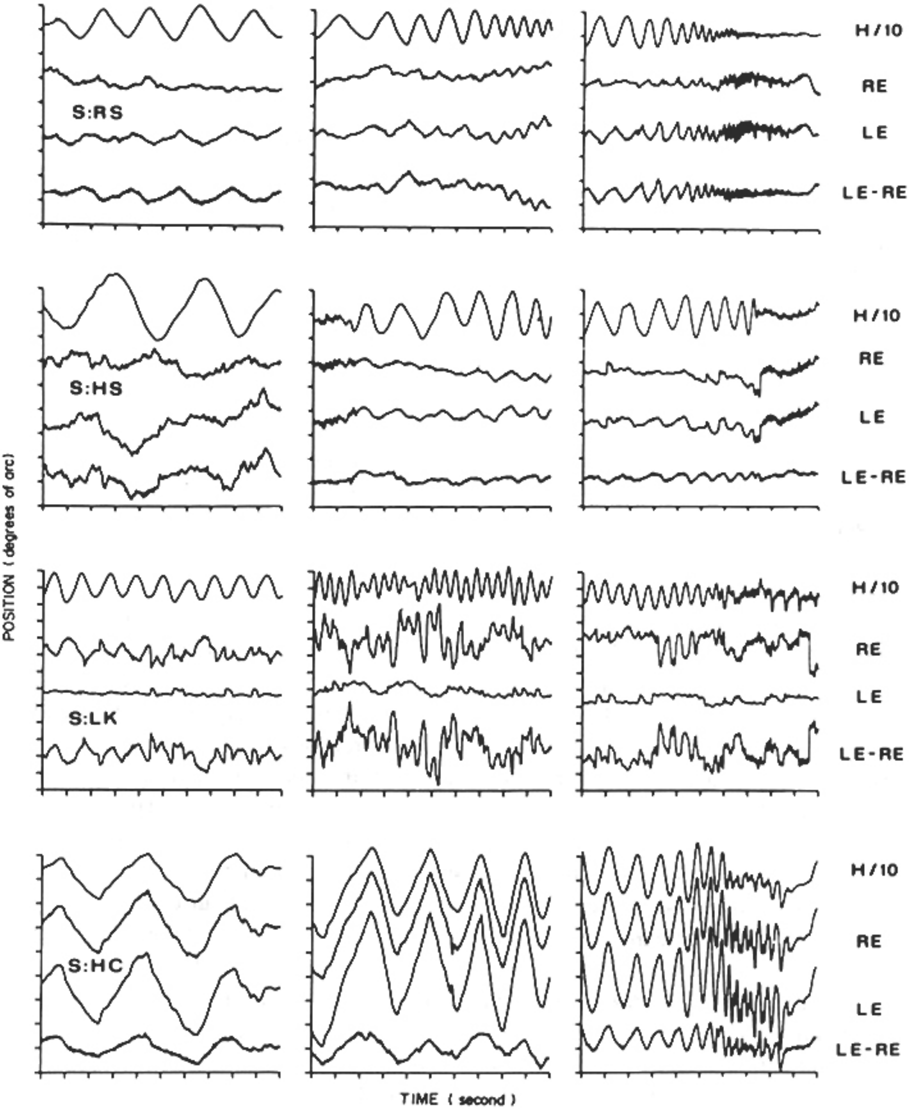


FIGURE 1.12. Representative recordings of horizontal head (H) and binocular gaze (retinal image position) of 4 subjects while they fixated a distant target and actively oscillated their heads about its vertical axis. Each of the 12 second records begins on the left and tick-marks on the abscissa indicate 1 sec intervals. Tick-marks on the ordinate indicate 1 degree of visual angle. The movements of the head have been scaled to 1/10 of their actual value and the trace LE-RE signifies vergence eye movements with convergence shown by upward changes in position. Upward changes of the right eye (RE), left eye (LE) and scaled head traces (H/10) signify movements to the right (from Steinman & Collewijn, 1980).

The eye and head traces in these recordings show the direction of the eye in an earth-fixed coordinate system (as they did in Fig. 1.9) which means that the eye traces would be horizontal straight lines whenever the line of sight stayed directly on the distant fixation target as the head oscillated. These eye-in-space (or "gaze") traces also represent the movement of the fixation target on the retina. Large excursions of eye position imply that the retinal image of the Rotterdam airport control tower or the image of the building in the suburbs of Den Haag, whichever target the subject was fixating, was dancing over large numbers of receptors in his foveal retinal mosaic. Very occasionally, retinal image motion was quite limited in extent, one might even say, stability was "virtually perfect". A few instances of this can be seen in these records (e.g., the final 4 seconds of subject RS's right eye trace in his left-hand panel and subject LK's first 4 seconds of his left eye trace in his left-hand panel). Such instances were confined to individual eyes of individual subjects. They were rare, indeed. Most often there was appreciable retinal image motion in each eye and appreciable differences of the motion between each of the eyes, resulting in large and continuous changes of vergence. Remember, these targets were fixed in space either 5,000 or 35,000 m away. Measurable vergence changes would not be required when the head oscillated while such distant targets were fixated. Note that the most striking features across all 4 subjects across the entire range of head frequencies and amplitudes were the large idiosyncracies shown by each subject in the degree of compensation for head movement by each of his eyes and, at the same time, the relative similarity among their vergence traces. The vergence traces of all 4 subjects oscillated at about the frequency of his head oscillations. This was accomplished in very different ways by each subject, for example, by having relatively modest compensation in each eye but, at the same time, a modest difference in compensation between them (subject HC), or by having excellent compensation in one eye and relatively incomplete compensation in the other eye (subjects RS and LK). Overall, there was much more retinal image motion than would be expected from conventional wisdom about compensatory eye movements during this period. Conventional wisdom had it that compensation was virtually perfect (see, e.g., Wilson & Melvill Jones, 1979, p.267).

