

90 Gaze Control under Natural Conditions

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Reason for studying the control of gaze

Little in visual neuroscience is of greater concern than a human being's ability to control the direction of *gaze* (the direction of the line of sight in spatial coordinates). Why? What could possibly make the human's control of gaze so important? The answer lies in the nature of the human *retina*, the receptor surface within the eye that *transduces* (translates) light, the *adequate* (most effective) stimulus for vision, into bio-electrical signals that are carried to the higher levels of the visual brain. These centers are responsible for our ability to see a world of colored objects, of various sizes and at various distances, moving or stationary with respect to each other, as well as moving or stationary with respect to ourselves. The retinal surface is very *heterogeneous* (diverse) with respect to its functional properties. A very small central depression (only about 1/40th of 1% of the retinal surface area), called the *fovea*, is responsible for our best visual acuity, that is, our ability to *discriminate* (distinguish) very fine details. The fovea is also responsible for our best color vision, while the regions outside of the fovea are particularly well suited for detecting very low levels of light and motion. The fact that the human retina had very heterogeneous functional properties was well established by the **last** quarter of the nineteenth century. (See Brindley, 1960, for many important older references and Oyster, 1999, for an up-to-date treatment of what is now known about the structure and function of the human eye.)

Why eye movements must be measured

One of the more intriguing aspects of human vision is the fact that the functional consequences of retinal heterogeneity are not experienced. Subjectively, our visual world is homogeneous. We perceive it as having good acuity and color representation throughout. Experiencing the visual world as homogeneous would not be possible if we could not move our eyes. Moving our eyes allows us to place selected visual objects in retinal regions specialized for processing different features. For example, we use the fovea for seeing colored details in brightly lighted environments, but shift to more peripheral retina when objects are too dim to be seen when they fall within the fovea (see Steinman and Cunitz, 1968, for the human oculomotor pattern near the absolute foveal threshold).

Two things were clear near the end of the nineteenth century, when the objective study of eye movements began. First, it was clear that the functional properties of the human retina were sufficiently heterogeneous to require the eye to move. Second, it had become clear from studies of reading, a particularly important and uniquely human eye movement behavior, that the way human beings move their eyes *cannot* be inferred from subjective impressions of what they were doing (Dodge and Cline, 1901; Huey, 1900; Javal, 1878). Objective measurement of human eye movements was required. This recognition encouraged the development of methods to measure human eye movements. These methods were developed and improved throughout the twentieth century, and a large body of knowledge about human eye movements was produced. See Collewijn (1998) for descriptions of many of the more popular contemporary methods of recording eye movements. See Hallett (1986), Steinman (1986), Kowler (1990), and Kowler (1991) for reviews of what has become a voluminous literature on human eye movements.

Why eye movements should be studied under ecologically relevant conditions

Virtually all of this knowledge was collected under unnatural, highly impoverished stimulating conditions. More often than not, the eye movements of only one eye were recorded. The head was immobilized on a biting board or a chin rest. The visual field was more often than not dark except for the fixation target, which was a tiny spot of light that lined up with the eye when it was centered in its orbit. Recordings were made while the single-point target remained stationary or moved during the recording. It is not clear, as we begin the second century of human eye movement research, that much of the knowledge we have, which is based on recordings made under such unnatural and highly impoverished conditions, applies to the way human beings actually control their gaze under more ecologically relevant conditions, that is, (1) when the human being's head and torso is free to move and (2) binocular gaze is recorded *accurately* as the human observes and manipulates (3) objects within arm's length in a (4) normally illuminated room. These conditions are particularly relevant for understanding the evolutionary success of our species. These are the conditions in which human beings fabricate and use tools, as well the conditions

in which they do most of their reading and other creative activities.

We have only just begun to study the way humans control their gaze under such natural conditions. I know of only five publications to date that meet the criteria listed above for studying human eye movements, *accurately* with respect to both space and time, under ecologically relevant conditions; namely, Epelboim (1998), Epelboim et al. (1995, 1997), Malinov et al. (2000), and Herst et al. (2001) (see Ballard et al. (1994), Land (1992), Land and Tatler (2001), Land et al. (1999), Smeets et al. (1996), and Land and Hayhoe (2001) for ecologically relevant experiments in which the eye movement recording methods were not sufficient to examine fine details of human performance). In addition, see Johansson et al. (2001) for an experiment in which objects were manipulated, condition (3) above, under less than ecologically relevant conditions. The authors recorded monocularly with a video-based eye-tracking system (effective bandwidth = 60 Hz) with the head immobilized on a biting board that “provided high stability of the head” (p. 6918). In short, we have just begun to study human eye movements accurately under the conditions in which humans evolved. At present, we still know very little about how gaze is actually controlled under natural conditions.

The first accurate, but unnatural, recordings of human fixation

It required half a century for investigators to get answers to two simpler questions, questions of interest ever since human eye movements were first recorded by Delabarre (1898): how well could gaze be kept on an attended target, and what kinds of eye movements were used to maintain gaze after fixation was achieved? Both of these questions had a bearing on a more fundamental question: how much does the image of an attended target move on the retina when the direction of gaze is maintained by rotations of the fixating eye within its orbit? This question was important because anatomical research early in the twentieth century revealed an even greater degree of retinal heterogeneity than was expected when human eye movement research began. There was a cellular specialization, called the *Central Bouquet* (Rochon-Duvigneaud, 1943) at the center of the fovea. It had a diameter of about only one-third of a degree of visual angle. This specialized region was filled with a densely packed group of rod-shaped cones. Clearly, the highest-quality human vision would require an exceptional ability to fixate an attended object. It had to be able to place the retinal image of the attended target exactly at the foveal center, and it had to be able to keep it there long enough for its finest details to be discriminated.

The problem encountered as soon as one tries to study the human being's control of gaze stems, in no small measure,

from the human's remarkable ability to control his or her gaze. Once it became possible to actually measure how good it was, free from artifacts, it became clear that gaze control was exquisite. Gaze could be placed and kept on an object with remarkably little variability, at least under the very unnatural conditions that were required to measure these minuscule behaviors. That is, the head had to be immobilized as much as possible, and the fixation target had to be placed on the line of sight when the eye was in its primary position in its orbit. Fixation did not seem nearly this good when measurements were first made by photographing light reflected from the curved surface of the cornea. This method, which was introduced by Dodge and Cline (1901), is called the *corneal reflex* method. It was used by Dodge, his collaborators, and many others, for 50 years, providing the bulk of the existing eye movement literature until 1950, when a new and much more accurate method came into vogue. Gaze during maintained fixation, as recorded with the corneal reflex method, was quite variable even when an experienced subject attempted to maintain gaze. But it was hard to know why because deviations in the direction of the beam reflected from the surface of the cornea could be caused by two motions: by a rotation of the eyeball or by a translation of the head. A translation of the head would bring the beam of light falling on the cornea to a different location on its curved surface. Changes in the position of the recording light falling on the photographic paper caused by rotations of the eyeball were of interest. Changes in position caused by head translations were not. They were artifacts. A technique was required to prevent them, or some way of recording them and subtracting them from the records was required (subtracting them was exceedingly difficult, perhaps even practically impossible; see Ratliff and Riggs, 1950). The human cornea is quite curved, which means that even a tiny translation of the head introduces a quite large artifact into the records. Clearly, the quality of human fixation, and the nature of retinal image motion, could not be known until this problem was solved. The very best biting board was not good enough to eliminate it (see Barlow, 1952, for a particularly heroic attempt to hold the head rigidly in place).

The first step toward the solution of this problem (known to the author) was made by Adler and Fliegelman (1934). They used the *optical lever technique* to measure human fixational eye movements. In this method, a very small, flat (plane) mirror is mounted on the eye, and eye movements are recorded when a beam of light, reflected from this mirror, falls onto photographic paper moving behind a slit at the front of a movie camera. The use of a *flat* mirror at the fulcrum of the optical lever, instead of the curved corneal surface, removes the head translation artifact from the records because the angle of incidence of the recording light beam does not change when the surface reflecting it to the photographic paper is flat. The angle of incidence does

change if the curved surface of the cornea is used, as had been the case in prior research. The optical lever technique easily produces records with very good spatial resolution because it has an inherent 2× magnification factor, that is, a 1 degree change in the angle of incidence results in a 2 degree change in the angle of reflectance (see Nachmias, 1959, for an explanation).

