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## The significance of microsaccades for vision and oculomotor control

Han Collewijn and

Department of Neuroscience, Erasmus University Medical Center, Rotterdam, The Netherlands

Eileen Kowler

Department of Psychology, Rutgers University, Piscataway, NJ, USA

### Abstract

Over the past decade several research groups have taken a renewed interest in the special role of a type of small eye movement, called ‘microsaccades’, in various visual processes, such as the activation of neurons in the central nervous system, or the prevention of image fading. As the study of microsaccades and their relation to visual processes goes back at least half a century, it seems appropriate to review the more recent reports in light of the history of research on maintained oculomotor fixation, in general, and on microsaccades in particular. Our review shows that there is no compelling evidence to support the view that microsaccades (or, fixation saccades more generally) serve a necessary role in improving oculomotor control or in keeping the visual world visible. The role of the retinal transients produced by small saccades during fixation needs to be evaluated in the context of both the brisk image motions present during active visual tasks performed by freely moving people, as well as the role of selective attention in modulating the strength of signals throughout the visual field.

### Keywords

microsaccade; oculomotor; vision; saccades; stabilized image; slow control; retinal image motion; VOR; attention; fixation

### Introduction

Over the past decade several research groups have taken a renewed interest in the special role of a type of small eye movement, called ‘microsaccades’, in various visual processes, such as the activation of neurons in the central nervous system, the prevention of image fading, or the allocation of attention. Epithets such as “window on the mind” (Martinez-Conde & Macknik, 2007) and “microcosm for research” (Engbert, 2006) have even been coined to emphasize the special significance of microsaccades. As the study of microsaccades and their relation to visual processes goes back at least half a century, it seems appropriate to review the more recent reports in light of the history of research on maintained oculomotor fixation, in general, and on microsaccades in particular.

Before beginning this review and analysis, it is important to underline the fact that most oculomotor research on microsaccades has been done under laboratory conditions that do

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Corresponding author: Eileen Kowler., kowler@rci.rutgers.edu., Address: Department of Psychology, Rutgers University, Piscataway, NJ 08854, USA.

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not begin to capture the richness and complexity of natural tasks. Subjects (human or animal) typically view sparse visual displays, doing simple and repetitive tasks, while movements of the head are restrained. Some of these restrictions were imposed in order to conform to the limitations of the instruments used to record eye movements (most of which could not deal adequately with head movements). Other restrictions emerged—as they do in visual science more generally—from the attempts to formulate testable hypotheses and establish precise experimental control over the stimulus and tasks. The optimistic view is that the results and conclusions obtained even under artificial experimental conditions will nevertheless reveal fundamental aspects of system characteristics that will generalize to more natural settings and pave the way for ultimate understanding of eye movements and vision as they operate under truly natural conditions. Developments over the past several years in instrumentation, analysis and modeling have enabled oculomotor research to be extended in productive ways to more complex and naturalistic experimental scenarios. The extent to which this expansion of work has affected the conclusions drawn from more traditional experimental settings will be addressed at the conclusion of this review.

## The historical roots of the microsaccade

### Classical studies of fixation

Serious attempts to study the eye movements during maintained fixation of stationary targets began in the early 1950s, sparked by a more general interest in theories of visual acuity and dynamic aspects of receptor responses. It was clear that testing theories of vision required answering a very fundamental question, namely, how much motion of the retinal image occurs when looking at stationary objects? This question inspired investigators—most notably Ditchburn in England, Riggs in the USA, and Yarbus in Russia—to develop the contact lens optical lever, a novel and effective instrument suitable for recording even the smallest possible movements of the eye at high spatial and temporal resolution.

There was remarkable agreement across a large number of studies done in different laboratories about the characteristics of fixational eye movements (Figure 1) (Boyce, 1967; Ditchburn & Foley-Fisher, 1967; Ditchburn & Ginsborg, 1953; Fiorentini & Ercoles, 1966; Krauskopf, Cornsweet, & Riggs, 1960; Nachmias, 1959, 1961; Ratliff & Riggs, 1950; St Cyr & Fender, 1969; Williams & Fender, 1977; Yarbus, 1967). Three types of eye movements during fixation were recognized:

1. *Saccades* ranging in size from about 2 to 12 min arc on single meridian, occurring at intervals ranging from 0.2 to 10 seconds. Saccades occurred simultaneously in both eyes and were always binocular, although they were not perfectly yoked in magnitude and direction. (The early authors always spoke of saccades, or “flicks.” The first use of the term “microsaccade” that we encountered is Zuber and Stark (1965), who used an analysis of velocity/amplitude relations to demonstrate that microsaccades are part of the continuous set of all saccades.) Histograms of the distributions of saccadic sizes (Figure 2) showed a sharp cut-off around 12 min arc with a few outliers around 20 min arc (Boyce, 1967; Ditchburn & Foley-Fisher, 1967). It is important to emphasize this narrow range because it defines the subset of saccades typical of fixation, and thus properly called “microsaccades.” Investigators until about 1980 have generally respected a maximum size of 10–12 min arc as the upper limit for microsaccades. Arbitrary and operational as this definition might appear to be, it is solidly founded on assembled data on human fixation, and defines the domain of the saccades whose functional significance was discussed and debated beginning in the 1950s. It is certainly completely out of context, and distorts the nature of the debate, to call (as some recent publications do) saccades of 0.5, 1.0, or even 2.0 deg, “microsaccades”.

2. *Drifts*, the comparatively slow movements occurring in the intersaccadic interval, ranging in amplitude from about 1.5 to 4 min arc, with median velocities around 4 min arc/s.
3. *Tremor*, rapid oscillatory movements with a frequency spectrum up to about 200 Hz and typical amplitudes of 5–30 sec arc. For a recent analysis of binocular tremor, recorded with miniature accelerometers, see Spauschus, Marsden, Halliday, Rosenberg, and Brown (1999); they observed spectral peaks at low (up to 25 Hz) and high (60–90 Hz) frequencies and found a high correlation between the two eyes, implicating an origin in the low-level neurons controlling the eye muscles. It is probably no more than a byproduct of the incompletely fused high-frequency firing of the fast extra-ocular motor units and will not be further treated in this review.

**A word about the contact lens optical lever**—It is a matter of justice to underline the technical accomplishments of the early researchers who developed and refined the contact lens optical lever method. Most of them had solid backgrounds in optics and physics, designed and perfected their own instruments, and reached precisions that are unrivalled by any commercial off-the-shelf equipment available today. Resolution was as good as 10 *sec arc* (e.g. Ditchburn & Ginsborg, 1953; Nachmias, 1959; Steinman, 1965); an order of magnitude better than the smallest microsaccades. In addition, simultaneous recording of horizontal and vertical components, even binocularly, had been achieved and computer processing of data had been introduced (e.g., Boyce, 1967; Krauskopf et al., 1960; Nachmias, 1959; St Cyr & Fender, 1969). Although the old techniques were laborious and not suitable for the collection of large volumes of data, their quality was fully adequate for the studies undertaken and it is very unlikely that the results were marred by subjectivity or poor signal-to-noise ratios. For a synopsis of the technical developments in the classical period, see Steinman (2003). More importantly, see the original papers to appreciate the care with which the authors protected their results against sources of error such as head movements or slip of the contact lens (e.g. Nachmias, 1959; Riggs, Armington, & Ratliff, 1954; Riggs & Schick, 1968<sup>1</sup>).

In the 1980s the contact lens-optical lever technique was revived by Schulz (1984) and Simon, Schulz, Rassow, and Haase (1984). They used X–Y sensitive photodetectors to record horizontal and vertical movements of both eyes. They reported microsaccades with amplitudes between 3 and 20 min arc occurring at rates of 1–3/s. The “main sequence” peak velocity–amplitude relation (Schulz, 1984, their Figure 7) confirmed Zuber and Stark (1965). Microsaccades occurred simultaneously in the two eyes, had roughly similar directions, although amplitudes might differ (Krauskopf et al., 1960), and did not strictly compensate for drift or re-center the gaze in 2-D diagrams. These findings confirm the classical evidence.

From the beginning, the functional interpretation of the different components of eye movements during fixation has focused on two main issues:

1. their role in maintaining stable fixation, and

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<sup>1</sup>Riggs and Schick (1968) performed the classical study on the stability of the contact lens. Using a psychophysical procedure that required alignment of a stabilized foveal line with that of an afterimage, they found that contact lens stability, even after attempts to perturb the lens by the execution of large (6 deg) saccades, was 30 seconds of arc. For a detailed discussion of the history of investigations of contact lens stability, see Steinman and Levinson (1990). Questions about contact lens stability have been raised recently as an excuse to dismiss whole cloth the studies of fixational eye movements using this method. However, the investigations of lens stability show that this method is entirely appropriate and suitable for measuring small fixational eye movements.

2. their role in optimizing vision, most often studied in relation to the fading (loss of perception) of retinal images that were stabilized on the retina.