Note that all of the subjects reported that they continued to see a phenomenally clear and stable world up until the very highest frequency oscillations, where the world remained clear but began to be seen as oscillating slightly. The reader should try this experiment himself by oscillating his head while fixating a distant target. The world will continue to look good under all conditions, providing only that the head oscillations remain in the range of frequencies and amplitudes illustrated in Fig. 1.12. We now know that perfection of oculomotor compensation is not the basis upon which the world looks fused and clear under such conditions. These results were quite unexpected by most, if not all, "experts" a decade ago. These days most, if not all, "experts" claim that they knew that it would come out the way that it did. Despite these claims, the fact remains that we are periodically asked to prove that our "generally expected" results do not reflect some artifact in our recording method (see Ferman, Collewijn, Jansen & van den Berg, 1987, for the most recent experiments designed to calm these fears).

The next direction our research would take was revealed in a phone call from New York. Bernie Cohen, from Mount Sinai (the medical school, not the mountain), was arranging the program for an International Meeting of the Barany Society to be held under the auspices of the New York Academy of Science in the Fall of 1980. The meeting would deal with oculomotor and vestibular physiology and we were invited to contribute something suitable. I am not sure after so many years whether I got the phone call or whether Han got it and then called me. In any case, the vestibular system was the way to go next. What should we do?

1.8 Retinal Image Slip Following Adaptation of the VOR

. . . was a perfect experiment. It was well within the theme of the meeting and was, at the same time, quite important for progress towards understanding natural retinal image motion. Our idea for the meeting followed, in part, from the work in Boston where we had proposed that the goal of oculomotor compensation might be some nonzero retinal image motion sufficient to prevent fading when the subject sat, as still as possible, without artificial supports for his head. It also followed on the work just completed in Rotterdam where the head had moved actively under relatively uncontrolled conditions while fixation was maintained on a distant target. Here I will describe what we did by quoting directly from our report (Collewijn et al., 1981): "First, we extended our results on natural retinal image motion to a larger sample of subjects, making these observations with passive, as well as active, rotations. Second, we measured binocular retinal image motion with sinusoidal stimulation of fixed frequencies and amplitude, allowing estimates of retinal image speed at each of several frequencies. Third, we determined the degree with which the VOR [the vestibulo-ocular response] (in the dark and when supplemented by vision) could be modified by changing the correlation between the amount of retinal image motion and a given degree of eye rotation. These adaptation experiments were undertaken to determine whether the observed departures from virtually perfect compensation arose from limitations inherent in the compensatory subsystems or from the desire of the compensatory subsystems to maintain retinal image motion at some nonzero value that might be optimal for vision" (p. 312). Fig. 1.13(A) illustrates the pre-adaptation natural eye and head movement records of a subject who had not served in the original experiments either in Boston or Rotterdam. His performance was similar to what had been seen earlier in other subjects in all important respects. Fig. 1.13(B) shows the results of experiments in which magnifying and minifying spectacles were used to require the VOR to adapt to novel arrangements. (See Collewijn et al., 1983; Steinman, Cushman & Martins, 1982, for more complete analyses then available in the original paper.)

The results illustrated in these figures were obtained at the University of Maryland at College Park where a new cube-surface, phase-detecting, eye and head monitoring instrument was under development. This instrument used primarily