By 1934 it was also possible to record on rapidly moving photographic paper. This allowed a high degree of temporal as well as spatial resolution. Even the very smallest fixational eye movements could be seen in Adler and Fliegelman's (1934) records. They reported that when a human being maintained fixation, eye movements consisted of *rapid shifts* averaging about 15 min arc; *waves*—inconsistent in direction, extent, and duration with peak-to-peak (p-p) displacements of 2½ to 5 min arc; and *fine vibratory movements*—50 to 100 per second, with p-p extents of about 2¼ min arc. These were important results, but their validity was still in doubt because Adler and Fliegelman's subjects had been required to maintain fixation on a relatively nearby target (only 2 m away). With such a target, the slightest movement of the subject's head with respect to the fixation stimulus would confound head translations relative to the fixation stimulus with motions of the image of the fixation target on the retina. The sizes of the various fixational eye movements they reported were also questionable. These authors apparently did not understand that their optical lever magnified the extent of eye rotation. Their quantitative descriptions were twice as big as those that should have been reported. These facts made the significance of Adler and Fliegelman's results uncertain at best. Ratliff and Riggs (1950) solved these problems and, in doing so, provided a valid method for studying the finest features of the human eye movement pattern. Their improvements also made it possible for them to make inferences about the nature and extent of the retinal image motions of their fixation targets. Ratliff and Riggs' technique also laid the foundation for stabilizing retinal images in the presence of fixational eye movements, a type of research that engaged many investigators between 1950 and 1980. Their landmark paper began by summarizing the status of knowledge about high-frequency tremor during maintained fixation. In the authors' words:

The summary of the studies of physiological nystagmus [one of the terms used to describe the small high-frequency component of the eye movement pattern during maintained fixation; *high frequency tremor* was the other] indicates that there is . . . evidence to support three different positions . . . (1) the eye is in motion . . . and there are fine vibratory motions . . . (2) the eye is in motion, but there is little evidence of vibratory motions . . . (3) The eye is essentially motionless during short periods of fixation. (Ratliff and Riggs, 1950, p. 690)

Why were things so unclear in 1950, after 50 years of objective human eye movement research? The big problem

stemmed from the fact that it was not possible to separate motions caused by head movements from those caused by eye movements. Ratliff and Riggs (1950) introduced a simple way to get around this. Again, in their words:

Originally it was planned to use the simultaneous records of head and eye movements to determine the exact motions of the retinal image [during maintained fixation], because . . . both . . . must be known to determine the motions of the image on the retina. However, it became apparent . . . that the center of rotation of the head is not even approximately a fixed point. At times the center of rotation may be at the point of contact of the upper teeth with the biting board [a dental impression used to restrict head movement]. At other times it may be at the point of articulation of the vertebral column with the cranium. Since the center of the head cannot be determined with accuracy, the angular movements which are recorded are of little use in determining the linear extent of the movement of the eye due to head movements . . . a better method . . . was needed. (Ratliff and Riggs, 1950, pp. 692–693)

They avoided the problem of eye translations by using the optical lever technique, introduced by Adler and Fliegelman (1934). They improved it, however, by mounting their small, flat mirror in a tight-fitting scleral contact lens. (Adler and Fliegelman had stuck their mirror directly on the eye and held it in place with a dab of vegetable gum.) The contact lens allowed Ratliff and Riggs to record for much longer periods of time. The contact lens also eliminated the need for the subject to hold the eyelid up with a finger while recordings were made. Ratliff and Riggs' most important contribution, however, was the way in which they eliminated the confound produced by head translations relative to the target. Head movement artifacts were eliminated simply by using a collimating lens in front of the eye. This lens placed the fixation target at optical infinity. This arrangement allowed the head to translate on the biting board without causing the retinal image of the target to be displaced on the retina. The fixation target, once it was viewed through the collimating lens, was simply too far away for head translations to affect the position of its retinal image significantly.

Ratliff and Riggs' (1950) records were valid, but they were hardly representative of natural fixation. The target was fixated monocularly while the head was immobilized as much as possible on a biting board. Even under these very restricted conditions, valid measurements could only be made of eye rotations on a single meridian, usually the horizontal. Nachmias (1959) introduced the first convenient variant of the optical lever method that could be used to make simultaneous, valid, albeit still very unnatural measurements of eye rotations on both horizontal and vertical meridians without confounding vertical with torsional eye rotations. Many important human oculomotor characteristics were observed under such unnatural conditions, and some of their physiological underpinnings have been worked out in primate models by recording electrophysiological brain activity in the oculomotor systems of monkeys while

they performed a variety of oculomotor tasks. The bulk of this research was done with a magnetic eye movement recording method introduced by Robinson (1963).

Instrumentation continued to develop, and by the last decade of the twentieth century, it finally became possible to observe how a human being controlled gaze under relatively natural conditions, that is, with the head and torso free to move naturally as objects within arm's reach were observed and manipulated. Doing this required solving the problem Ratliff and Riggs (1950) had managed to get around by putting their targets at optical infinity. Observing gaze control with nearby objects requires measuring the smallest translations (<0.1 mm) of the head, as well as its roll, pitch, yaw, and two-dimensional binocular eye movements. All of these angles have to be measured to at least 1 arc min for the measurements of gaze to be at least twice as good as the performance of the oculomotor system, the biological system under study. See Epelboim et al. (1995) for a brief description of the instrumentation developed to do this. This unique instrumentation made possible the first accurate, natural studies of human gaze control. These studies have called into question the significance of many observations that had been made earlier under less natural conditions. These new naturalistic observations will be described after some highlights from earlier, somewhat less natural, research are reported. These observations clearly implied that studying the human being's control of gaze under unnatural conditions could be perilous. They could mislead the investigators. There were clear hints that this might be the case as early as 1953 when Riggs et al. published their pioneering study of stabilized retinal images. Their study reported a result whose significance was not appreciated for more than 25 years. This publication will be described in some detail after some necessary background and definitions are presented.

Background and definitions

Foveal creatures like ourselves make two very different kinds, or types, of eye movements. In the simplest classification, proposed by Steinman et al. (1990), these two kinds of eye movements are simply called *fast* and *slow*. This reduces the number of postulated oculomotor subsystems from five or more to only two (see Dodge, 1903; Hallett, 1986; Robinson, 1968, for descriptions of many more oculomotor subsystems). Steinman et al. (1990) justify their reduction by pointing out that the traditional classifications are based primarily on the stimulating conditions usually used to study one or another of these putative subsystems. The classifications do not seem to be based on any well-established differences in oculomotor performance, physiology, or anatomy. The simpler classification seems to be catching on, as evidenced by its adoption in a popular introductory perception text (Sekuler and Blake, 2002, pp. 364–370). In this

classification, eye movements are simply called either fast or slow on the basis of three oculomotor performance characteristics, namely, their (1) peak velocities, (2) acceleration characteristics, and (3) susceptibility to voluntary control. The initiation, size, and direction of the fast eye movements, which are called *saccades*, are under voluntary control. They accelerate very rapidly and attain their relatively high peak velocities early. Saccades do not require visual targets. Their peak velocities are somewhat lower, and the size of the smallest voluntary saccade is larger when no targets are visible, but their main performance characteristics are the same. As a consequence, humans can shift their gaze to look at something that may appear anywhere in a completely dark visual field almost as well as they can shift their gaze to look at something visible in peripheral vision. Said differently, saccades are not influenced by properties of the visual field. The eye will drift in an idiosyncratic direction in total darkness (often down) when the head is immobilized, however, because the low-velocity compensatory eye movements, called *slow control*, require input from a visible stimulus moving on the retina (Steinman et al., 1967, 1973).

Slow (or *smooth*) eye movements are different. They accelerate gradually, and their maximum velocity is less than half of that achieved by the fastest saccades. The susceptibility of these slow eye movements to voluntary control is also much more limited. Normally, they cannot be initiated voluntarily if nothing is moving on the retina. Smooth eye movements will respond reflexively to a moving object or frame in the visual field, *but only if* the observer is not provided with a stationary object which can be used to keep gaze in place. Objects or frames that are moving in the visual field can be ignored, but gaze can stay in place only if the visual field contains a visible stationary target. Head movements can also cause the retinal images of objects and frames to move, and if, *but only if*, the subject attends to these motions will they be tracked with smooth eye movements. If smooth eye movements are made by paying attention to a moving object, the response is called *smooth pursuit*. If smooth eye movements are made by paying attention to a large frame rather than to an object, many oculomotor researchers call these slow eye movements *optokinetic reflexes* (OKN), rather than smooth pursuits. This distinction seems to be based entirely on tradition, and not on the characteristics of the eye movements themselves or any known differences in their anatomical or physiological underpinnings. Note, however, that if the subject chooses to attend to a stationary object or frame, smooth eye movements will not be observed. Gaze will be maintained. So, what the person wants to attend to is under voluntary control, but when it comes to slow, or smooth, eye movements, properties of the attended stimulus determine the nature of the oculomotor response once the subject selects the stimulus. (See Kowler et al., 1984, for experimental results showing the degree to which selective atten-

tion determines the outcome when moving and stationary stimuli are present in the visual field at the same time, and see Kowler, 1990, for the most comprehensive treatment available of the importance of cognitive factors in controlling human eye movements.)

Head movements also provide another kind of input to the oculomotor system. The oculomotor system receives input from the hair cells in the semicircular canals of the vestibular system as well as from the retina. These hair cells respond to accelerations of the head, causing the eye to rotate in the direction opposite to the head's rotation. The eye's angular velocity, resulting from vestibular stimulation, is similar (~95%) to the head's angular velocity (Collewijn et al., 1983). These involuntary counterrolling eye movements, called the *vestibulo-ocular reflex* (VOR), can be canceled almost completely if the observer fixates an object attached to the head, such as the tip of the nose if it is illuminated and if it is long enough to be seen. The VOR cannot be made to operate voluntarily if the head is not allowed to move. Once it can move, what VOR does depends on what the subject is attending to. The velocity of the slow eye movements (smooth pursuits or OKN) that a subject uses to track a smoothly moving object or frame *can* be adjusted voluntarily to specified fractions of the target's velocity, but smooth eye movements *cannot* be made voluntarily without a target moving on the retina, and smooth pursuit velocity *cannot* exceed the velocity of the moving target. Subjects asked to get ahead of a smoothly moving target can do this, but only by making saccades ahead of the target. They cannot lead the target with smooth pursuits (Steinman et al., 1969).

Each type of eye movement accomplishes different things. The fast, voluntary eye movements, saccades, are used to fixate an attended object, that is, to place its retinal image within the fovea. Said differently, saccades are used to place gaze where, within the visual field, we want gaze to fall. Human saccades can attain peak velocities of about 550 deg/sec. Their peak velocity depends on their size. Larger saccades are faster. This velocity/amplitude relationship has been dubbed the *main sequence*, a term borrowed from star brightness magnitudes in astronomy which was probably introduced to impute some kind of special significance to this rather common phenomenon. Very small saccades, called *microsaccades* (smaller than 10 or 12 min arc), have velocities of only a few degrees per second. These tiny saccades are the smallest voluntary human behaviors (see Haddad and Steinman, 1973; Steinman et al., 1973, for a discussion of their nature and functional significance).