### Fixation stability

The main function of saccades in foveated species is to bring a selected target to the fovea. In this light, it was perfectly plausible to interpret microsaccades as corrections that would re-foveate the target after it had drifted away during the intersaccadic interval. This is, in fact, what Cornsweet concluded in 1956. This interpretation turned out to be only partly true once Cornsweet's measurements, which were restricted to horizontal movements, were extended to both dimensions. Nachmias (1959) (see also Boyce, 1967), added vertical measurements and established that saccades could correct fixation errors along certain meridians, while in other directions the correction by saccades was poor, and correction by drift was appreciable. Thus, drift was not just noise, but also corrective, and the occurrence of a saccade could be predicted not only by a positional error, but equally well by the passage of time since the previous saccade.

A more direct demonstration that slow intersaccadic eye movements were able to account for stable fixation was provided by Steinman, Cunitz, Timberlake, and Herman (1967), who showed that the occurrence of microsaccades could be reduced from 2 to 3 per second to approximately one every 2 seconds by simple instruction, with no loss in fixation stability. These results were extended to larger populations of subjects by Ciuffreda, Kenyon, and Stark (1979), Schor and Hallmark (1978), and Winterson and Collewijn (1976), along with reports of individuals who rarely make microsaccades during fixation (Fiorentini & Ercoles, 1966; Snodderly, 1987; Winterson & Collewijn, 1976). In the absence of saccades, fixation was maintained by 'drift' alone, now renamed *slow control* to emphasize its functional significance (Steinman, Haddad, Skavenski, & Wyman, 1973). Without microsaccades, the stability of maintained fixation was excellent, with standard deviations of eye position on each meridian on the order of 4 min arc. Slow control was found to be effective for relatively large visual targets, regardless of shape (Epelboim & Kowler, 1993; Murphy, Haddad, & Steinman, 1974; Sansbury, Skavenski, Haddad, & Steinman, 1973).

One thing these early studies could not achieve was a determination of the preferred retinal locus of fixation. The historical identification of the locus of preferred fixation with the locus of highest cone density has been maintained until recently as the most reasonable assumption. A direct verification of the retinal locus of fixation has now been achieved in the elegant work of Putnam et al. (2005), who managed to obtain—using high-resolution adaptive optics—registered images of a fixation target amidst the foveal cone mosaic. Two remarkable results were obtained. A sample of fixation positions showed an average dispersion (S.D.) of 3.4 min arc, confirming earlier estimates made with the contact lens method (e.g., Steinman, 1965). However, the mean fixation position did *not* coincide with the locus of highest cone density, but was displaced from this locus by an average of 10 min arc (with idiosyncratic topography; see Figure 3).

Slow control is also seen in non-foveated animals such as the cat (Winterson & Robinson, 1975) and the rabbit (Collewijn, 1981). These animals (that never show anything like a microsaccade) maintain ocular stability quite well in a structured visual surround. They do so by a control system that corrects for excessive retinal image motion, much like optokinetic stabilization (although not at unity gain). Likewise, human slow control is also a velocity compensating system that acts to reduce retinal image motion rather than correct for errors in position from some presumed optimal retinal locus. Epelboim and Kowler (1993) studied slow control with stationary targets located at various retinal eccentricities and found that while slow control was position-sensitive, i.e., stability deteriorated with eccentricity (as

might be expected from a motion-sensitive system in a heterogeneous retina), slow control was not position-corrective and did not carry the line of sight toward the eccentric target.

In the meantime, evidence grew that microsaccades were saccades like any other, and, more specifically, amenable to the same sort of voluntary control that characterizes larger saccades. For example, microsaccades can be made to accurately track small displacements in target position (Timberlake, Wyman, Skavenski, & Steinman, 1972; Wyman & Steinman, 1973) and to look away in specified directions from stationary targets (Haddad & Steinman, 1973). People may be unaware of making microsaccades, but this does not put microsaccades in a special class of involuntary movements, as the same can be said of large saccades as well.<sup>2</sup>

### Fixational eye movements and the quality of perception

One surprising outcome of the initial fixation studies was the discovery that visual targets faded in the absence of motion of the retinal image (Ditchburn & Ginsborg, 1953; Riggs, Ratliff, Cornsweet, & Cornsweet, 1953; Yarbus, 1967). The contact lens-optical lever lent itself, in the hands of the optical experts that had developed it, to a method of eliminating the retinal displacements caused by eye movements. This was done typically by making the optical-lever mirror, attached to the contact lens, a part of the visual pathway in such a way that the visual target could be moved by an amount equal to the rotation of the eye.

Thus originated the study of “stabilized images”, which could then subsequently be unstabilized again by specific, imposed motions of the stimulus, including, but not limited to, those that simulated the miniature eye movements typical of fixation. The topic of vision with stabilized images has been reviewed extensively (see, for example, Arend & Timberlake, 1986; Kowler, 1991; Martinez-Conde, Macknik, & Hubel, 2004; Steinman et al., 1973), and there have been some newer investigations, such as by Rucci, Iovin, Poletti, and Santini (2007). Steinman and Levinson (1990) discussed vision with stabilized images within the framework of the relation between retinal image motion and visual thresholds for perceiving contrast and detail. The relation between retinal image motion and visibility is complex, with factors such as retinal eccentricity, spatial frequency, contrast, brightness, color and the duration of the exposure coming into play, along with the pattern retinal motion itself.

The literature on vision with stabilized images showed no evidence for a unique function for saccades or microsaccades in preventing image fading. Any type of image movement could restore vision to some extent, as one would expect (e.g., Figure 4). Slow or smooth movements could be sufficient by themselves, depending on speed or amplitude. The advantage of smooth movements is that they are continuous and cover (in principle) all directions. Saccade-like movements in the microsaccade size range also contribute, but their disadvantage is that the effects are transient and oriented, so that only a high rate of saccades in many directions would substantially improve overall visibility.

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<sup>2</sup>People are generally not aware of the eye movements, including saccades, made during fixation. This is often cited as support for the involuntary or reflexive nature of microsaccades. Awareness, however, is not the best way to classify movements as either voluntary or involuntary. In normal life, saccades, large or small, are made without explicit awareness (people are often surprised to discover that during reading, the eye executes a series of discrete movements across the line of text). The voluntary vs. involuntary character of saccades may be compared to the automatism of walking. Normally, a person will walk from A to B without ever thinking about the details of his stepping movements, guided mainly by the lay-out of the surroundings and the level of urgency (determining his speed). On the other hand, he can be instructed to follow a specified manner of stepping, or a marked trajectory, but such cognitively controlled performance is not necessarily representative of typical behavior. Not only are people generally unaware of the repertoire of eye movements that are executed all the time, but the effects of these eye movements on the retinal image are typically completely filtered out of the visual percept. For instance, the perceived image of the surroundings or a text that is being scanned remains completely stable, despite the numerous saccadic displacements of the retinal image (for discussion of such perceptual issues, see Murakami & Cavanagh, 2001).

Interestingly, there was agreement that the 'typical' fixational eye movements were not necessarily optimal for vision. Visibility was often better with imposed retinal image movements, including smooth oscillations, that were faster and ranged over larger amplitudes than the typical eye movements of fixation (Ditchburn & Drysdale, 1977a, 1977b; Gerrits & Vendrik, 1974; King-Smith & Riggs, 1978; Riggs et al., 1953). Although the source of such faster image motions was not known at the time, later work (to be discussed below) showed that fixational eye movements and retinal motions are considerably faster when the head is free to move.

### Microsaccades and the perception of fine foveal details

Given no special role for microsaccades in visibility, researchers turned to other possible functions. One obvious candidate is, in fact, no different from the role of any other saccade in vision, namely, to serve as an adjunct to visual attention and bring the line of sight (and the presumed locus of best acuity) to those visual details that are most relevant to the task at hand.

Attempts to evaluate this idea included observations of microsaccades in a variety of visual tasks. Microsaccades (again using the classical definition of a saccade smaller than 12 min arc) almost never occur during reading (Cunitz & Steinman, 1969; Kowler & Anton, 1987; Schnitzer & Kowler, 2006) and are rare during visual search (e.g., Hoge & Erkelens, 1996; Motter & Belky, 1998), tasks that are typically carried out by sequences of saccades of about a half degree to several degrees in length (see below for confirmation of this result for visuomotor tasks). Microsaccades might be expected in such tasks if only to clean up any errors in landing position left behind by large, primary saccades. However, microsaccades—and corrective saccades in general—are rare when saccadic targets are spatially extended shapes, rather than small target points (Kowler & Blaser, 1995; Melcher & Kowler, 1999; Vishwanath & Kowler, 2003).

A more fruitful way to uncover a useful function for microsaccades would be to choose tasks in which shifts of attention between small details (small enough to fit within the central half degree of the retina) would be expected to be crucial. Winterson and Collewijn (1976) measured eye movements of naïve subjects who were asked to aim and shoot a rifle (no bullets) or thread a needle. During the interval of about 2–4 seconds when they performed these tasks, microsaccade rate was never greater than their baseline rate during steady fixation (2/s) and in fact dropped to about 0.5/s during the final portions of the trials. Bridgeman and Palca (1980) obtained a similar result in a comparable task that required a high acuity visual judgment without a directly related motor activity. Specifically, subjects had to judge whether the tip of a moving horizontally oriented "thread" would have ended above or below the tip of a stationary, vertical "needle". Like Winterson and Collewijn (1976), Bridgeman and Palca (1980) found a progressive decline in the frequency of microsaccades during the 8 s trials, with the minimum saccade rates occurring at the very end when the final judgment had to be made. In a different task, Kowler and Steinman (1977, 1979) found that saccades of about 25–30 min arc (larger than microsaccades) improved the accuracy of counting randomly positioned small shapes in a 2 deg diameter region (see also, Kowler & Anton, 1987), but smaller saccades (10–13 min arc), used when the counting region was compressed to a diameter of 30 min arc, made no difference to performance. Finally, Kowler and Sperling (1980) found no effects of small (16 min arc), saccade-like stimulus motions on visual search, and showed that the acquisition of visual information continues at the same rate over time, with no special role for retinal image transients in initiating periods of information acquisition.