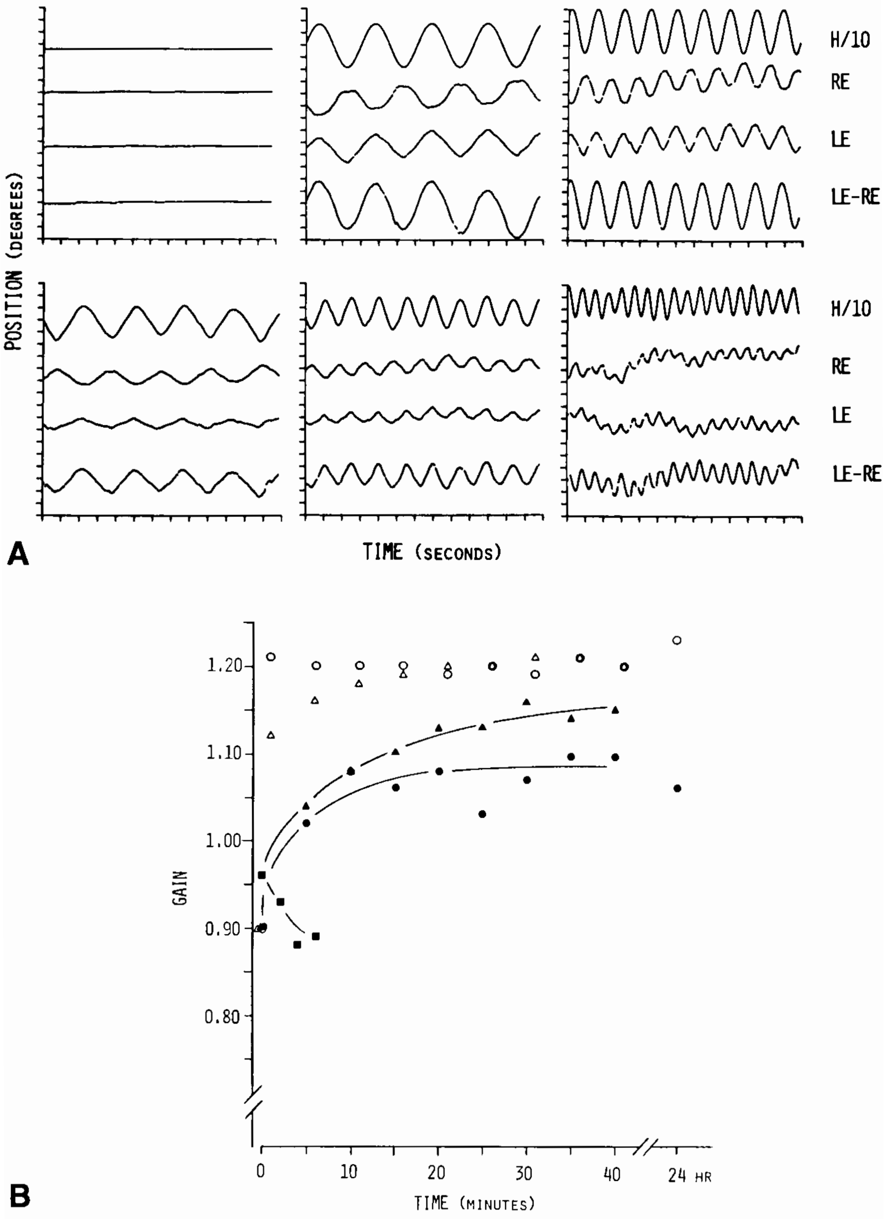


FIGURE 1.13. (A) Six representative records of horizontal head position and gaze (retinal image position) of Albert Martins, fixating a target while his head was passively or actively oscillated (from Collewijn et al., 1981). (B) VOR gain in the light (open symbols) and in the dark (closed symbols) as a function of adaptation time. Collewijn's performance is shown by circles, Martins' by triangles and Steinman's by squares.

digital circuitry and, a decade ago when this work was done, its noise level and "dead band" were less than 1 minute of arc, its bandwidth was 178 Hz (−3 dB) and its linearity was 1%. It only operated along the horizontal meridian, but its dynamic range on the horizontal was 360° with the characteristics just described. In short, this new instrument at an early stage of development was good enough to provide the best measurements of these kinds of phenomena available at the time. There were two findings that went beyond confirmation and extension of the general features of natural retinal image motion reported by Skavenski and colleagues (1979) and Steinman and Collewijn (1978, 1980). First, there was our discovery that the adaptation of the VOR (in the dark as well as in the light) was virtually complete in minutes rather than incomplete after days, providing the requirements for adaptation were kept modest, that is, less than 40%, rather than the +100% or −50% (i.e., 2 times or 1/2 magnification) requirement used by prior investigators. Second, we found that each subject adapted to his idiosyncratic level of natural retinal image motion (2–8% of head speed). When he did this, the experimental conditions had forced the amount of retinal image motion to pass through a value approximating zero retinal image motion during the course of adaptation. All 3 subjects tested in this experiment continued to adapt, ending at their preferred, clearly nonzero, value of retinal image motion they had before magnifying or minifying spectacles were put in front of their eyes. Both of our findings depended heavily on having much better instrumentation for measuring eye movements than had been used by prior investigators. All prior primate research on adaptation of the VOR had used EOG [electro-oculography], a poor technique for anything beyond crude clinical observations (see Collewijn et al., 1985, for a comparison of EOG with his sensor coil method and also for other references that highlight limitations of this outdated, but unfortunately still used, methodology.)

Time was running out on one of our often repeated claims. In Boston, in Rotterdam and now in College Park, we had found incomplete oculomotor compensation for head movement and had noted that the visual world remained phenomenally clear and stable despite all these perturbations of the retinal image. We had just reported an experiment designed to show explicitly that the goal of oculomotor compensation was some nonzero amount of retinal image slip and went on to claim that this motion might be beneficial for vision because it could prevent fading of the visual scene when a human being was not moving about. Where were the visual psychophysical measurements to support these claims? All we actually had were informal subjective reports of a phenomenally clear and stable world while we were moving. Where were our concurrent visual threshold measurements?

1.9 An Intramural Phone Call

. . . announced that it was time to "fish or cut bait." This call came from Jack Levinson, a colleague in my department's Program in Sensory and Perceptual Processes. Jack had been asked to organize a symposium on the detection of contrast in the presence of motion for the Annual Meeting of the Optical Society to be held in New Orleans in October, 1983. Jack phoned from across the hall in the Spring, and I agreed to participate with one proviso. Namely, I explained to Jack that we would need his help. It's one thing to say that we must study visual processing in the presence of natural retinal image motion to oculomotorists (or to journal referees with such background) and quite another to make visual psychophysical measurements properly and then get up in front of a group of hard-nosed professional visionaries and tell them how natural image motion affects basic visual processing. Collewijn and I (and our collaborators) were mere oculomotorists, members of a much younger specialty than physiological optics (Helmholtz's term) or visual science (a currently popular label). Oculomotoring is in its intellectual infancy. We don't even have real quantitative models. Our "models", such as they are, are only minor variations of circuit designs taught in the "How to do Electronics" manuals issued by the Armed Forces just after World War II (see Steinman, 1986b, for an evaluation of the value of the linear systems engineering approach introduced into the study of the oculomotor system in the decade following the end of the war). How could we advise a group, working in traditions begun by Helmholtz, Maxwell and Mach, about their own specialized research area. This was a tradition in which real natural scientists discussed real universal problems, not the just-emerging oculomotor traditions where fads launched by the half-baked ideas of the odd assortment of dentists, psychologists, physicians and engineers, who work on eye movements, were discussed. Jack (a genuine, card-carrying physicist) was reassuring. He promised to keep us from making fools of ourselves. He went even further and offered to make the measurements of contrast sensitivity in the presence of natural retinal image motion that we would need for his symposium. A set of these threshold measurements is summarized in Fig. 1.14(A–C).