Saccades of all sizes are used to bring attended objects to fall at the *center of best vision* or *optimal locus* (Cornsweet, 1956) at the foveal center. Saccades of about 0.5 to 1.5 degrees of visual angle are used to read a line of ordinary text. Saccades can also be used to reestablish fixation quickly if an object suddenly moves away from the optimal locus.

Saccades can shift gaze among objects in the visual field very rapidly. We are not ordinarily aware of making these rapid gaze shifts, and it came as a surprise when it was discovered that such high-velocity jumps were used to read. Subjectively, one has the impression that our eyes glide smoothly across the text as we read each line of words. We can easily make ourselves aware of the relatively large gaze shift we use to move from the end of one line to the beginning of the next, but the jumps among the words are perceived as being smooth. They are not. The reading eye movement pattern is shown in Figure 90.1. This figure is somewhat unusual because it shows the reading eye movement pattern of a subject who is reading under relatively natural conditions. The subject is seated with the head and torso free as he reads a standard text located about 30 cm in front of his eyes. Only left eye movements are reproduced in this figure, but recording was binocular (the right eye movements were very similar to the left). Translations as well as rotations of the head are shown. The top graph in Figure 90.1 shows head rotations; the bottom graph shows rotations of the left eye. The pattern of head rotations varied during the trial. A 2 degree head rotation to the right was made during the third and fourth seconds as the eyes moved to the right across a line of text. There was a fast, large saccade (~25 degrees = about 10 cm on the page) that moved gaze to the left to the beginning of the next line of text near the middle of the fifth second, but the movement of the head was much slower, which meant that the head was still *moving* to the left as the eye was moving to the right as it read the new line of text. So, for about 0.5 second, the head and eye were moving in opposite directions.

Different head-eye coordinations were observed during other reading trials, and the second subject, who served in these experiments, also showed different kinds of head-eye coordination. Kowler et al. (1991) drew the following conclusions from this research:

Head rotations were larger when the head was free than when the head was on a the bite board [and] the S.D.s of head rotations with the head free are about twice what is observed when subjects try to hold the head as still as possible without artificial support during maintained fixation. . . . The head moves during reading but not in a stereotypical pattern . . . in some instances it moved in the same direction as the reading saccades; in other instances it moved in the opposite direction. Eye rotations compensated well for head movements, producing a fairly stable line of sight during intersaccadic intervals. (pp. 421-422)

None of these head and eye movements are perceived subjectively when one reads, a fact which seems as remarkable now as it *did* when it was first discovered a little over a century ago.

The human being's slow, or smooth, eye movements have velocities ranging from as little as 3 minutes of arc per second up to peak velocities of about 200 degrees of arc per second.

Kowler, 1990, for a review of her research on anticipatory smooth eye movements). We also speak of *involuntary* or *noisy drifts*. Adler and Fliegelman (1934) called these slow eye movements *waves*. They are involuntary slow shifts of gaze. They are observed in the intervals between small saccades, which are made when an adult subject maintains fixation on a stationary object with the head immobilized. The involuntary slow eye movements, which have been shown to correct such noisy drifts, have been described as smooth pursuit of a stationary object whose retinal image moves because of noisy drifts (Nachmias, 1959). Steinman et al. (1973) ascribed these compensatory fixational slow eye movements to the operation of an oculomotor subsystem they dubbed *slow control*.

Findings encouraging questions about the relevance of unnatural research

THE ROLE OF NATURAL AND UNNATURAL RETINAL IMAGE MOTION IN VISUAL PROCESSING Riggs et al. (1953), who initiated a long line of research on stabilized retinal images, reported an unexpected result whose significance would not be appreciated for 26 years. They used the contact lens optical lever technique to allow a subject to view a simple fixation target under three conditions. The first condition allowed what they called *normal* vision, in which the subject viewed the stimulus monocularly with the head fixed on a biting board. They called this vision normal because the retinal image displacements of the fixating eye were the same as the displacements present under the fixation conditions they normally used, that is, with the head immobilized on a biting board. In the second condition, a mirror path in the optical arrangements stabilized the retinal image of the fixation target. When the eye moved, the target moved with it by the same amount, so its retinal image did not move on the retina. In the third condition, called *exaggerated motion*, the mirror path was arranged so that an eye movement caused the fixation target to move on the retina twice as much as it moved during normal fixation. The subject indicated whether the fixation target was visible during fixation trials, which lasted for many seconds. As expected, the stabilized target disappeared often and remained invisible for the longest period of time. The target also disappeared occasionally during normal viewing. This was not surprising. Many observers had noticed periodic fading of fixation targets (and more complicated displays) when they stared at them for many seconds with the head immobilized artificially. Fading was least likely in the exaggerated retinal image motion condition. This result came as a surprise, but little was made of it at the time. It clearly meant that transient stimulation was useful for visual processing, but its implications were otherwise ignored. It became important 26 years later when Skavenski et al. (1979) published the first accurate monocular recordings of the head and eye movements

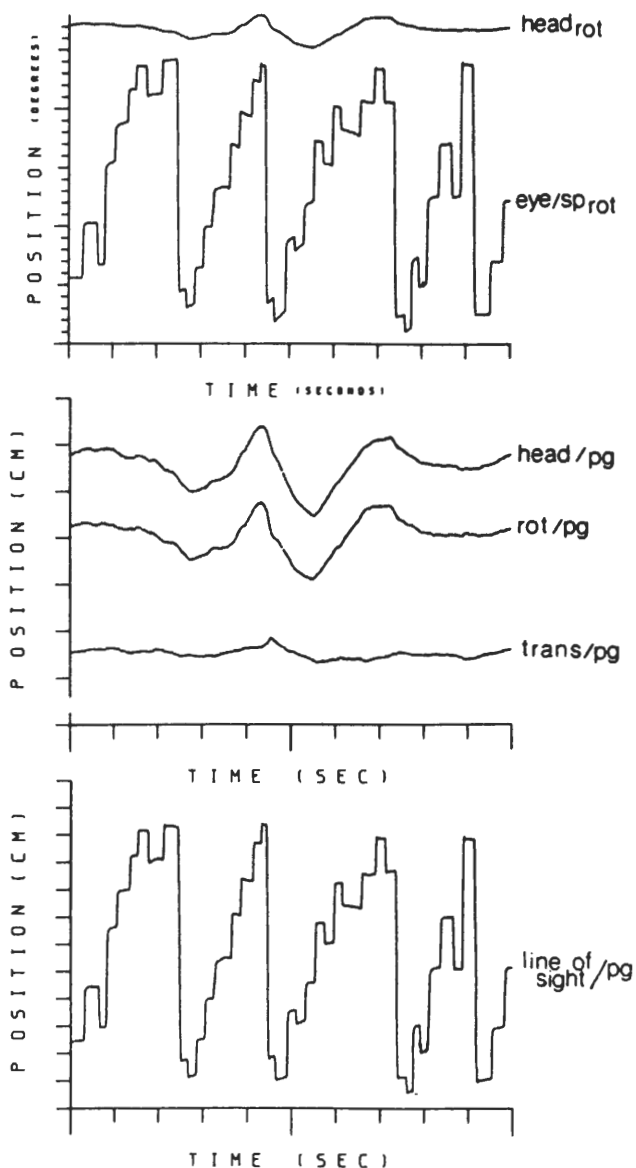


FIGURE 90.1. Results of a sample reading trial. *Top*: Horizontal rotation of the left eye and the head as a function of time during reading. Upward deflection of the traces indicates rightward eye or head motion. *Middle*: Total movement of the head (head/pg), the rotational component (rot/pg), and the translational component (trans/pg) on the page of text. These traces represent the positions of an imaginary line connecting the midpoint of the center of rotation of the left eye with the page. *Bottom*: Horizontal position of the line of sight of the left eye on the page of text. (From Kowler et al., 1991.)

They tend to be involuntary in the sense that normally they cannot be made by willing them in the absence of something moving in the visual field. They will, however, always be made in anticipation of a future target motion. These *anticipatory smooth eye movements* can be as fast as 60 deg/sec (see Steinman et al., 1990, for records showing very fast anticipatory smooth eye movements, and see