Several recent studies have suggested that saccades during fixation are correlated with shifts of attention to peripheral targets (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock,

Engbert, Rolfs, & Kliegl, 2007). Given the connection between saccadic planning and attention shifts (Deubel & Schneider, 1996; Gersch, Kowler, Schnitzer, & Doshier, 2008; Hoffman & Subramaniam, 1995; Kowler, Andersen, Doshier, & Blaser, 1995), it does not seem surprising that some small saccades might occur when trying to shift attention to a peripheral target without fully breaking fixation. Nevertheless, the issue has been controversial, with different studies producing different results (see Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007). While under some circumstances small saccades could be prompted by shifts of attention to eccentric locations, evidence indicates that this relationship is not obligatory, nor does it have necessary consequences for perception (Tse, Caplovitz, & Hsieh, 2006).

To summarize: The functional role of saccades as small as 20 min arc has never been in dispute because even saccades this small are needed to bring crucial details to more central regions of the retina. But there has been no evidence for a useful role for shifts of the line of sight in the range of sizes characteristic of fixational microsaccades (<12 to 15 min arc).

### Fixation with unrestrained heads

Studies of maintained fixation until about 1980 were carried out exclusively in experiments that restrained the head. Although many laboratories had been studying the relationship between head and eye movements during controlled head oscillations (typically, by movements of chairs while head movements relative to the chair were restrained), the question of how head and eye would behave when free to move in chosen patterns had not been addressed.

Recordings of oculomotor behavior without restraint of the head were made possible by several new developments in the magnetic sensor coil technique that was developed in its classical form by Robinson (1963) and modified by Collewijn, van der Mark, and Jansen (1975). By using larger fields (Skavenski, Hansen, Steinman, & Winterson, 1979), and changing measurement to the phase of the signal induced in the sensor coil rather than amplitude (Collewijn, 1977; Collewijn, Martins, & Steinman, 1983; Hartmann & Klinke, 1976), it became possible to precisely record binocular gaze angles as well as head rotations in spatial coordinates (Steinman & Collewijn, 1980). Additional developments (Ferman, Collewijn, Jansen, & Van den Berg, 1987) made it possible to measure torsional movements as well. Finally, the addition of an acoustic location system (Epelboim et al., 1995) allowed measurement of concurrent head translations. All of this was accomplished at resolutions of 1 min arc for rotation and 1 mm for translation, sampled at frequencies of at least 488 Hz.<sup>3</sup>

### Effects of head movements on fixation stability while sitting or standing as still as possible

In the first free-head study with the magnetic sensor coil technique, Skavenski et al. (1979) compared the stability of the head and gaze with and without head restraints (i.e., bite-

<sup>3</sup>For many years, the scleral sensor coil has been considered as the “gold standard” in contemporary studies of eye movements (human or animal) that require high precision. Stability of the coil on the eye when properly applied, even throughout a series of horizontal and vertical saccades (of 20 deg) was demonstrated in its first description (Collewijn et al., 1975, their Figure 3). A major advantage of the coil technique is its large flexibility: with suitable magnetic fields and electronic instrumentation it can be adapted to a wide range of sensitivities and angular ranges, even with free head movements. Its spatial and temporal resolution are, for all practical purposes, unlimited. In the main text we have already referred to the main papers that document all its applications. An essential disadvantage of the coil (in its present stage) is its intrusive nature, that limits useful measuring time (to about 30 minutes in most subjects), especially when maintained maximum visual acuity is important. In this respect, the newest generation video-trackers are superior, however, at the cost of spatial and temporal resolution. In some recent investigations a direct comparison has been made between the scleral coil and video-tracker systems; they reveal some subtle differences that are of interest, but generally conform to the characteristics mentioned above (Frens & van der Geest, 2002; Houben, Goumans, & van der Steen, 2006; Smeets & Hooge, 2003; van der Geest & Frens, 2002).

boards). (For reasons connected to the non-uniformity of the magnetic fields, it was necessary to limit head position to a  $\pm 1$  cm region, which was done by placing the head inside a wooden frame). Note that in free-head experiments, eye- and head angles are measured with respect to earth (gaze = eye orientation in space). The head has 6 degrees of freedom: 3 angular and 3 translational. Because of the translational freedom, gaze angles alone can be directly related to the position of a target provided that the latter is viewed at optically infinite distance (as was the case in Skavenski et al., 1979); for nearer targets, complex spatial calculations have to be made incorporating both rotation and translation (see Epelboim et al., 1995).

The unrestrained head showed considerable motion, even when attempts were made to keep it as still as possible. Typically, head orientation had a standard deviation on a single meridian of about 11 min arc when sitting and about 22 min arc when standing. These head motions resulted in less stable gaze, most notably, increases in the speed of the eye (Figure 5A). Mean eye speeds (derived from successive positions at 50 ms intervals during 40 s trials) were 13–15 min arc/s on the bite-board, increasing to 21–26 min arc/s when sitting and 22–38 min arc/s when standing.

Implicit in such findings was that oculomotor compensatory mechanisms, such as the vestibular-ocular response, OKN, or smooth pursuit, were only partly effective. Skavenski et al. (1979) imposed a range of oscillatory head movements and found that compensation was at best about 90% of the head rotations—good, but not perfect.

Novel as these findings were, a precedent of some kind can be found for them. Ditchburn and Ginsborg (1953), in their classical study of “Involuntary eye movements during fixation”, using the contact lens—flat mirror—optical lever technique, included a—little noticed—section on “Records with the head free”. One fundamental advantage of the flat mirror on the lens was that it allowed very small head translations without disturbing the eye recording, and for this reason a subject could, in principle, be allowed to get off the bite-board and move his head, although the size of the mirror (3 mm) called for enormous discipline. Some successful recordings were obtained “attempting to keep his head as still as possible...during slow rotations of the head from side to side through angles of about 1 deg...during jerky head movements of similar magnitude”. The records (their Figure 6) showed “appearance of undulations in the drifts synchronous with those of the head. These indicate that the eye is rotating to some extent together with its orbit.” In short, Ditchburn himself produced evidence that oculomotor behavior, in particular slow eye movement velocity, became different once the bite-board was abandoned. It is remarkable that he did not fully appreciate the implications of this finding in his later work on stabilized images and the prevention of fading.

### **Fixation stability during small, deliberate head oscillations**

The incompleteness of gaze stabilization during head movements was further confirmed by Steinman and Collewijn (1980), who recorded binocular, horizontal eye, and head movements during active head oscillations at frequencies between 0.25 and 5 Hz (peak-to-peak amplitudes 30–0.25 deg) while attempting to keep looking at a target at optical infinity. By the use of a homogeneous magnetic field, the range of allowable head positions no longer needed to be restricted.

Gaze was far from stable under these conditions: head velocities around 30 deg/s caused gaze velocities (equivalent to retinal image velocities) around 3 deg/s, compensation by the VOR not being better than about 90%. In addition, gaze motions were rarely equal in the two eyes, so that large vergence motions were present as well. Vision was not noticeably affected and remained single, clear and stable except during the most violent head shaking.



The implication of these findings was that, in normal, active visuomotor behavior, retinal image speeds could easily rise to several deg/sec (see Figures 5B and 5C).

Ferman et al. (1987) confirmed these findings in a larger population of subjects, where gaze was measured around all 3 axes of rotation (horizontal, vertical and torsion eye movements) while they freely moved their heads. By that time, scleral sensor coils had become available that allowed measurement of the gaze position in all 3 axes within a range of  $\pm 25$  deg and with a resolution of about 3 min arc. In addition, the mathematics had been worked out to transform the raw signals to veridical coordinates that were free of any artifacts, such as crosstalk between the axes due to misalignment of the coil on the eye. Mean gaze speeds during horizontal head movements amounted to 23 min arc/s when the head was held still, and 34–56 min arc/s during active head oscillation. For vertical head oscillations, speeds were marginally larger. For torsion (oscillation around an axis parallel to the line of sight) the results were very different; compensation on this axis was only on the order of 50% and mean torsional gaze velocities reached up to 8.6 deg/s.

One of the notable consequences of freeing the head was that the microsaccade, the hallmark of steady fixation performance, appeared suddenly to be irrelevant. Although some microsaccades still occurred during fixation with the head free (Figure 5A), saccades of any size were infrequent during active oscillations of the head (Steinman & Collewijn, 1980). As will be shown below, quantitative analysis in active and much more natural tasks showed that microsaccades were very rare once classical strict demands for fixation are released.