These graphs show the contrast required for each of 3 subjects (Eileen Kowler, a; the author, b; and Han Collewijn, c) to detect the presence of a sinusoidally-modulated raster in a CRT display as a function of the spatial frequency of the bars. The parameter separating the 3 functions in each graph shows whether the head was supported artificially (triangles) or whether the subjects were oscillating their heads in time to a metronome beating at 1/3 or 4/3 Hz (Xs or diamonds, respectively). These particular subjects and particular paced head movements were used because we knew a lot about the natural retinal image motion they produced (Collewijn et al., 1981). Each subject had a typical contrast sensitivity function (CSF) when the head was supported artificially, namely, they were most sensitive somewhere between 3 and 6 cycles/degree and needed more contrast at lower spatial frequencies. Their high frequency cut-offs lay between 40 and 60 cycles/degree. The intersubject differences, which are apparent in Fig. 1.14(A–C), would be expected because a and c were myopes, who had worn spectacle corrections since childhood. This is known to make them relatively insensitive to high spatial frequencies when compared to b, who had no history of refractive errors.

The interesting results are to be found within each subject's performance, namely, by looking for differences between the CSFs measured with the head stationary and when it was moving. First, we see higher sensitivity for moving low

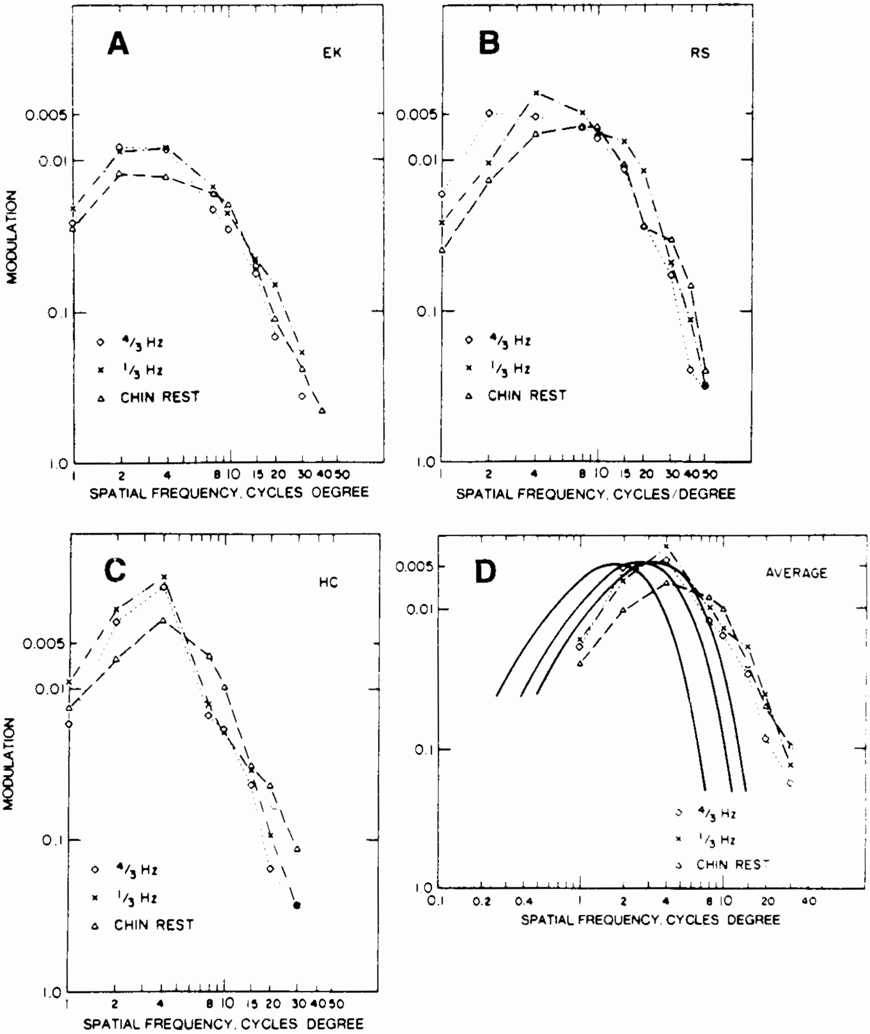


FIGURE 1.14. Threshold grating contrast-modulation settings as fractions of 100% contrast at various spatial frequencies. Three frequencies of head oscillations about its vertical axis were used, namely, near 0 with the head supported by a chin-rest or oscillating at 1/3 and 4/3 Hz. (A) shows the CSFs obtained under these conditions for subject EK, (B) for subject RS and (C) for subject HC. (D) shows their average CSF (the geometric mean) as broken lines with plotting symbols. Values and extrapolations from Kelly's model of the spatio-temporal transfer surface are shown as solid lines. These hypothetical functions are based on unidirectional motion of similar speed imposed on a grating "stabilized" with a Stage III, SRI Eyetracker. See the text for a discussion of these functions (from Steinman, Levinson, Collewijn & van der Steen, 1985).

spatial frequency gratings. Van Nes (1968) was the first to demonstrate beneficial effects of motion (imposed by drifting a grating while the subject tried to maintain fixation of the stationary CRT aperture). So, our beneficial effect of motion at low spatial frequencies was not news except for the fact that the patterns of retinal image motion were quite different, that is, unidirectional, constant velocity motion for van Nes and a variable, essentially sinusoidal, oscillation in the natural retinal image motion pattern we observed (see Fig. 1.13(A)).