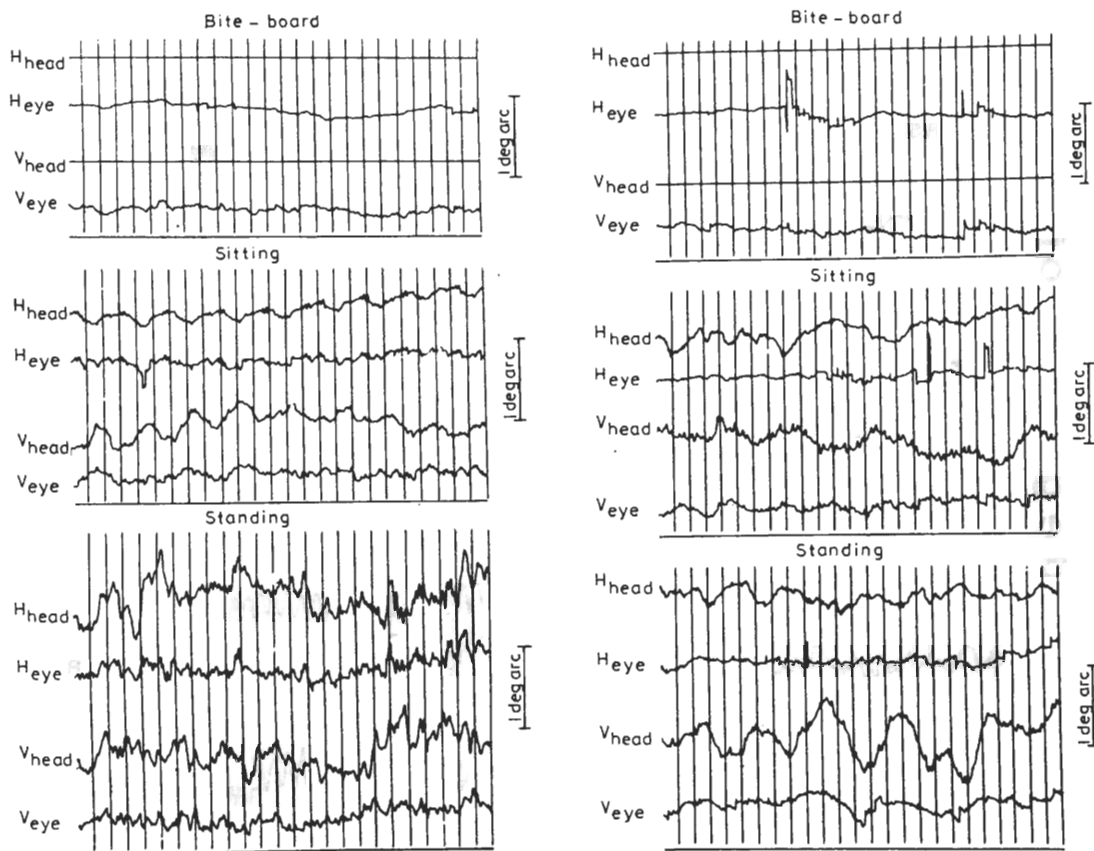


FIGURE 90.2. Representative horizontal (H) and vertical (V) head position and gaze of subject AAS (*left*) and RMS (*right*) while they fixated a target at optical infinity with their heads supported on a biting board or while they were standing as still as possible. Records

of seated and standing subjects fixating a target located at optical infinity.

Figure 90.2 clearly shows that the head moves quite a lot when a human being tries to sit or stand as still as possible. A good deal of this head movement is compensated for by eye movements, but considerable retinal image motion remains. The eye traces in the records reproduced in Figure 90.2 show gaze. They would be horizontal straight lines if head movements were compensated for perfectly. There are very few instances where this can be seen in the records of both subjects when they sat or stood. Their gaze was considerably more stable when their heads had artificial support, as shown by the top two records in Figure 90.2. Note that in the two more natural conditions in which the subjects were sitting or standing still without artificial support, there was considerable uncompensated head motion. This led to considerable retinal image motion—enough to minimize, perhaps even to prevent, any fading of the fixation target. The retinal image velocities observed while they were sitting and standing were quite similar to those which had proved to be so effective in preventing fading in the exaggerated retinal image motion condition in the Riggs et al. (1953)

begin on the left. The vertical lines show 1 second intervals, and the vertical scales on the right show 1 degree of visual angle. Upward changes in these position traces signify rightward or upward rotations. (From Skavenski et al., 1979.)

publication about stabilized images. The implications of these results, in the authors' words, were as follows:

[T]he gain of the compensatory machinery is tuned to guarantee that the retinal image will always move at some appreciable speed which would not be the case if the gain of compensation approached 1 when the amplitude of body rotation was small. . . . Note that subjects whose heads are supported on bite-boards occasionally report periods of target fading which means that retinal image speeds seen on a bite-board are only marginal for maintaining vision . . . [and] once we pay attention to the fact that compensation is mostly less than perfect . . . we are forced to consider how we see a perceptually clear world during such image motion. Oculomotorists have assumed that the quality of vision is a consequence of the stability of the retinal image [caused by the virtual perfection of oculomotor compensation]. The retinal image is not actually stable so perceptual clarity must depend in part on visual as well as on oculomotor activities. (Skavenski et al., 1979, pp. 681–682)

The significance of Figure 90.3 is quite similar to that of Figure 90.2. Here we see recordings made under even more natural conditions. Figure 90.3 shows head and binocular eye recordings of four subjects who attempted to maintain

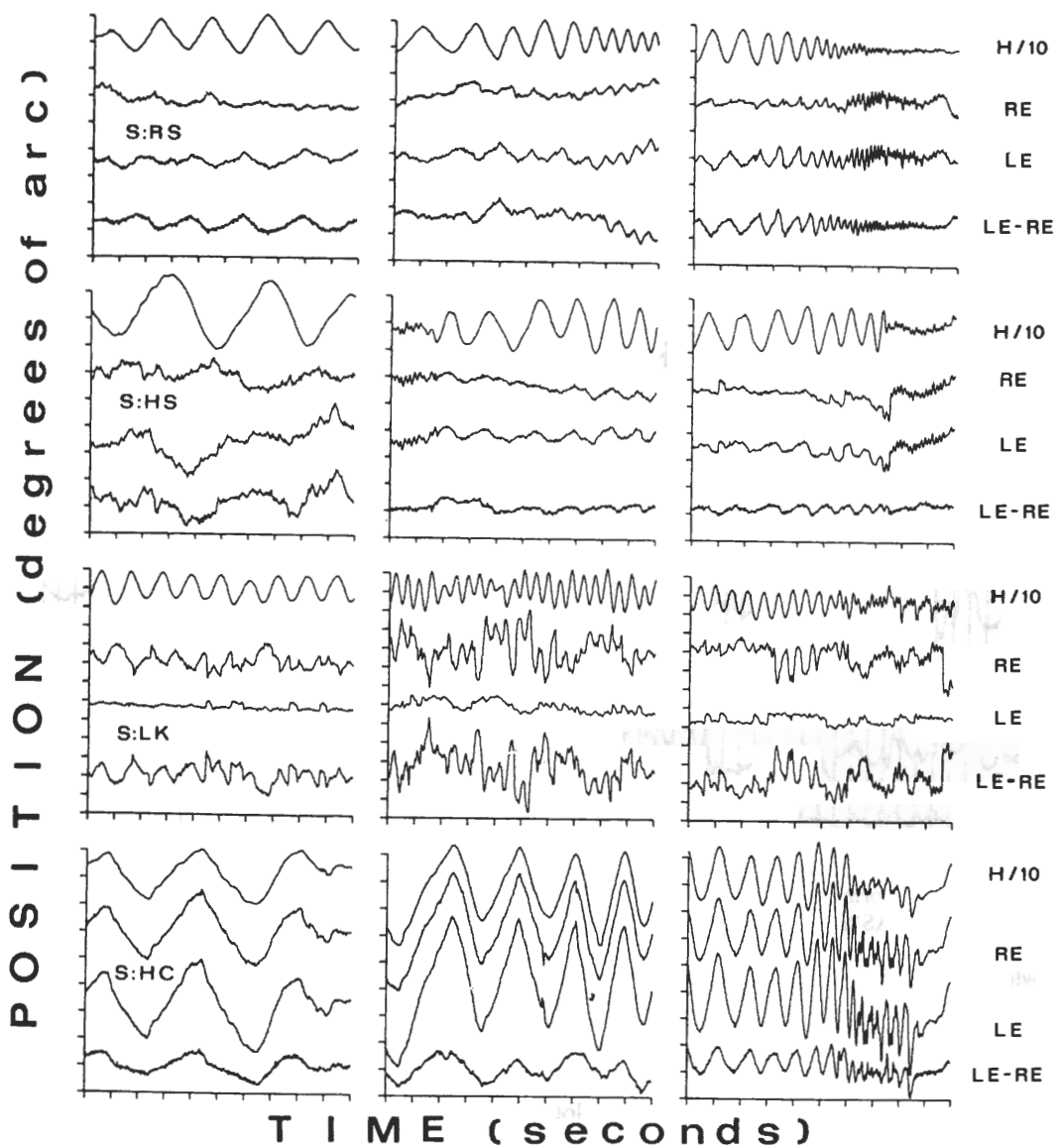


FIGURE 90.3. Representative horizontal eye and head movements of four subjects (R.S., H.S., L.K., and H.C.) while they fixated a distant object as they moved their heads. Records begins on the left, and the time-scale marks signify 1/10 second intervals. The head position trace (H/10) shows the position of the head to 1/10th of its actual value. Right eye position (RE) is just below the head, with

left eye position (LE) just below it, and the bottom trace in each graph (LE-RE) shows vergence. Upward changes in position traces in these records show rightward movements, and upward changes in vergence traces signify convergence. (From Steinman and Collewijn, 1980.)

fixation on distant targets (5000 or 35,000 m away) as they actively oscillated their heads about their vertical axis at different frequencies and amplitudes. Once again we see considerable oculomotor compensation for head rotations, but it is far from perfect, which means that there was considerable residual retinal image motion. All four subjects reported seeing clearly throughout these trials. Some jitter of the visual field was reported at the highest head oscillation frequencies, but vision was always fused and clear despite such violent retinal image motions. Now that binocular record-

ings were finally made, a very surprising result can be seen: there was considerable difference in the degree of compensation by each of the subjects' eyes. This led to considerable variation in their vergence angles (the oscillations evident in the bottom trace in each subject's graphs, labeled "LE-RE," for "left eye-right eye"). This result was not expected. Such large variations in vergence angles should not have been observed when binocular fixation was maintained on such distant targets. The implications of these results, in the authors' words, were as follows:

It is not easy to study binocular eye movements accurately in freely moving subjects or to stabilize retinal images under such conditions. Furthermore, it was not believed to be necessary to study freely moving subjects. Almost all investigators . . . believed that natural visual and oculomotor performance, and their interaction, could be understood despite the fact that their subjects' heads were immobilized. Two assumptions underlie this belief. First, it is assumed that the oculomotor system compensates almost perfectly for motions of the body. . . . Second, it is assumed that compensatory oculomotor activities are almost perfectly yoked in the two eyes. Once these two assumptions are made, the fusion, stability and clarity of the visual world during normal activity can be explained. These explanations, however, rest on what we now know is an idealized view of the operation of the oculomotor system. (Steinman and Collewijn, 1980, pp. 427–428)

These results also suggest that much will be found under natural conditions that could not have been anticipated from what was known from research performed under the more common, much less natural conditions usually employed.