To sum up: with the head unrestrained, retinal image velocities of at least .3–.5 deg/s were found to occur during fixation of a target at infinity. Head oscillation augmented these velocities even more.

### Microsaccades and gaze shifts during natural visuomotor tasks

Studies of eye movements without head restraints became more popular beginning in the 1990s, with most of these done using head-mounted video-based eye trackers, with the objective of either finding out where people look during active visual tasks (e.g. Ballard, Hayhoe, & Pelz, 1995; Land & Hayhoe, 2001; Land, Mennie, & Rusted, 1999; Pelz & Canosa, 2001), or, studying the coordination of head and eye during shifts of gaze (Berthoz, 1985; Freedman & Sparks, 1997, 2000; Sparks, Freedman, Chen, & Gandhi, 2001).

Epelboim (1998) used the sensor coil system, combined with translation measurement (Epelboim et al., 1995; see also above), to study eye and head movements made while tapping a series of stationary color-coded rods, presented on a table in front of the subject. The results confirmed that the high image velocities characteristic of fixation with unrestrained head persisted when head movements were made to accomplish a purposeful task. Retinal image speeds during pauses between gaze shifts were high: up to 5 deg/s. In a comparison task, where subjects shifted gaze between the same targets without tapping, head movements were slower and retinal image velocities were about 1.5 deg/s. These values were about the same as image speeds during reading—a task with substantial visual demands—with the head free (Kowler et al., 1992).

Thus, the degree of oculomotor compensation for active head movements varied over a large range, depending on the task being performed. The variation in compensation for head movements affected not only the accuracy and dynamics of the gaze shifts, but also the amount of retinal motion during the intersaccadic pauses. Epelboim (1998) suggested that this adjustment in the compensation for head movements was a rational process, driven by the need to optimize both gaze shift dynamics, as well as inter-saccadic retinal speed.

Findings like these suggest that under natural conditions, people can produce a wide range of retinal conditions, and will do so depending on task goals.

At the same time, microsaccades were rare. Malinov, Epelboim, Herst, and Steinman (2000), analyzing 3375 saccades sampled from the same data set, reported that most saccades (83%) were smaller than 15 deg (in agreement with Bahill, Adler, & Stark, 1975), with about a third smaller than 2 deg. Saccades were rarely smaller than 0.5 deg and only 2 qualified as genuine microsaccades, i.e., their 2-D size was smaller than 12 min arc (Figure 6). Repeating the experiment with smaller targets to increase the required spatial precision of the task and perhaps encourage use of smaller saccades, did not change the outcome: only 4 of 3258 saccades sampled were smaller than 17 min arc (Steinman, Pizlo, Forofonova, & Epelboim, 2003).

## Microsaccades and visual neurophysiology

The studies of eye movements summarized in the preceding two sections revealed no special role for microsaccades (i.e., saccades less than about 15 min arc) in maintaining image visibility, in maintaining fixation, or in carrying out visual or visuomotor tasks. By “no special role” we mean that no oculomotor or visual task had emerged that could not be done as well, or better, by an appropriate pattern of smooth eye movements or slow control. A special role for microsaccades seemed particularly unlikely to emerge under natural conditions, when head movements are permitted during either fixation or during the performance of active visual tasks, and retinal image speeds take on values from a half to several deg/second, depending on the head movements and on the task.

Interest in microsaccades has revived over the past decade, due in part to new studies of the relationship between the activity of visual neurons in monkey and the eye movements of fixation.

### Neural responses in visual areas during maintained fixation

The study of the relation between eye movements and the neurophysiology of visual receptive fields in the awake monkey was started by Wurtz (1969a), who designed a method for training monkeys to fixate a small target. In Wurtz's technique, the monkey learned to press a bar in response to the dimming of a target. As the target was decreased in size, the monkey became more proficient in the task, and the quality of fixation improved. Using such behavioral methods to control the monkeys' eye movements, Wurtz (1969b, 1969c) compared the effects of retinal image motions produced by large saccades to those produced by equivalent motions of the stimulus on the activity of neurons in V1. Neural responses were similar under both conditions, giving no evidence for 'extraretinal' (corollary discharge) influences. (For more recent examples of studies on the effects of large saccades on visual neurons in monkey, see DiCarlo & Maunsell, 2000; Gallant, Connor, & Van Essen, 1998; Livingstone, Freeman, & Hubel, 1996; MacEvoy, Hanks, & Paradiso, 2008.)

What about the effects of the eye movements of fixation? Monkeys can fixate like humans: they make microsaccades and possess a visually driven slow control system that can be used to maintain the line of sight (Motter & Poggio, 1984; Skavenski, Robinson, Steinman, & Timberlake, 1975; Snodderly & Kurtz, 1985). These eye movements can affect neural firing. Gur, Beylin, and Snodderly (1997) showed that at least some of the variability of the responses of neurons in V1 could be attributed to fluctuations in eye position (smooth or saccadic) during fixation. This result demonstrated the sensitivity of V1 cells to even very small retinal image motions, and set the stage for further investigations of the effects of the different types of eye movements of fixation on neural responses.

Three studies relating neural activity to fixational eye movements, each done under somewhat different conditions, produced conflicting patterns of results. Leopold and Logothetis (1998) investigated the effects of microsaccades (median amplitude 10 min arc) on the activity of V1 neurons with centrally located receptive fields and found that cells showed either suppressed (37% of cells) or enhanced (17% of cells) activity following microsaccades. Enhancement was more common in area V2, and also in V4, where most cells showed excitatory bursts after saccades. Martinez-Conde, Macknik, and Hubel (2000), using a different stimulus, task, and set of receptive field locations, found no suppression in V1, but rather an increased probability of bursts during the intervals following saccades ranging up to 2 degrees in size (see Martinez-Conde, Macknik, & Hubel, 2002; Reppas, Usrey, & Reid, 2002, for evidence for saccade-related bursts in LGN). In still another pattern of results, Snodderly, Kagan, and Gur (2001) found 3 classes of neurons in V1:

1. *position/drift cells*, showing a sustained discharge during intersaccadic periods;
2. *saccadic cells*, producing burst responses (often directionally selective) after a saccade swept the stimulus on, off, or across the receptive field; and
3. *mixed cells*, firing bursts of spikes both after saccades, and during intersaccadic periods.

Even very small saccades (in the genuine microsaccade-range) were effective in activating some of these cells.

Finding fluctuations in neural activity correlated with fixation saccades, even in only a subset of visual cells, reopened the discussion of the functional role of microsaccades. One proposal was that the saccade-linked changes in firing patterns could contribute to a temporal synchronization of activity in large populations of visual neurons (Leopold & Logothetis, 1998). Another hypothesis (emerging from studies of the effects of large saccades, but conceivably applying to small saccades as well) is that post-saccadic activity could contribute to the integration of information across saccades (MacEvoy et al., 2008). Finally, a third proposal was that the retinal transients produced by saccades would revive visual signals whose strength was diminishing over time (Martinez-Conde et al., 2002). This last idea led to new psychophysical tests of the role of saccades in visibility.

## Saccades and visibility

### Instrumentation

Before considering the results of recent studies of eye movements during fixation, and their relation to perception, it is necessary to briefly discuss issues of measurement. Many recent studies have employed eyetrackers which, unlike the optical lever or sensor coil, do not require an attachment to the eye. As a result, experiments can be performed on a larger number of observers, often naïve subjects, who participate in experiments for a relatively short amount of time. This is clearly useful. But are these devices optimally suited to the study of miniature eye movements during fixation?

Figure 7 shows examples of recordings of fixation made with a Dual Purkinje Tracker (head stabilized by a bitebar) and with a video-based eyetracker (Eyelink 1000, using a chinrest). Figure 8 shows a published figure from Møller, Laursen, Tygesen, and Sjølie (2002), also made with a video eyetracker (Eyelink II). Saccades as small as about 4–5 min arc can be seen in the records. At the same time the recordings show, as expected, greater noise than recordings made with the contact lens optical lever. An analysis of a sample of video recordings made with the Eyelink II showed a noise level in the velocity trace of about  $\pm 3$  to 6 deg/s (see Appendix A). This is similar to the peak velocities of small (2–5 min arc) saccades on a single meridian, thus making detection of such small saccades (<5 min arc)

unreliable. Some genuine microsaccades might escape detection, and spurious high velocity events could be erroneously classified as saccades.

Investigators were aware of the problems created by the noise, and went to considerable effort to develop statistical methods in the attempt to avoid falsely labeling instances of high velocity noise as saccades (Engbert & Kliegl, 2004; Engbert & Mergenthaler, 2006). One way to reliably distinguish genuine saccades from noise is their simultaneous occurrence in both eyes, a reasonable criterion given that saccades are virtually always binocular (although not necessarily perfectly yoked in amplitude and direction) (e.g., Krauskopf et al., 1960; see also Schulz, 1984). A telltale sign of the problematic detection of microsaccades in video-tracker signals was the occurrence of monocular saccades in the recordings (e.g., Engbert & Kliegl, 2003; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). Engbert and Kliegl (2003, 2004) used binocularity as a criterion to accept a detected saccade as genuine. Martinez-Conde et al. (2006) did not, but did report that only the binocular saccades were correlated with visual performance (see below), reinforcing the suspicion that the monocular saccades might be noise.