The more interesting result was the rather modest detrimental effect of motion on the high spatial frequency limbs of the CSFs measured while the head was moving. Differences between supporting the head and oscillating it at 4/3 Hz were small. This meant that moving high spatial frequency gratings could be seen well while they were moving on the retina. We knew that the virtual perfection of oculomotor compensation could not explain the psychophysical thresholds we had measured. The crossover points between the stationary and moving CSFs are also interesting. These show the spatial frequencies where moving the target is beneficial (on the left) and where it begins to be detrimental, albeit moderately (on the right). The crossovers for the 3 subjects shown in Fig. 1.14(A–C) were between about 8 and 15 cycles/degree. Their averaged CSFs (geometrical means) are shown as lines connecting data points in Fig. 1.14(D). Here the average crossovers occur at 10 cycles/degree and the high spatial frequency cut-offs are all at or slightly above 40 cycles/degree. The solid lines plotted in Fig. 1.14(D) are taken from Kelly's (1979a, 1979b) "spatio-temporal surface model" of the effects of motion on contrast. There are some striking differences between predictions from his model, which was developed on the basis of psychophysical measurements of CSFs obtained after imposing constant velocity motion on a "stabilized" sinusoidal grating, and our results where motion was generated by natural failures of oculomotor compensation during head movement. His predicted high spatial frequency cut-offs (stationary, as well as moving!) were half of the cut-offs we measured and his predicted detrimental effects of image motion were also much larger. Furthermore, his predicted crossovers were at about 1 cycle/degree while ours were seen almost an order of magnitude higher. Discussion of possible reasons for these differences will be postponed until after the rest of the material we collected for the October 1983 Optical Society Meeting is described. We did at lot more than measure CSFs and, as will be seen, this other work was much more interesting than the most-likely reasons for the discrepancies between our results and the predictions of Kelly's (1979a, 1979b) model. We were taking Kelly's model much more seriously than it deserved when we first reported our measurements. Reasons for saying this will be given later.

The CSF measurements were made in College Park just before the annual ARVO meeting in 1983. Only psychophysical thresholds were measured at the time (i.e., no concurrent eye movement recordings were made) because the 1-D, phase-detecting system in College Park was in its final phase of development, which made it a unique, 2-D, phase-detecting instrument. Bandwidth and linearity were also improved in this period (effective bandwidth was raised to 244 Hz and linearity

FIGURE 1.15. (A) Collewijn's large cube-surface field coil phase-detecting apparatus in Rotterdam. See the text for details. (B) Close-up of a subject in the apparatus shown in (A) wearing binocular eye coils beneath a pair of spectacles with a lowpass filter in front of one eye and a highpass filter in front of the other eye. These filters made it possible to present different stimuli to each eye, allowing psychophysical measurement of stereoacuity while head and eye movements were recorded.

made better than 0.01%). These improvements took several years and the first 2-D work with the completed instrument was published in 1988[2].

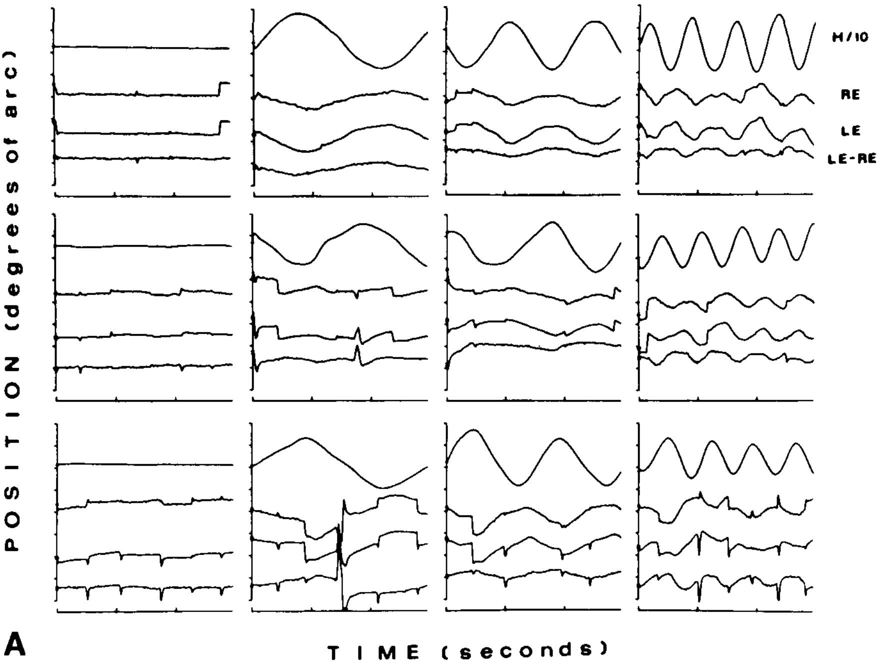
The rest of our data collection for the Optical Society Symposium was done in Rotterdam where Collewijn had just completed the new cube-surface field coil, 1-D phase-detecting system illustrated in Fig. 1.15. This was a large set-up, designed specifically for human beings, who could now sit in a comfortable chair near the center of the field coils rather than straddle a narrow wooden beam at the center of the much smaller rabbit apparatus. In the photo reproduced in Fig. 1.15(A), Han Collewijn (wearing spectacles) can be seen on the right. The back of Hans van der Steen's head (like Han, serving as an experimenter in this photo) can be seen in the foreground. I can be seen on the left side, just outside the field coils where I am preparing data sheets for psychophysical measurements of stereoacuity thresholds. The subject (Dusan Poboda) is faintly visible within the coils. Two slide projectors

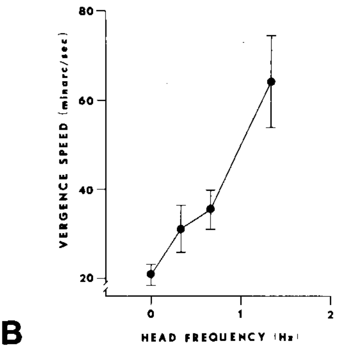
[2]See Collewijn and colleagues (1988a, 1988b) for a description of the completed 2-D instrument, which can measure, simultaneously, by means of the phase-detection principle, rotations on the N-S and E-W vertical, as well as on the horizontal, meridian. Also, see Collewijn and colleagues (1990) and Kowler and colleagues (1990) for its first uses after the addition of a device, which uses acoustic propagation times, to measure translations of the head to better than 1 mm. This most recent addition finally made it possible to work with nearby targets while the head was free. This new capability paves the way for beginning to try to answer the question that Prof. Volkmann had posed over the telephone 16 years earlier. Also, see Edwards and colleagues (1994) for a complete treatment of the unique 3-D eye/head monitor now in use.