THE MICROSACCADE, FUNDAMENTAL OCULOMOTOR ACTION OR LABORATORY CURIOSITY The microsaccade has a long history in the study of human eye movements research. It first became prominent as what Adler and Fliegelman (1934) called *rapid shifts*, which were observed during attempts to maintain fixation. Adler and Fliegelman claimed that their extent was about “15 minutes of arc.” Once this value is corrected for their computational error (see above), these saccades would be 7.5 min arc, an acceptable value for what has been called a *microsaccade* since Zuber et al. (1965) introduced this term. Generally speaking, saccades smaller than 10 or 12 min arc along a single meridian have been placed in this category ever since accurate estimates of fixational eye movements began to be made about 50 years ago. Ditchburn (1955), who trained as a physicist and shifted his research interests to human vision after World War II, believed that transient stimulation provided by these microsaccades, which he called *flicks*, was essential for maintaining clear, high-quality color vision. Many subjects, but by no means all, whose fixational eye movements have been recorded since the optical lever technique came into vogue showed microsaccades in their eye movement pattern during maintained fixation. The status and significance of microsaccades came into question when Steinman et al. (1967) reported that simple instructions would reduce their frequency appreciably (by 50% or more) and even eliminate them completely. These reductions in microsaccade rates had no adverse effects on the quality of vision. This observation was followed by a series of publications, including some which showed that saccades as small as microsaccades were in the voluntary behavioral repertoire and others which showed that microsaccades could be used to track small target steps reliably. These experiments were summarized by Steinman et al. In 1973, by which time it was generally

accepted by most oculomotorists that microsaccades, which are present only in the behavior of adult human beings whose heads are being held artificially while they attempt to maintain fixation, were a laboratory curiosity rather than an important oculomotor behavior (Kowler and Steinman, 1979). Ditchburn (1980) preferred to believe otherwise, and his comment on one of the papers in this series led to an exchange of letters (Kowler and Steinman, 1980). This exchange should be of interest to anyone wondering about the significance of microsaccades. The significance of microsaccades for processing visual contrast and spatial detail was discussed in Steinman and Levinson (1990). This review also claims that microsaccades are not likely to contribute to any kind of visual processing. In addition, it reviews the extensive literature on stabilized images and also claims that microsaccades do not play a significant role in vision. When it first became possible to study the control of gaze under relatively natural conditions (Steinman and Collewijn, 1980), it became clear to the investigators that microsaccades were not common, perhaps even absent, in the fixational eye movement pattern once the head was free to move naturally. Nailing this down has become important now that microsaccades are beginning to be taken seriously in the primate oculomotor community (e.g., Bair and O’Keefe, 1998; Martinez-Conde et al., 2000; Rucci et al., 2000). For this reason, we randomly sampled 3375 saccades made by four subjects in two naturalistic sequential looking tasks and found that only 2 (0.06%) could be classified as microsaccades, that is, smaller than 12 min arc (Malinov et al., 2000). The implications of these results, in the authors’ words, were as follows:

We have another reportable, albeit expected result. Namely, microsaccades were extremely unlikely. . . . Those, who have studied human eye movements under natural conditions with instrumentation sufficiently sensitive (noise $\leq 2'$) to measure microsaccades, have rarely seen microsaccades (Steinman & Collewijn, 1980, were probably the first). **But** as far as we know, the actual likelihood of finding a microsaccade under natural conditions has never been reported, in part because: (i) other issues were under study; and microsaccades had lost their significance by 1980. They were laboratory curiosities, confined to human adults, whose head were supported artificially. (Malinov et al., 2000, p. 2089)

There is no reason to believe at this time that the situation has changed, so I would be cautious about accepting work imputing an important role to such behaviors in infrahuman primates, particularly inasmuch as it takes a lot of fixation training before monkeys even begin to show microsaccades in their fixational eye movement pattern (Skavenski et al., 1975; Steinman et al., 1973). We turn next to some relatively recent work on a subject that has forced a major revision of our thinking about the performance characteristics of one of the classical oculomotor subsystems: vergence.

NATURAL SMOOTH AND SACCADIC VERGENCE The oculomotor *vergence subsystem* was one of Dodge's (1903, 1907) five types of eye movement. He described these eye movements, which he called *type V*, in the following way:

The fifth type is in several respects unique. It consists, primarily, of movements of convergence and divergence . . . [when] the stimulus falls on disparate points of the two retinae, and the movements of the two eyes are consequently not in the same but in opposite directions. The most conspicuous of the differentiae of this type are the relative slowness of the movements. . . . Whereas movements of the first type [saccades] through 10° occupy about 40σ [msec]; eye movements of the fifth type . . . occupy about 400σ [msec]. (Dodge, 1903, pp. 327–328)

The slowness and smoothness of Dodge's type V eye movement were stressed in the oculomotor literature until quite recently, when Erkelens et al. (1989a) used the unique eye movement recording system developed at the University of Maryland to examine how vergence actually operated under much more natural conditions than had been possible before. These observations made it clear that studying human eye movements under unnatural conditions had given a very misleading impression of how the human oculomotor systems performs when it adjusts gaze in three dimensions. These experiments and the implications of their results, in the authors' words, were as follows:

We studied ocular vergence responses made under relatively natural viewing conditions as a first attempt to determine whether vergence responses obtained under such conditions could be predicted from descriptions of vergence responses to the isolated motion-in-depth cues that had been studied separately in previous experiments. We undertook to study vergence under relatively natural conditions because it has become increasingly clear in recent years that oculomotor performance, as well as its visual consequences cannot be predicted from studies undertaken under constraints that had been necessary and eventually became traditional in laboratory settings (Skavenski et al., 1979; Steinman and Collewijn, 1980; Collewijn et al. 1983; Steinman et al., 1985). . . . We found that ocular vergence in response to a target seen to be changing its position in depth in a normally lighted room, replete with natural cues to depth, had shorter delays and better dynamics than could have been expected from reports of previous experiments. . . . Changes in vergence often preceded changes in the distance of the target when the distance of the target was under control of the subject. The most accurate vergence tracking (smallest tracking error) was observed when voluntary movements of the upper torso . . . provided the changes in the distance of the target. (Erkelens et al., 1989b, pp. 418–419)

Figure 90.4 shows an example of one subject's slow or smooth vergence eye movements produced by changing the distance between the subject and the target in this experiment.

The next publication in this series of naturalistic experiments, by Erkelens et al. (1989a), yielded even more surprising results. Once again, the experiment and the

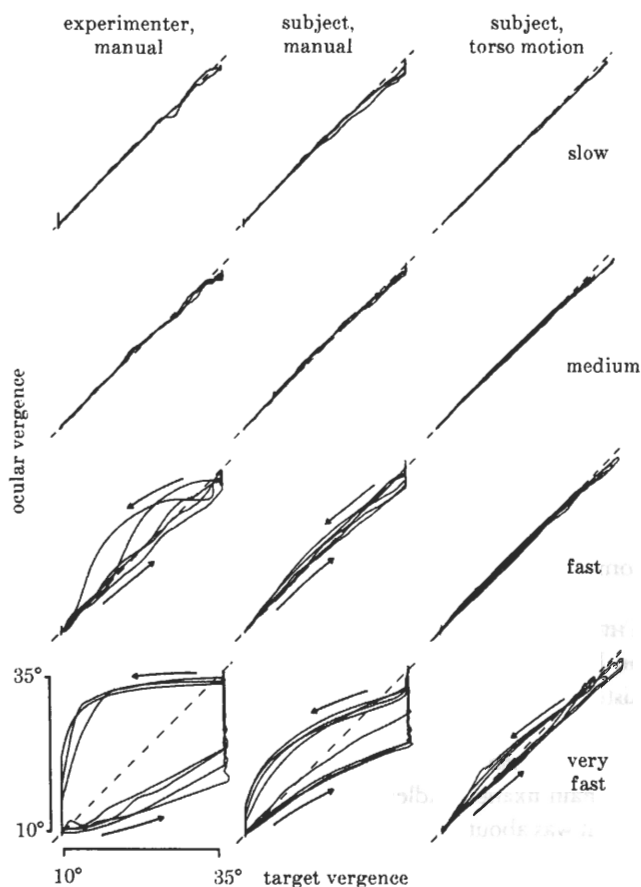


FIGURE 90.4. Typical relations between ocular-vergence and target-vergence angle of subject H.C. in response to slow (first row), medium (second row), fast (third row), and very fast (bottom row) changes in target distance. The three columns represent the three ways in which the distance of the target was varied. The diagonal dashed lines represent perfectly accurate vergence tracking. (From Erkelens et al., 1989b.)

implications of its results will be given in the authors' words:

In the preceding paper . . . we reported that the vergence subsystem makes timely and fast responses over a large dynamic range when it is provided with its 'natural input'. . . . We also showed that the vergence subsystem, like other oculomotor subsystems, is largely under voluntary control once it is provided with its natural input. . . . The present experiments . . . examined (1) shifts of gaze between stationary target objects . . . at different distances . . . along the median plane . . . and (2) shifts of gaze between objects that lay off to the side of the median plane as well as at different distances. . . . We examined . . . both [because they] are required for effective functioning in natural situations. We had no basis for predicting the quality of oculomotor performance. . . . We found that symmetrical vergence responses, as large as 30° , were largely smooth and attained maximum speeds as high as 200°s^{-1} . When . . . targets required asymmetrical vergence responses . . . vergence responses . . . were mediated almost exclusively by unequal saccades. . . . Such a dominant role for saccades in producing large vergence responses consistently has been rarely suspected. . . . We

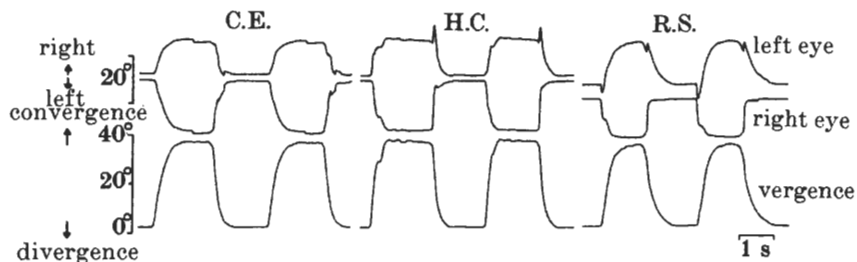


FIGURE 90.5. Representative binocular eye movements of three subjects (C.E., H.C., and R.S.) when they shifted gaze between light-emitting diodes (LEDs) located along each subject's median

plane. The small bar on the lower right shows a 1 second interval. The vergence shifts shown were mainly smooth. They were also very fast. (From Erkelens et al., 1989b.)

conclude that unequal saccades are generated normally in asymmetric vergence, and that traditional schemes . . . are incorrect. (pp. 442–443)

Figure 90.5 shows the very fast *smooth* vergence responses made by each of the three subjects, who shifted gaze between two targets located at different distances along their median plane. Figure 90.6 shows their asymmetrical *saccadic* vergence responses made when they shifted gaze between targets which were not located on their median plane. Note that under natural conditions, virtually all vergence changes are asymmetric and saccadic because targets are rarely located along the median plane and never stay there very long. The slightest movement of the body creates conditions favorable for saccadic rather than smooth vergence changes. Once this is appreciated, smooth vergence, like microsaccades, seems to be primarily a laboratory curiosity. It can be demonstrated, but it is hard to set up and almost impossible to maintain if the subject's head is not immobilized artificially.

The second paper on vergence under naturalistic conditions concluded as follows:

There is a great deal left to do now that we have shown that the control of vergence can be studied in the laboratory in ways that make sense with respect to the way vergence must operate in everyday life. We must now determine with our accurate, high-

bandwidth instrumentation, how the saccadic and slow subsystems function, synergistically, when gaze shifts between stationary objects . . . within the three-dimensional visual field in which human beings locate, track and manipulate objects of interest to them. We must refine our techniques to allow the subject's head to be free while he interacts with objects within reach of his hands. Once this is done, we will begin to have some idea of how cognitive, oculomotor and manual motor skills interact to guarantee our success as a species. (p. 464)

The reader should consult Judge (1991), who reviewed the status of vergence eye movements shortly after these two papers were published to gauge the novelty of these results with respect to how they fit with the traditional vergence literature, a literature that began with what Dodge (1903) called type V eye movements.

SUMMARY OF RECENT ECOLOGICALLY RELEVANT RESEARCH
The instrumentation developments required to study gaze under natural conditions were finished in 1992 and the first publication based on its use appeared in 1995, 3 years shy of the hundredth anniversary of the first publication reporting a method for recording human eye movements (Delabarre, 1898). In all, five papers meeting the requirements for studying gaze control under *natural* conditions have appeared so far (Epelboim, 1998; Epelboim et al., 1995, 1997; Herst et al., 2001; Malinov et al., 2000; see Steinman, 1995, for a detailed explanation of why and how the unique

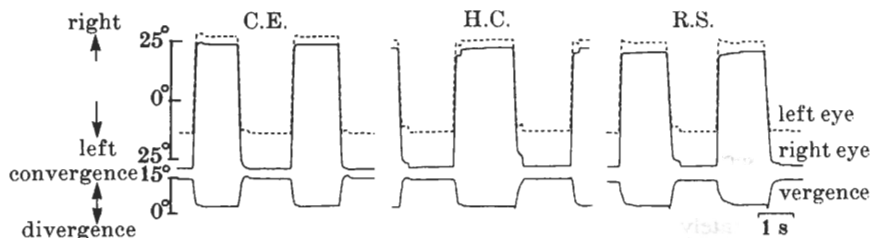


FIGURE 90.6. Representative binocular eye movements of three subjects (C.E., H.C., and R.S.) when they shifted gaze between a LED far away and to the right of the subject's median plane and a LED nearer and to the left of the subject's median plane. This target arrangement required asymmetrical vergence responses. The

dashed trace shows the position of the left eye; the solid trace shows the position of the right eye and vergence, that is, the difference between the positions of each eye. The small bar on the lower right shows a 1 second interval. The vergence shifts shown were mainly smooth. They were also very fast. (From Erkelens et al., 1989a.)

eye movement recording instrumentation at the University of Maryland was developed). In this series of experiments, the subject's head and torso were completely free as two-dimensional binocular gaze was recorded. The subject either looked at a sequence of targets in a specified order (look-only condition) or tapped a similar sequence of targets (tap condition). They were required to complete each sequence as rapidly as possible without making any errors. The targets were arranged in randomly selected locations on a work table in a well-illuminated chamber, which contained many objects and frames that provided excellent information about the location of the subject and targets within the three dimensions of the workplace. Data were also collected when the subject chose the order in which the targets would be fixated or tapped.

Only the main findings of these experiments will be summarized here. The source papers (listed just above) should be consulted for details. These results could not have been expected on the basis of prior work done under much less natural conditions. Highlights of the analyses completed and published so far are as follows: (1) just looking at a sequence of targets, solely to fixate each target accurately, and looking at a similar sequence to guide tapping, are fundamentally different tasks. The seemingly more complicated task, using vision to guide tapping, was easier, more pleasant, and took less time to complete than the task in which the subject did much less, namely, simply fixate each target in a sequence; (2) visual search (using a saccade to *find* the next target) is a separate and different saccadic activity from *looking from one target to the next in the sequence* in both looking and tapping tasks; (3) looking for its own sake, looking to guide tapping, and visual searching are synergistic, interacting in beneficial ways; (4) subjects almost *always* look at the target they are about to tap before tapping it, but are *convinced* that they do not do this often once a particular target pattern has been learned; (5) cyclopean gaze, on average, is more accurate than gaze from either eye, demonstrating that under natural conditions (6) subjects show no sign of a *dominant eye* when they use their eyes to perform visually guided motor tasks despite the fact that they do show a dominant eye when a conventional *phoria cover test* is performed; (7) microsaccades, when the head is free, are exceedingly rare (see the section "The Microsaccade, Fundamental Oculomotor Action or Laboratory Curiosity"); (8) vergence tends to be set 25% to 45% *beyond* the attended plane; in other words, subjects do *not* adjust binocular gaze to intersect at the attended target, but rather adjust their eyes to intersect much farther away; (9) subjects fixate no more accurately than a given task demands, implying that at least for ordinary visuomotor tasks, any part of the foveal floor which is good enough to do the job will be used; (10) the *main sequence*, like other characteristic oculomotor performance, is controlled from the top down, that is, high-level task demands, such as its objec-

tives or goals, set the control parameters in the oculomotor *plant* (its physiological machinery) automatically; it does this without any conscious effort; and (11) once the head, as well as the eye, is free from restraint, the head is most likely to begin to move before, or at the same time, as the eye. The way the four subjects of these experiments actually controlled their gaze when they only looked at and when they tapped sequences of targets can be visualized by going to the following web page: <http://brissweb.umd.edu>.

Some highlights of these publications, the first accurate reports of how human beings control gaze under ecologically relevant conditions, are reproduced in Figures 90.7 to 90.10. The reader should consult the source papers (cited above) for detailed explanations of how these data were collected and what they have been taken to mean. Examining the visualizations available at the web page (cited just above) after reading these source papers will also promote understanding of the significance of these figures.

The basis for achieving accurate gaze control lies in the human being's ability to call upon one or the other compensatory subsystem at different times and to varying degrees. This ability is built in. Choosing a particular behavioral objective (goal or purpose) sets the parameters in the oculomotor plant without any explicit, conscious efforts on the subject's part. Furthermore, under natural conditions, gaze control is lax, perhaps even lazy. One could just as easily call it *efficient*. Why should the oculomotor system set its parameters so as to make it do more work than is needed to get a particular job done? In short, it should not come as a surprise that gaze is not set to be as accurate as possible *all* the time. Evidence for this, as well as demonstrations of the human being's control of gaze by adjusting parameters of oculomotor subsystems, is clear when gaze is studied *under* conditions approximating those that are commonplace *in* the workaday world. It may be here, *and only here*, that the nature and extent of the human being's exquisite control gaze becomes apparent. Much of the oculomotor literature, which is based on research done with the head restrained and targets beyond arm's reach, has probably told us very little of lasting value despite a century of active research. Fortunately, methods are now available which make accurate, ecologically relevant research possible, so one can hope that a second century of oculomotor research will not be needed before we actually *know* how human beings control gaze as they do other things that are important for their success as a species.