### What happened to the microsaccades?

Another noteworthy feature of recent studies of fixational eye movements has been the unexplained shift in reported saccade amplitudes toward substantially larger values than found in the extensive classical literature. In the classical work, saccades during fixation rarely exceeded 12–15 min arc. In more recent work, the saccades are much larger. Møller et al. (2002), for example, found mean amplitudes of 14–16 min arc in the subjects with the smallest saccades. Engbert and Kliegl (2003) reported a “main-sequence” diagram (their Figure 2) showing the traditional increase in peak saccadic velocities with amplitude, but very few saccades in the genuine micro-range (<12 min arc).

What happened to the microsaccades? Møller et al. (2002) suggested that the larger size of their reported saccades was due to the greater freedom of head movement with a chin rest in comparison to the bitebar used in the contact lens studies. Other possible explanations of the shift to larger saccade sizes include a change in behavioral strategies (perhaps the contact lens optical lever subjects were fixating more carefully), effects of different visual environments (fixation points in darkness vs. fully illuminated rooms), and, finally, the possibility that small saccades were lost in the instrument noise (this could account for the missing microsaccades, but would not, by itself, explain why the maximum observed size of the saccades during fixation increased). The change in the reported properties of the eye movements shows that the contemporary work is being done under different conditions than the earlier work to which it is often compared.

Unfortunately, the response to the unexplained shift to larger fixation saccades was to re-define the concept of a microsaccade. Engbert and Kliegl (2004, p. 431), for example, defined microsaccades as “rapid small-amplitude movements (Ditchburn, 1973) which typically occur at a rate of one to two per second, and have amplitudes that are rarely larger than 1 deg.”

We think this re-definition of microsaccades creates confusion. In the classical work, microsaccades had a median size of about 4.5 min arc, reaching a maximum of about 10–12 min arc (Boyce, 1967; Cunitz & Steinman, 1969; Ditchburn & Foley-Fisher, 1967). The debates about the role of microsaccades in vision, in fixation, or in visual tasks, centered around saccades of this magnitude. No one has ever denied a function for saccades 20 min arc or larger, nor questioned why they are a necessary part of the normal oculomotor repertoire (e.g., Cunitz & Steinman, 1969; Kowler & Anton, 1987; Kowler & Steinman, 1977). These saccades are needed for the same reason that any saccades are needed, namely,

to move images to a portion of the retina where spatial resolution is optimal. Could such saccades have any additional functional roles in vision?

### Fixation saccades and Troxler fading

Martinez-Conde et al. (2006) studied the relationship between saccades observed during fixation and the fading of eccentric targets. Troxler fading—the disappearance of low contrast eccentric stimuli during prolonged periods of steady fixation—is a well-known and robust phenomenon that can be connected to neurophysiological results (see above) describing visual responses outside the central fovea.

Martinez-Conde et al. (2006) had subjects fixate a central point target while a small, medium-contrast Gabor patch was presented at eccentricities of 3 to 9 degrees. The Gabor would periodically fade from view during the 30 second periods of fixation, and subjects continuously reported, by means of button presses, whether the Gabor was fading or intensifying. Analyses of the eye movement recordings showed a higher rate of occurrence of saccades, and larger sizes of saccades, during periods of perceived intensification than during periods of perceived fading. The results supported a role for saccades in periodically reviving the visibility of the eccentric stimulus after many seconds of fixation.

If saccades are important for visibility, then perhaps their occurrence is triggered by instances of low retinal image speed. This idea had been proposed and rejected earlier by Cornsweet (1956) and Fiorentini and Ercoles (1966), and was recently re-examined by Engbert and Mergenthaler (2006). They reported a small reduction (<10%) in the measured speed of the eye just prior to the occurrence of saccades during fixation. However, interpretation of this finding is complicated by the fact that the baseline retinal displacements Engbert and Mergenthaler (2006) reported were about 8 min arc in 50 ms, or 2.6 deg/s. This value is a factor of 10–40 higher than the velocity of slow eye movements reported in the optical lever studies (see above), and similar to the expected velocity noise in the video eye trace after optimal differentiation of the position signals (see Appendix A).

A role for saccades in preventing Troxler fading, as Martinez-Conde et al. noted, was not a new notion. Clarke and Belcher (1962) showed that a 1 deg wide Troxler-faded target at an eccentricity of 20 degrees became visible again after step-displacements of the fixation target. The probability of restoring visibility increased with step amplitude from 3 to 22 min arc.

Clark and Belcher's results suggest that saccades would need to be larger than the classical microsaccades in order to reliably prevent peripheral fading. In agreement with these observations, the saccades that Martinez-Conde et al. (2006) found to prevent fading were well out of the microsaccade range. Saccades as large as 2 degrees were included in the analyses, and the saccades that were effective in restoring visibility were about 20 min arc in size. Thus, although the experiments were presented in the context of attempting to resolve debates about the role of microsaccades (e.g., Ditchburn, 1980; Kowler & Steinman, 1980), the saccades at issue were considerably larger than genuine microsaccades, and larger than the saccades found in the classical studies of fixation. It is, of course, possible that smaller saccades would have played a role in maintaining visibility had the Gabor targets been smaller and shown at smaller eccentricities. But under such conditions, the slower retinal movements during intersaccadic intervals may begin to come into play (e.g., Rucci et al., 2007).

The key question raised by these recent results is whether the transient changes in the retinal image produced by the saccades of fixation are crucial for visibility, or whether, as earlier researchers on vision with stabilized images concluded (see above), smooth image motions

will do as well if their speed and amplitude are sufficient. In an attempt to address this central question in the context of Troxler fading, Martinez-Conde et al. (2006) noted that their results were similar with the head removed from the chin rest, suggesting that the expected increase in smooth eye velocity resulting from uncompensated head motions (Skavenski et al., 1979) did not yield the same benefits to vision as the abrupt displacements produced by saccades. However, since intersaccadic retinal velocities were not reported, and head movements were not monitored, the authors did not draw firm conclusions about the role of smooth image motions, and proposed that further work would be needed. Such further work needs to explore the effects of different patterns of natural image motions on visibility and contrast sensitivity for a variety of visual tasks and retinal eccentricities (e.g., Steinman, Levinson, Collewijn, & van der Steen, 1985). Our own informal observations with Troxler-type stimuli shows that fading can be prevented by rotating the head.

### **Do we need microsaccades to keep the visual world from fading?**

There is no shortage of retinal image motion during normal viewing.

Under natural conditions—with moving heads, and active people—retinal image velocities of several degrees per second are the norm. Even during reading, a relatively sedate activity, intersaccadic image velocities average about 1 deg/sec. Confronted with these velocities, it makes sense for visual neurons to have evolved a tolerance for significant retinal motion. It is the typical case. Substantial image motions are present during most normal human activities, and the visual world is in no danger of fading from view. As a result, we do not think it reasonable to regard fixational eye movements, including the microsaccades, as having evolved in order to prevent images from fading. We think that evolutionary pressures acted in the opposite direction, namely, to compel the visual system to develop a tolerance, and even a preference, for the image motions that would be nearly impossible to avoid in any realistic setting. Image motions are inevitable because of the imperfections inherent to biological compensatory systems of any kind. Perfect, real-time compensation cannot be realistically expected from any system, biological or engineered, because it would require the absence of any noise, threshold, processing time or calibration error. Studies of compensatory systems have shown that, not only is compensation for head motion imperfect, but it often operates at surprisingly low levels (low gain), with considerable adjustments of gain carried out depending on the task (Epelboim, 1998).

Of course, people are not always in motion. There are many visual tasks that require periods of sustained vigilance, when we sit still and focus our attention and gaze on a small, stationary visual array. Under these conditions fixation is at its most stable levels, and the motion of the retinal image is slowest. There is agreement across studies, old and new, that under these conditions, with deliberate and careful sustained fixation, the visibility of eccentric images may suffer (foveal targets do not fade). But is the reduction in the visibility of eccentric images under the conditions of sustained fixation and attention to a central stimulus necessarily a problem for vision? We suspect such fading, if it occurs in natural vision, is barely noticed, and could even be useful.

When a visual task requires sustained attention to a central target, signals from the periphery, originating from objects irrelevant to the task at hand, will be attenuated. Psychophysical and neurophysiological studies agree that foveal animals possess powerful attentional filters to reduce sensitivity to unwanted, task-irrelevant visual details (Bahcall & Kowler, 1999; Carrasco, Ling, & Read, 2004; Doshier & Lu, 2000; Huang & Dobkins, 2005; Morrone, Denti, & Spinelli, 2004; Reynolds, Pasternak, & Desimone, 2000; Schwartz et al., 2005; Williford & Maunsell, 2006). Even vivid, high-contrast patterns can fail to be identified when attention is occupied elsewhere (Wilder, Kowler, Schnitzer, Gersch, & Doshier, 2008). We require these attentional filters because of inherent limits in the capacity

of perception and memory. Thus, even if retinal image motions were always adequate to support contrast sensitivity and visual resolution throughout the visual field, perception of these same peripheral stimuli would be attenuated due to the focus of attention on the fovea.