were located behind the large disk with 2 apertures that can be seen in front of and below the subject in Fig. 1.15(A). The output of these projectors passed through either a highpass (red appearing) or a lowpass (green appearing) gelatin filter that permitted separate visual input for each eye (<1% crosstalk) because the subject wore a matching pair of filters in front of his eyes. The filters in front of the slide projectors could be interchanged quickly by rotating the disk. This made it possible to vary the eye that received each half of a particular stereo-pair. Changing the slide shown to each eye had the effect of making the critical detail (a bright thin line surrounded by a haphazard arrangement of bright and dark rectangles) to appear either in front or in back of the plane of the rectangles when the display was fused. These arrangements allowed a forced-choice psychophysical technique to be used (i.e., the subject always responded, saying either "front" or "back" on all trials; he was forced to choose regardless of the confidence he had about the relative depth of the line target, whose disparity was varied randomly from trial to trial). This kind of psychophysical procedure is probably the easiest way of getting a reliable threshold estimate within the 40 minute session-length imposed by wearing silicone annuli. One of the 3 subjects, who is ready to participate in the experiment (i.e., wearing a head coil and binocular eye coils beneath a pair of goggles serving to mount the red and green filters), is shown in Fig. 1.15(B). During the experiment he either sat still or oscillated his head in pace with a metronome beating at 1/3, 2/3 or 4/3 Hz. The head and eye movements of the 3 subjects who served in these experiments are illustrated in Fig. 1.16(A). All showed considerable retinal image motion within each eye and considerable perturbation of vergence (differences between each eye's motion) — expected results in light of our prior work.

Fig. 1.16(B) shows their average vergence speed under the 4 conditions of movement and Fig. 1.16(C) shows their averaged psychophysical performance (i.e., percent correct reports of relative depth as a function of the disparity of the line target). Conventional thresholds (e.g., 75% correct) could not be measured with the disparities available. Our smallest disparity was 11.4 seconds of visual angle (somewhere between 1/2 to 1/3 the diameter of the finest human foveal cone receptor). All 3 subjects got the stereo-depth plane correct more than 80% of the time with this disparity both when they moved their heads and when they sat still. Moving the head with the resulting vergence perturbations had no measurable effect on the subjects' ability to report the relative depth of the line target. In fact, all 3 subjects said that it was easier to see the relative depth of the line when they moved the head then when they sat still. Their subjective impressions, however, did not show up in the likelihood of their making a correct response. Moving and sitting still gave essentially the same results.

To sum up, retinal image motion in each eye and differences in image motion between the eyes had no measurable effects on stereoacuity. The implications of these results for theories of stereovision are discussed in detail in Collewijn and Erkelens (1990) and Collewijn and colleagues (1990). Here, it is sufficient to realize that our results show that the human visual system not only solves what computer scientists and machine visionaries like to call the "correspondence problem", but





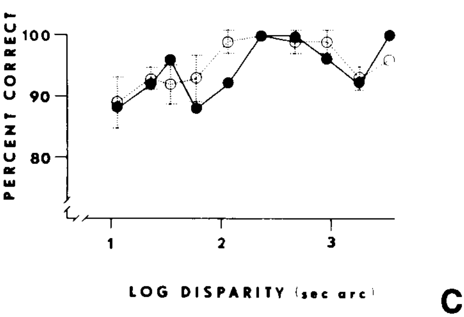


FIGURE 1.16. (A) Head and binocular eye movements of three subjects while psychophysical stereoacuity thresholds were measured during four conditions of head oscillation; sitting still on the left and oscillating about a vertical axis at 1/3, 2/3 and 4/3 Hz in the records to the right. LE-RE is vergence, the eye movement of significance in this experiment. See the text for details (from Steinman et al., 1985.). (B) Mean vergence speed (absolute velocity) as a function of head frequency for the three subjects whose eye and head movements are illustrated in (A). The error bars (standard deviations) show intersubject variability (from Steinman et al., 1985). (C) Accuracy of report (percent correct) as a function of the disparity of the stimuli. Data points show the averaged performance of the three subjects shown in (A) and (B). The closed symbols show accuracy when the subjects sat still. The open symbols show accuracy when they oscillated their heads. The error bars (standard deviations) show the variability associated with moving the head at three frequencies (from Steinman et al., 1985).

that it solves this problem at an exceedingly fine scale. Stereoacuity thresholds, had we had targets with sufficiently small disparities to actually measure them conventionally (75% correct), would have come out to something like 5 seconds of arc. This is the expected threshold value for stereoacuity with stationary test targets. Our subjects maintained this level of performance in the presence of changes of alignment of the eyes occurring, on average, with speeds greater than 3600 seconds of arc/second. I present this result as a problem for the Computer Scientists, fully confident that someone will come up with a satisfactory solution soon.

Another result of this series of experiments in Rotterdam, which may have significance for or may help in the design of binocular vision machines, was the demonstration that random dot stereograms could be fused and fusion could be maintained in the presence of the most violent possible head oscillations (Steinman, Levinson, Collewijn & van der Steen, 1985). This result encouraged Erkelens (1988) to reexamine the work of Fender and Julesz (1967) on fusion. These authors used contact lenses to stabilize stereograms on the retina and then slowly pulled the stereograms apart until fusion broke (i.e., the subjects "saw double") at somewhat more than 2° separations. Next, they slowly brought the stereograms together until fusion was reestablished. Separation had to be reduced to less than 10' before fusion was reestablished. Fender and Julesz called this difference in the disparity required to break fusion and the disparity required to reestablish fusion, "hysteresis". Erkelens was able to replicate these results but found that "hysteresis" depended on the particular experimental design, that is, it depended on the preceding fusional history. Fusion over large disparities was possible if brief, randomized tests were employed. Erkelens' result suggests that "hysteresis" is not likely to be significant for binocular vision in everyday life. Furthermore, Erkelens' results are compatible with our observations of natural binocular eye movements during head movement. It would be easier for the visual system to tolerate the kinds of vergence perturbations we observed (i.e., allow the percept of a single, fused visual world) if fusion could be established, as well as maintained, across disparities as large as 2° (see Collewijn & Erkelens, 1990; Collewijn et al., 1990, for a discussion of "hysteresis" in binocular vision).