Acknowledgments

This chapter is dedicated to the *memory* of Dr. Julie Epelboim (1964–2001), who *contributed enormously* to making the ecologically relevant *research referred to in this* chapter possible, as well as using this approach to collect the

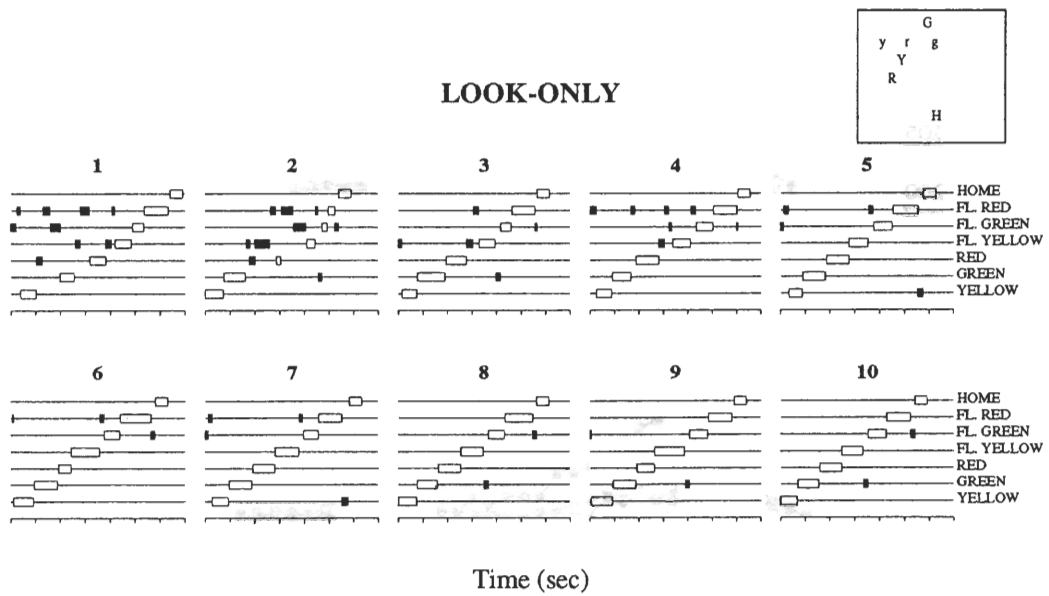
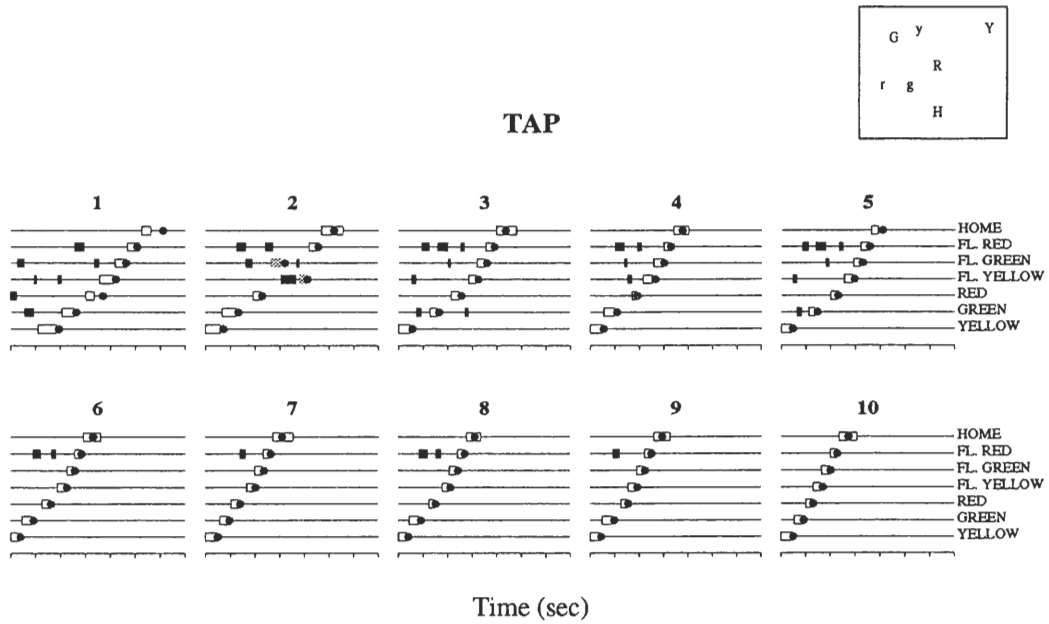


FIGURE 90.7. Look/tap diagrams for a 10 blocks of tapping trials and 10 blocks of looking-only trials. Each diagram represents one repetition with the same target configuration. The repetitions are numbered 1 to 10 above each diagram. The positions of targets on the work table for each block are shown in the rectangle signifying the colors of the six LED targets and a home button: Y, yellow; G, green; R, red; y, flashing yellow; g, flashing green; r, flashing red; H, home. Time is shown on the abscissa. Each horizontal line above the abscissa represents one target, labeled with its color on

the right. Boxes and dots on each horizontal line show when the subject looked at or tapped that target. Open boxes show sequence episodes, solid boxes show search episodes, and shaded boxes show looking episodes preceding tapping errors (see text). Widths of boxes show durations of looking episodes. Solid circles show the times of the taps. See the text for a full explanation, but it is clear that the visuomotor coordination during the two tasks was different. Looking for its own sake was not the same as looking to guide tapping. (From Epelboim et al., 1995.)

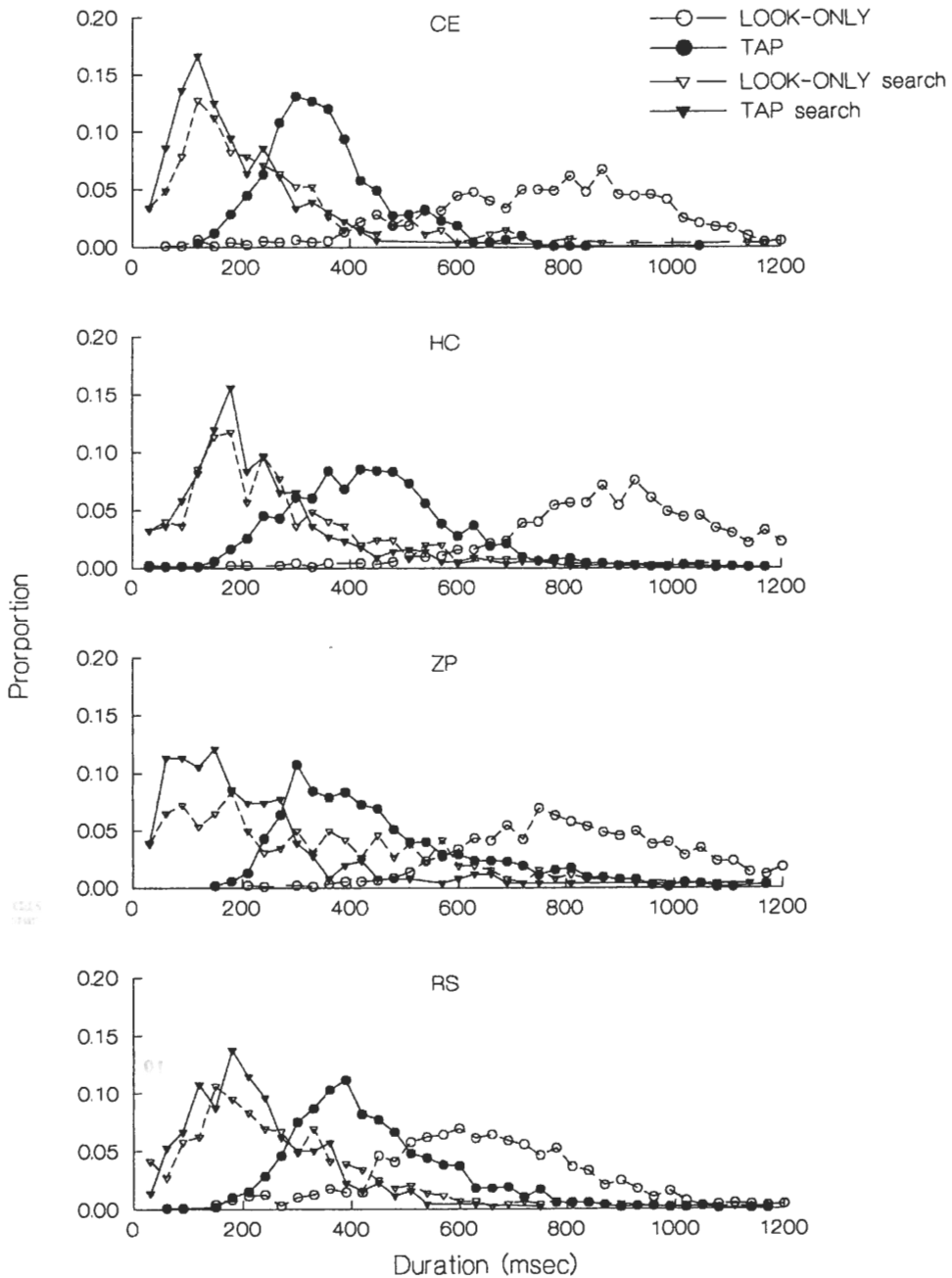


FIGURE 90.8. Distributions of sequence (*circles*) and search (*triangles*) episode durations (milliseconds). Data for tapping are shown as solid lines and solid symbols, and data for looking only are shown as dashed lines and open symbols. Bin width is 30 msec. Data for four subjects are shown in rows labeled C.E., H.C., Z.P., and R.S., Each distribution is based on 950 to 1396 observations for sequence episodes and 247 to 552 observations for search episodes. All four

subjects showed that dwell-time distributions for search episodes were short and the same in both tasks, and dwell times were much longer during look-only trials. These results were taken to mean that saccades made to find targets are different from saccades made to move gaze through a sequence of targets. (From Epelboim et al., 1995.)