Oculomotor and motor activities that affect the quality of the retinal image—including saccades, microsaccades, compensatory eye movements and head movements—can be seen as operating alongside visual attention, modulating the visibility of different regions of the visual array as needed by the task. In active tasks, retinal speed can be controlled by adjusting the level of compensation for head movements (Epelboim, 1998). When it becomes important to maintain the line of sight, and attention, on small, central foveal details, people tend to stop moving around: they sit still, keep their head still, and—most relevant to the present discussion—reduce the production of saccades (Bridgeman & Palca, 1980; Winterson & Collewijn, 1976). The inactivity reduces the velocity and amplitude of image motions, supplementing the work of attention in decreasing the visibility and contrast sensitivity of potentially distracting eccentric objects. If improving the visibility or resolution of an object in the periphery should become necessary, we need only to turn our heads and shift our gaze.

## Conclusions

The ability to maintain oculomotor stability for prolonged periods of time is one of the most appreciated and most important of our oculomotor skills. Considerable effort has been devoted to understanding the mechanisms responsible for stable fixation and its relation to vision. This review summarized and evaluated these efforts, going back to the seminal work in the 1950's, and extending to research published over the past few years. Much of this review focused on one feature of the pattern of fixational eye movements, namely, the microsaccade.

Microsaccades have long been a topic of interest, and frankly, curiosity, because on the face of things they would appear to be an unnecessary addition to the repertoire of oculomotor abilities. Humans (along with other species) have a variety of effective oculomotor responses to perturbations in the position of the retinal image produced by movements of objects themselves, or by motions of head or body. Saccades can correct for sudden displacements of images, or change the point of fixation to new objects. Smooth eye movements can compensate well for motions of the head or motion of images. Each of these types of eye movements handles its particular job in a timely fashion, with high levels of accuracy and precision.

Yet microsaccades, and saccades more generally, occur periodically during maintained fixation. Why do we need them? Do they serve any essential function, or are they “noise” in the saccadic system (not doing much of value, but not particularly harmful either)? Our review leads us to the following conclusions:

1. Microsaccades are in general not essential for maintaining a stable line of sight. Smooth eye movements (slow control) carry out this function well. Only in rare situations where slow control is ineffective—e.g. in individuals with slow continuous drifts in one or another direction—microsaccades will correct periodically for retinal error and restore the image to a preferred fixation locus.
2. Microsaccades are not essential for keeping foveal images visible. Details imaged in the central fovea will fade from view only when special means are used to eliminate as much retinal motion as possible (“stabilized images”). Efforts to fixate carefully, including elimination of head movements, along with a voluntary reduction or elimination of microsaccades for seconds on end, produce no fading.

We emphasize this point about foveal images because the need for stable fixation for seconds on end is likely to be most critical when doing tasks that require judgments about foveal images, where large saccades would have to be avoided.

3. Recent studies of eye movements of fixation have reported saccades that are considerably larger than the microsaccades found in the classical work that was done with the contact lens optical lever. In the original studies, saccades during fixation rarely exceeded about 15 min arc. In the more recent studies, sizes of fixation saccades extend to about one degree. The shift in saccade size is puzzling and has created confusion. Specifically, there has never been controversy about the role of saccades greater than 20 minutes of arc in visual tasks. These saccades serve the same role as any saccade, namely, bringing the image to a more central retinal location. Saccades smaller than about 15 min arc (genuine microsaccades) have, so far, been found to be useless for tasks requiring judgments about details imaged within the central portion (about 30 min arc) of the retina. These include visual and visuomotor tasks, representative of typical activities, that are carried out over several seconds, where shifts of attention are presumably involved. Further attempts to explore the role of fixation saccades in vision or visual tasks would benefit from distinguishing between the effects of saccades larger and smaller than about 20 minutes of arc, a functional 'dividing line' that has emerged from studies thus far.
4. Retinally stabilized images, and some unstabilized images (low-contrast, low-spatial frequency images in the periphery), will fade when retinal motions are restricted. In these cases saccades can produce transient changes that restore visibility. In normal situations, however, the motion of the retinal image is substantial, either during fixation or during the pauses between shifts of gaze, because the oculomotor compensation for head motion is not perfect. Even compensation of better than 90% will result in image motion of several degrees per second during modest activity. Thus, the visual system appears to be confronted with the task of coping with too much image motion, not too little. In cases where sustained attention needs to be maintained on the foveal target to accomplish a visual task, fixating a target with a stable head (to minimize smooth retinal motion) and a reduced rate of saccades, may work alongside perceptual attention to attenuate peripheral images and allow limited perceptual resources to remain focused on the fovea.
5. Much is still to be learned about the role of natural image motions in vision (smooth and saccadic), both in terms of the perceptual effects, as well as the consequences for the activity of visual neurons. Under natural conditions, people can produce a remarkably wide range of retinal conditions, by, for example, changing the pattern of head motion, adjusting the gain of oculomotor compensatory responses, or altering the sizes and frequency of saccades. How such adjustments are made in response to the momentary and ongoing needs of the perceptual task is a significant unsolved problem in vision and oculomotor control.

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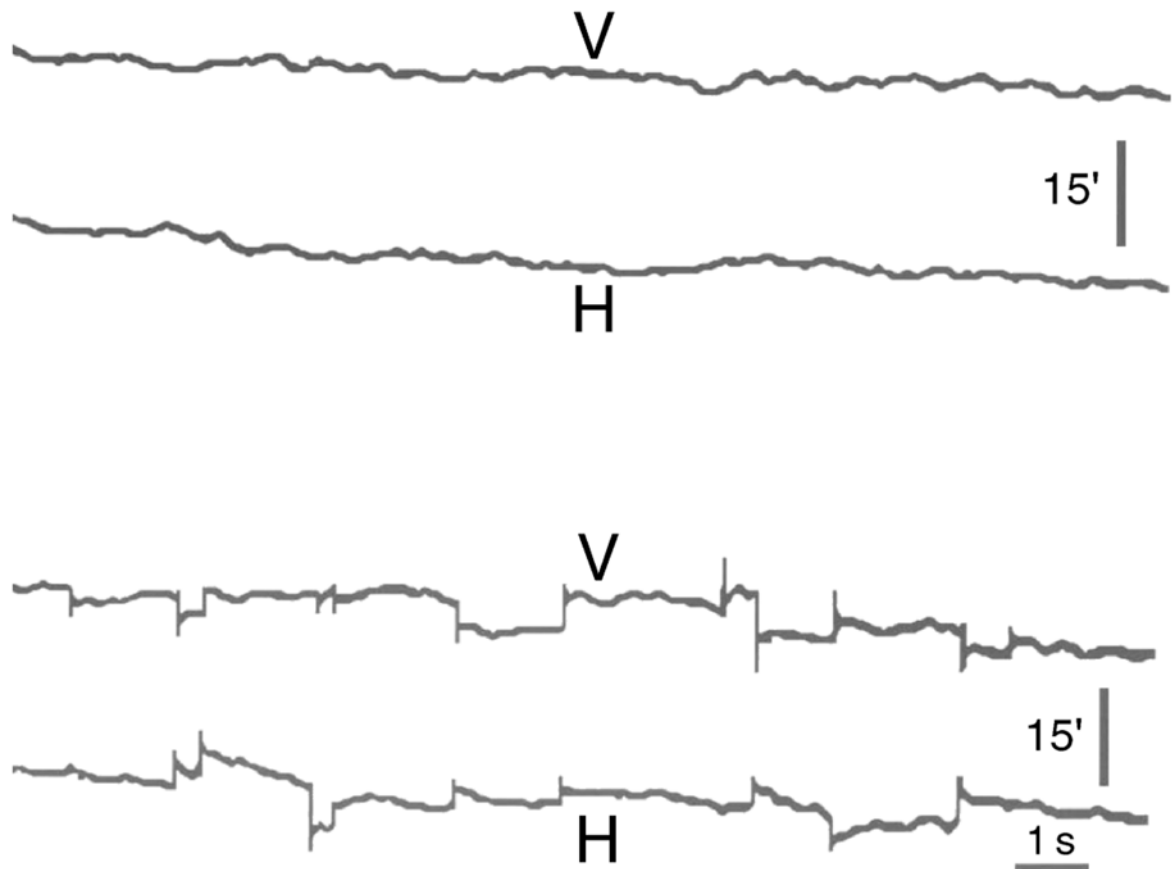
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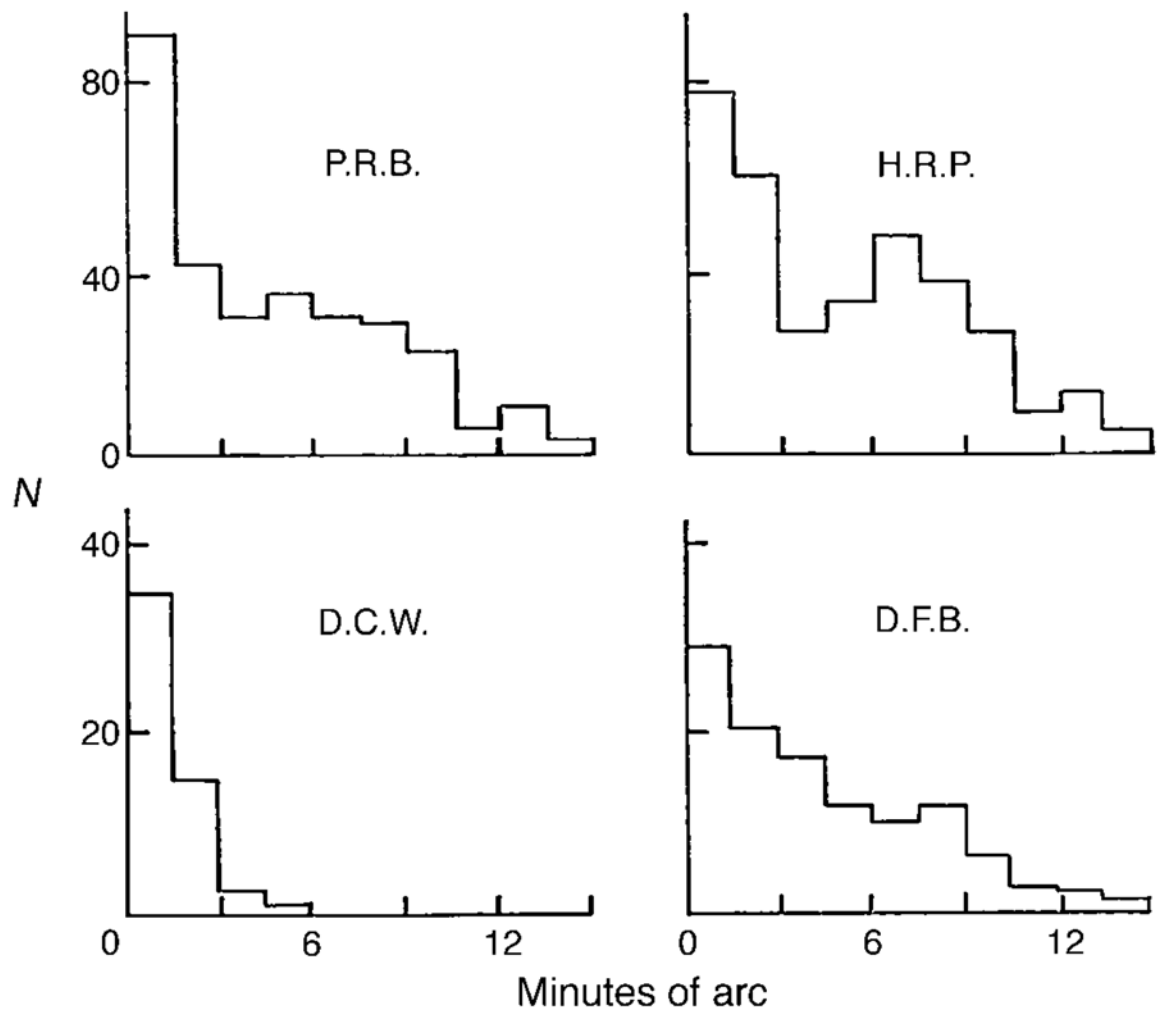
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## Appendix A