Our report at the Optical Society Meeting was successful. No one booed or threw rotten vegetables. In fact, only a few seemed to realize that our novel results mattered a lot for the way the brain does visual processing. Why? Well, first off, no one in the audience, or elsewhere for that matter, was in a position to make the kind of measurements we had made. So, even if the listener believed our results, what could he do experimentally along these lines in his own lab? Also, even if he accepted our results and did theoretical, rather than experimental work, how could he model these results? Retinal images were moving too far and too fast on the retinas to be incorporated readily into contemporary models of visual processing. In time, what seemed at first to be benign acceptance gave way to benign skepticism. Our CSF measurements were the easiest to doubt because we had not at the time been able to make eye movement recordings while we measured psychophysical thresholds. Could it be that the CSFs, measured in the presence of natural retinal image motion, contained an artifact? Could we be sure that the subjects (ourselves) had followed the instructions and made threshold judgments near the center of their head oscillations when its velocity, and consequently, the gratings slip on the retina, was at its highest value? Maybe we cheated. In its more friendly form, one might say that we inadvertently failed to follow instructions and made our judgments when the head, and consequently the retinal image of the grating, slowed down just before and after the head changed direction. Said more succinctly, can we really be sure that we didn't sneak a peek as we turned about? If we had done this, our failure to find marked, adverse effects of image motion with high spatial frequency gratings would be an artifact. The high spatial frequency gratings were actually moving more slowly than we believed. This hypothesis is not as straightforward as it seems at first once it is realized that we would have had to use a different strategy with low spatial frequency gratings. Here, we would have had to make our judgments at the center of our head swings to obtain the enhancement of contrast sensitivity by motion known ever since van Nes (1968). Human beings can, of course, be this devious and this skillful. They might even be capable of behaving this way without realizing they were doing so.

This artifact was ruled out recently (Steinman & Levinson, 1990) by using the eye monitoring instrumentation at College Park to do control experiments that precluded such devious strategems. A dedicated microprocessor was used to calculate head and retinal image speed in real-time during oscillations of the head. The minimum amount of contrast available on the display was made contingent on how fast either the head or retinal image was moving. The experimenter set the maximum contrast available on a given trial when the head moved and used these settings to estimate contrast thresholds. The results of these experiments are summarized in Fig. 1.17. In Fig. 1.17(A), head speed set the lower limit of contrast available (i.e., No speed, no contrast. No contrast, no bars in the display). In Fig. 1.17(B), retinal image speed, rather than head speed, controlled contrast with the same consequences for the display. The experiment in which the lower limit of contrast was controlled by the head allowed very complete threshold measurements because no silicone annulus was worn on the eye and thresholds could be estimated in sessions that lasted 2 hours. Psychophysical sessions in which retinal image speed controlled contrast were much shorter (20–30 minutes). These thresholds are, therefore, necessarily noisier, but they, like the head thresholds, are good enough to rule out the possibility that our prior thresholds were artifactual (compare Figs. 1.17(A,B) with Fig. 1.14(B), which shows the same subject's CSFs when he could sneak a peek at turnabouts). The visual system does actually tolerate appreciable retinal image motion much more than has been observed in experiments in which constant velocity motion was imposed on a "stabilized" grating display.

Now that we were sure that we had no artifact in the main features of the CSFs in our original report, it becomes reasonable to ask why did natural retinal image motion have different effects on contrast sensitivity than imposed image motion? When we published our original work (Steinman et al., 1985), we sought explanation in subtle differences, such as differences in the waveforms of the natural and imposed motions and different light levels in the several experiments.

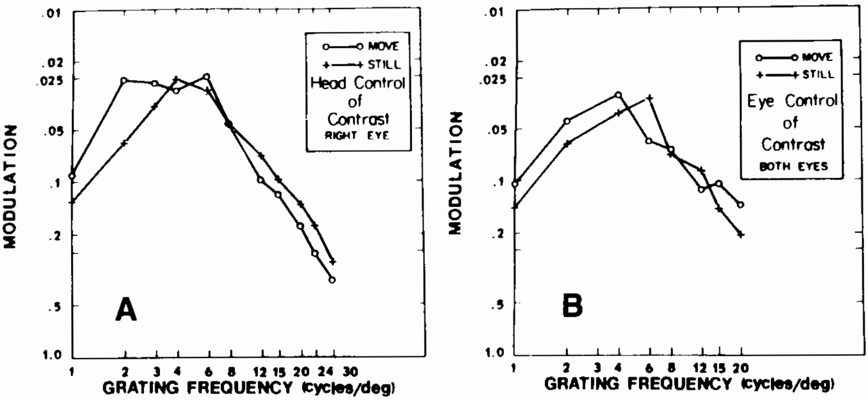


FIGURE 1.17. (A) Threshold grating contrast-modulation settings as fractions of 100% contrast at 11 spatial frequencies. These contrast sensitivity functions were obtained either while Steinman sat still, shown by the filled circles, or while he oscillated his head about its vertical axis, shown by the open circles. When he oscillated his head, the speed with which the head was moving determined the maximum available contrast. See the text for a discussion of these functions (from Steinman & Levinson, 1990). (B) Threshold grating contrast-modulation settings as fractions of 100% contrast at 8 spatial frequencies. These contrast sensitivity functions were obtained either while Steinman sat still, shown by the filled circles, or while he oscillated his head about its vertical axis, shown by the open circles. When he oscillated his head, the speed with which the retinal image was moving in either the right or left eye determined the maximum available contrast. The functions during movement are the mean of the threshold settings made with each eye at a separate session. See the text for a discussion of the significance of these functions and details about how these observations were made (from Steinman & Levinson, 1990).