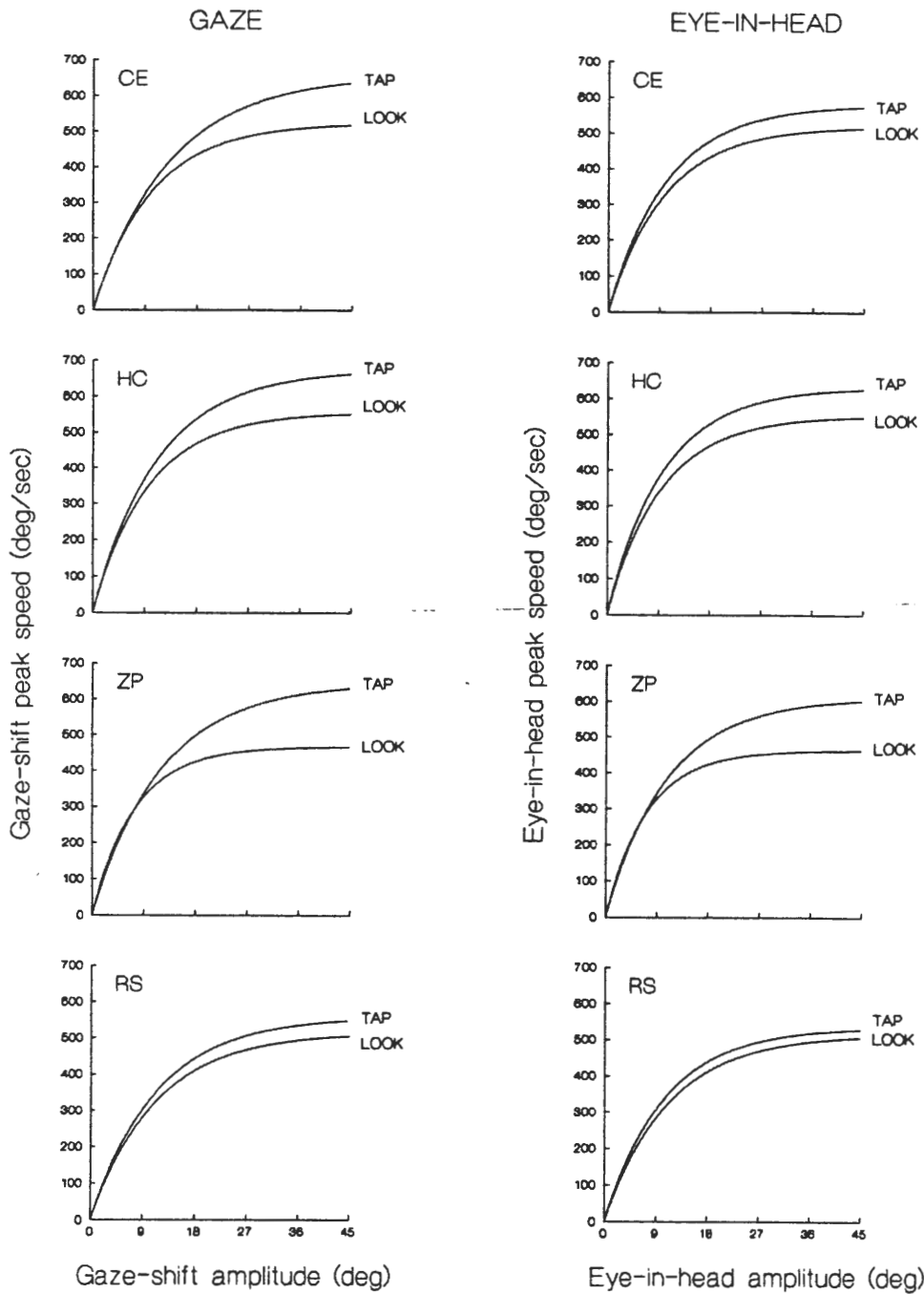


Figure 90.9. Gaze-shift peak speed (*left*) as a function of amplitude in space and eye-in-head peak speed (*right*) as a function of amplitude within the head of four subjects labeled C.E., H.C., Z.P., and R.S. These smooth curves are least square fits of the data. They show that the nature of the main sequence depends on the nature of the task, with higher velocities being found during

tapping than during looking only. The relatively small difference between the tasks shown by subject RS (bottom pair of graphs) can be explained by his age. He was 65 when these data were collected, so it was not surprising that his peak saccadic velocity was considerably lower than the highest velocities of the younger subjects. (From Epelboim et al., 1997.)

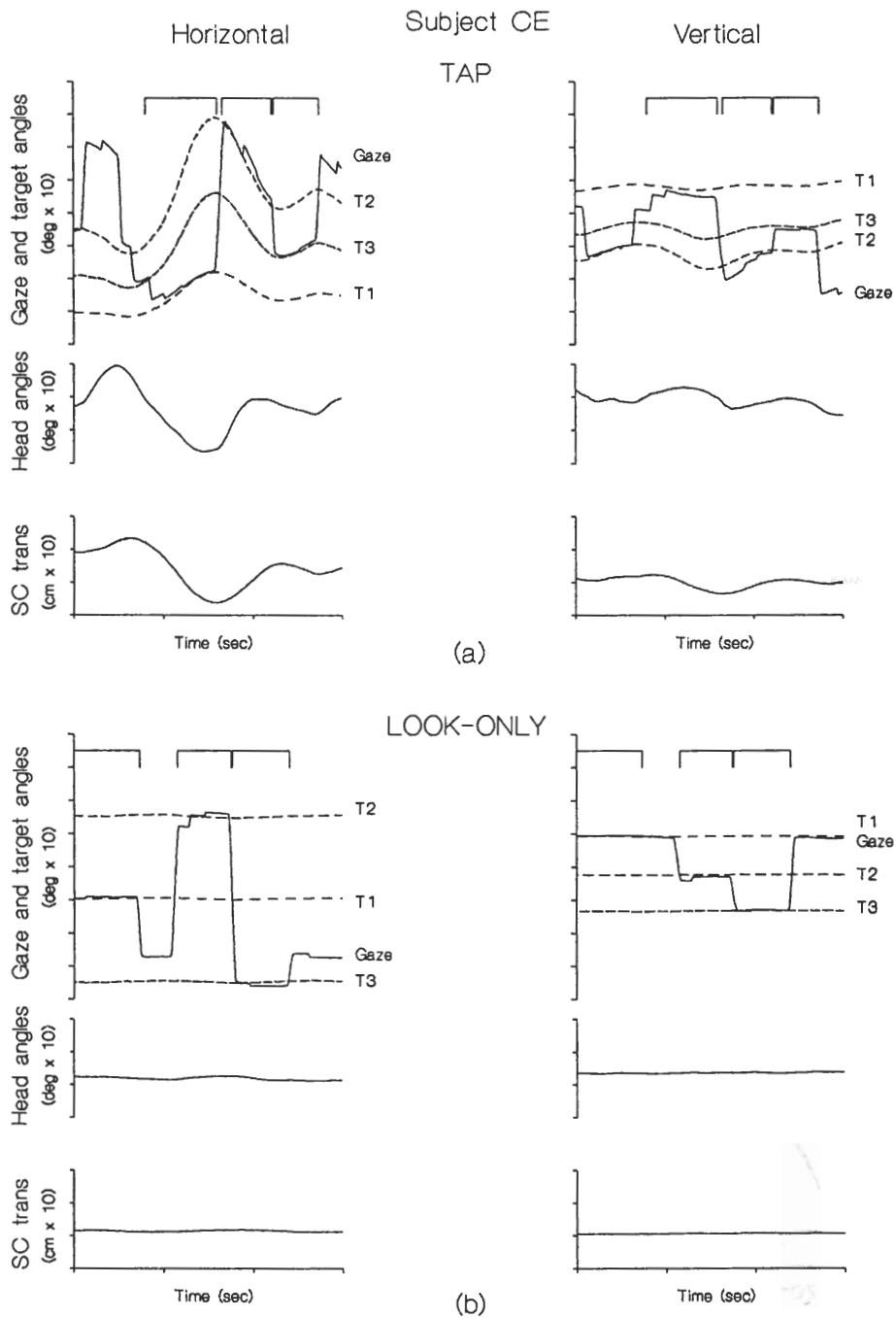


FIGURE 90.10. Analog records for subject C.E. during three segments of a tapping trial (a) and a looking-only trial (b). Horizontal components are shown on the left, and vertical components are shown on the right. The layout is the same for a and b. The top row shows gaze (solid lines) and target angles (dashed lines) for the right eye plotted as a function of time. Brackets above the graph show episodes during which CE was looking at each of the three targets

whose traces are shown. The second row shows head angles as a function of time. The bottom row shows translations of the sighting center of the right eye as a function of time. Gaze and head movements were used quite differently with respect to controlling the amount of retinal image motion when fixation was maintained during each task. (From Epelboim, 1998.)

data for her doctoral dissertation. Her obituary, including a list of her main publications, can be found in Herst et al. (2001). The research described in this chapter was supported, in part, by grants from the Chemistry and Life Sciences Directorate of the Air Force Office of Scientific Research, most recently AFOSR Grant No. F496200210143.

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