One of us (Collewijn) analyzed a number of trials with experienced subjects in an Eyelink II facility at the Neuroscience Department at the Erasmus Medical Center in Rotterdam (we acknowledge the assistance of Drs. M. A. Frens and A. Lutgheid). A bite-board was used to get the most stable results. Position signals were differentiated with a modified two-point central difference algorithm, using the two position samples preceding and the two following each moment for which velocity was calculated, according to the equation published by Collewijn, Erkelens, and Steinman (1995) that was used also by Engbert and Kliegl (2003). This resulted in a velocity signal with a peak-to-peak noise level of  $\pm 3$  deg/s on the horizontal meridian and somewhat higher levels (up to 6 deg/s) on the vertical, without additional filtering. A frequency response analysis of this differencing routine, following Bahill, Kallman, and Lieberman (1982), showed that the obtained velocity signal had (for a sampling frequency of 500/s) a bandwidth of 74 Hz ( $-3$  dB), which is fully adequate for the analysis of saccades. In these data, microsaccades as small as 10 min arc were unambiguously identified in position as well as velocity plots (peak velocity about 13 deg/s). However, the noise levels of about 3 and 6 deg/s on the two meridians are similar to peak velocities of saccades of about 2.3–4.5 min arc. In view of this noise (in both position and velocity signals) the detection of saccades smaller than about 5 min arc will be unreliable, no matter whether it is done by simple human inspection or by any computerized routine: noise remains noise and is a fundamental limit for the detection of single events that occur at random times. This seems to make the technique of somewhat borderline quality in relation to the traditional size range of microsaccades.

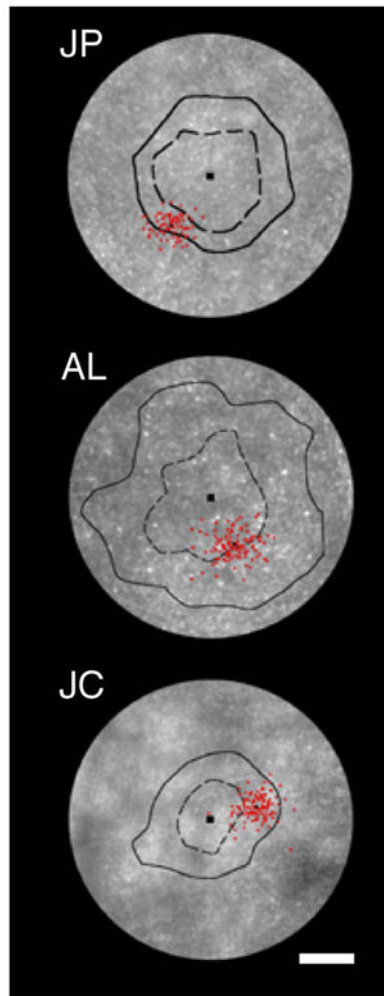


**Figure 1.** Horizontal and vertical eye movements over time, as measured with the contact lens optical lever, while fixating a small point target showing a stable line of sight maintained either with (bottom traces) or without (top traces) the occurrence of microsaccades (from Steinman et al., 1973, *Science*, 181, 810–819). Reproduced with permission.

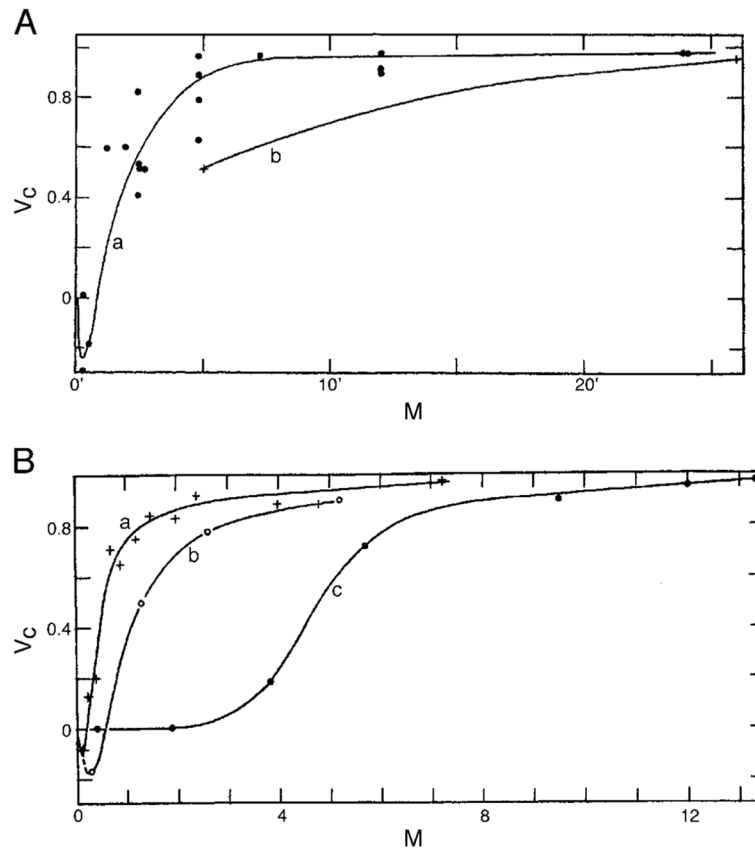


**Figure 2.** Distribution of sizes of microsaccades of 4 fixating human subjects, recorded with the contact lens technique (taken from Boyce, 1967, *Proceedings of the Royal Society of London B*, 167, 293–315). Reproduced with permission.