Looking harder at this question over a period of several years, we now believe that the explanation lies in deficiencies in Kelly's (1979a, 1979b) stabilizing instrument. In short, we do not actually have any meaningful measurements of CSFs with imposed motion to compare with our measurements with natural motion. Kelly used a Stage III SRI Double Purkinje Image Eyetracker to stabilize his gratings prior to imposing constant velocity motion. This instrument cannot be used with sine wave gratings above 12 cycles/degree (only about 1/4 of the way to the normal high spatial frequency cutoff of the human visual system) in the most suitable subject described to date (Kelly himself). It has not been found to be useful above 7 or 8 cycles/degree in other subjects. Only a brief justification of these assertions is possible here and the reader is directed to Steinman and Levinson (1990) for a more complete treatment. I will start with a brief description of Kelly's stabilizing instrument.

The SRI Eyetracker is a very ingenious and complicated, noninvasive, instrument for measuring 2-D eye rotations. In principle, this makes it ideal for psychophysical research because very long periods of data collection, not possible with any invasive method, are possible. Its principle of operation is as follows: The SRI Eyetracker measures changes in the distance between the first Purkinje

Image (the light reflected from the cornea) and the fourth Purkinje Image (the light reflected from the concave surface at the back of the crystalline lens within the eye). When a collimated beam enters the eye, a real image of its source is formed, within the eye, by reflection from the concave surface of the crystalline lens. A virtual image of the source is also formed by the convex outer surface of the cornea. This virtual image from the cornea is also located within the eye in a position near to the virtual image formed by the crystalline lens. These reflecting surfaces, which form the first and fourth Purkinje Images, are at different distances from the center of rotation of the eye. This causes the distance between the first and fourth images to change as the eye rotates. This distance does not change when the eye translates relative to the source, allowing an instrument built on this principle to measure eye rotation free from translational artifacts. The degree, size and location of regions of relative linearity of the eye position output of this instrument depend on anatomical structures of each individual's eye.

The device is electromechanical with voltages proportional to eye position being derived from the X and Y position of mirrors mounted on 2-D servomotors that track the first and very faint fourth images so as to keep them centered on silicon quadrant detectors. The indications of eye position along the horizontal and vertical meridians come from piezo-electric crystals mounted on the tracking servo mirror mountings. These crystals must resolve displacements as small as 1 micrometer or better. There are many sources of noise inherent in such instrumentation, ranging from shot noise in the photodetectors to nonstationary variations of the reflecting properties of a given individual's eyes. It is not possible to determine the noise spectrum of the instrument independently of noise contributed by a particular individual's eyes.

Herein lies the main problem. It is easy to show (as Kelly, 1979a, did), by determining the highest spatial frequency that the instrument can stabilize sufficiently well to make an afterimage with discriminable bars, that inherent noise is such as to limit its use as a stabilizer to gratings of 12 cycles/degree in Kelly's eye, and 7 cycles/degree in his subject's eye. Subsequent work with the latest version of this instrument (Arend & Timberlake, 1986) also has found its use to be restricted to spatial frequencies under 10 cycles/degree. Accepting Kelly's data (1979a) and his model of the effects of motion on contrast sensitivity (Kelly, 1979b), as we did in our original report, is only plausible if one is ready to assume the SRI Eyetracker, which serves as a lowpass filter when used for stabilization, does not distort the shape of the CSFs measured with different amounts of imposed motion with spatial frequencies below 12 or 7 cycles/degree, depending on the subject. This is asking a lot, particularly inasmuch as the actual noise spectrum of the Eyetracker has not, and probably cannot be measured because it includes unpredictable contributions from properties of each individual subject's eye.

To sum up, the noise spectrum of the SRI Eyetracker can distort the CSFs in unknown (and probably unknowable ways) with lower spatial frequency gratings and it is useless across the most interesting range we studied (above 10 cycles/degree). We did not appreciate these limitations when we prepared our original report and the predictions from Kelly's model shown in Fig. 1.14(D) are, in retrospect, meaningless. Once this pointless comparison is put aside, we are left with an intriguing problem. Namely, how does the visual system manage to tolerate (or, perhaps, even put to good use) the relatively large, fast displacements of light distributions on the retinal surface that accompany all natural bodily movements? The new and particularly intriguing fact, here, is that this tolerance for motion extends down to the lowest, most primitive level of visual processing, that is, the discrimination of threshold differences of contrast in a single eye. This discovery is harder to understand than the tolerance we found for vergence perturbations on stereoacuity thresholds or the fusion of random dot stereograms. These situations are far less mysterious because relative positions of relevant target details are preserved when vergence changes. If the important stimulus feature underlying the percept is the relative positions of target details, vergence perturbations are of little or no consequence and should, therefore, be tolerated (see Collewijn & Erkelens, 1990; and Collewijn, Steinman, Erkelens & Regan, 1992, for elaboration of this point). But note, both stereoacuity and stereofusion are binocular accomplishments that require processing at relatively high levels in the visual system after input from the two eyes is combined. The tolerance of appreciable retinal image motion contrast thresholds within a single eye is harder to understand at this point in time.

It is hard to predict, with any degree of certainty, what the future holds for the role of eye movement in visual processing because this role has changed so frequently during the past 136 years. At present it is possible to say with reasonable certainty that eye movement is useful for seeing very sharp edges or small details we wish to inspect for more than 2/10ths of a second. It is also possible to say with reasonable certainty that the retinal image is, fortunately, in no danger of standing still in any natural situation. It is even possible to assert with reasonable certainty that vision continues to function at near capacity levels without virtual perfection of oculomotor control. Finally, it is possible to say with reasonable certainty that the role of eye movement in maintaining a phenomenally clear and stable world can now be studied with techniques that may, one day, make it possible to do more then shake one's head or look upwards with raised, outstretched arms whenever the telephone rings.

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