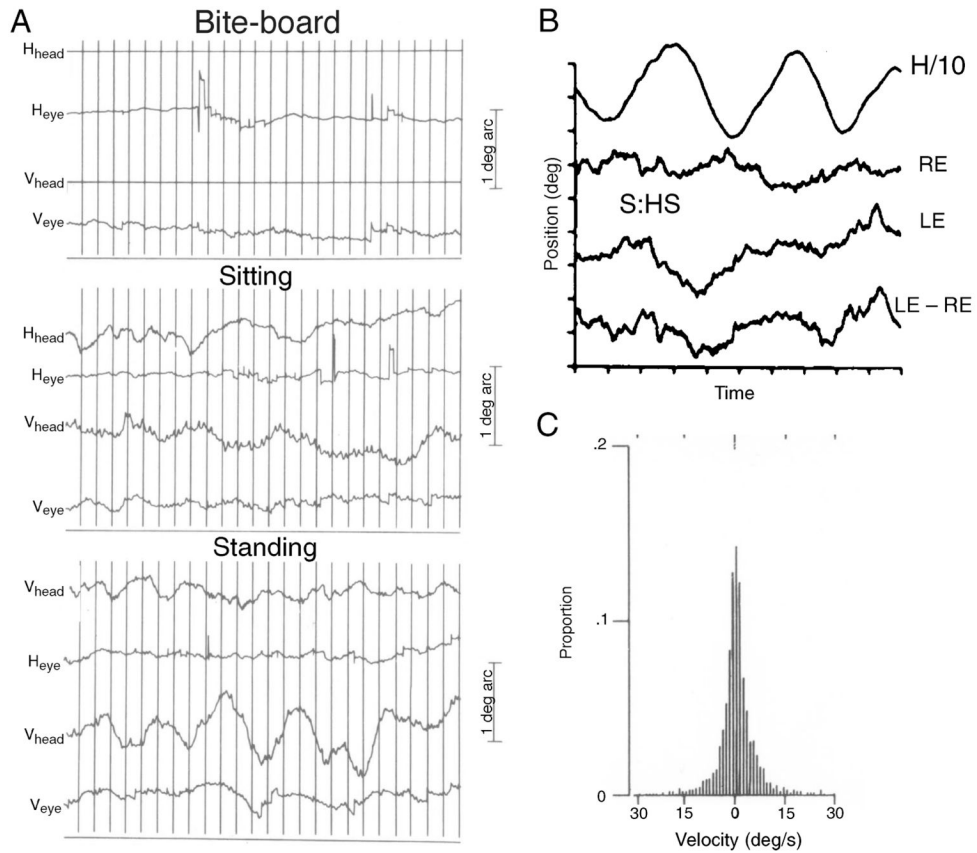


**Figure 3.** Area of highest cone density is not always used for fixation. Shown are retinal montages of the foveal cone mosaic for three subjects. The black square represents the foveal center of each subject. The dashed black line is the isodensity contour line representing a 5% increase in cone spacing, and the solid black line is the isodensity contour line representing a 15% increase in cone spacing. Red dots are individual fixation locations. Scale bar is 50  $\mu\text{m}$  (from Putnam et al., 2005).



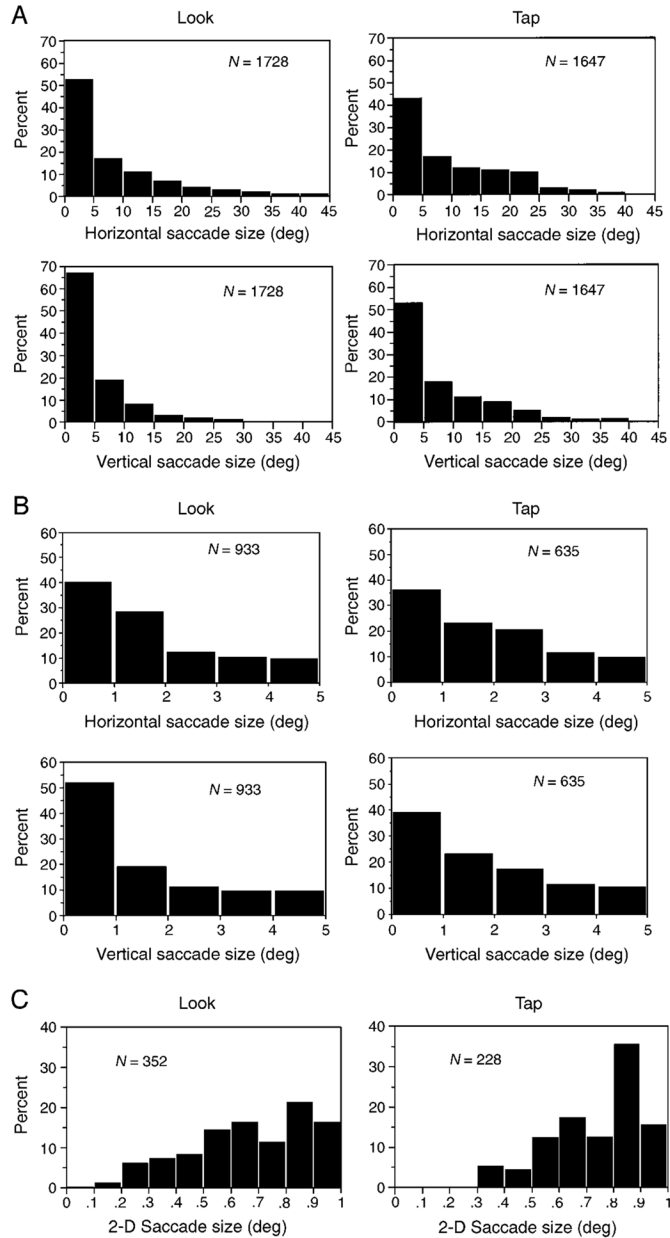
**Figure 4.**

The effects of small, imposed target motion on a stabilized (foveal) image in restoring visibility. Figures taken from Ditchburn and Drysdale (1977b), *Proceedings of the Royal Society of London B*, 167, 385–406. Reproduced with permission. The Y-axis shows the level of visibility ( $V_c$ ) to the subject; the X-axis shows the (peak-to-peak) magnitude (in min arc) of the imposed movement. Upper panel: effect of sinusoidal motion at 0.55 Hz (graph *b* refers to previous measurements by Ditchburn, Fender, & Mayne). Lower panel: effect of square wave motion (0.5 Hz). Graphs *a* and *b* refer to sharp targets; graph *c* to a low contrast target.

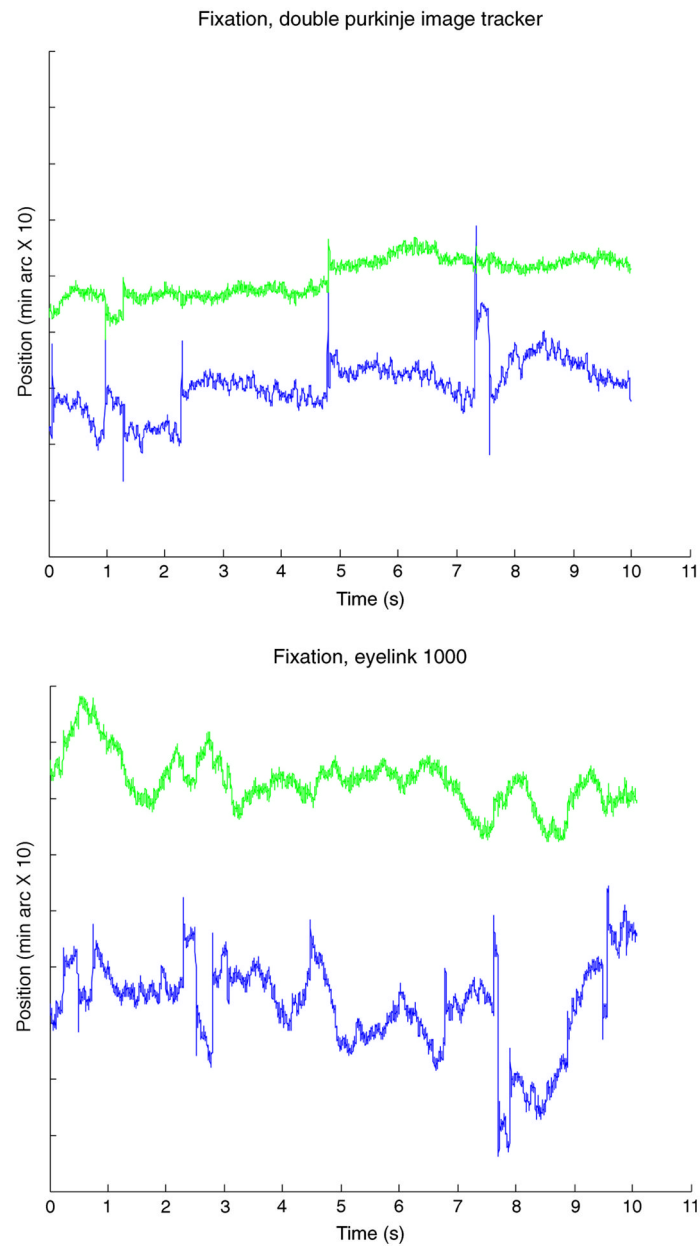


**Figure 5.**

(A) Movements of eye and head during fixation while the head was either supported by a bite-board or was free to move while the subject was either sitting or standing as still as possible. Repetitive vertical stripes are 1-s time markers (from Skavenski et al., 1979). (B) Horizontal eye movements of one subject fixating a distant target while freely moving the head over small amplitudes. The head position trace shows head position scaled to 1/10 of its value. (C) Distribution of retinal image velocities (right eye) during small active head motions, as in (B). (B, C from Steinman & Collewijn, 1980, *Vision Research*, 20, 415–429). Reproduced with permission.

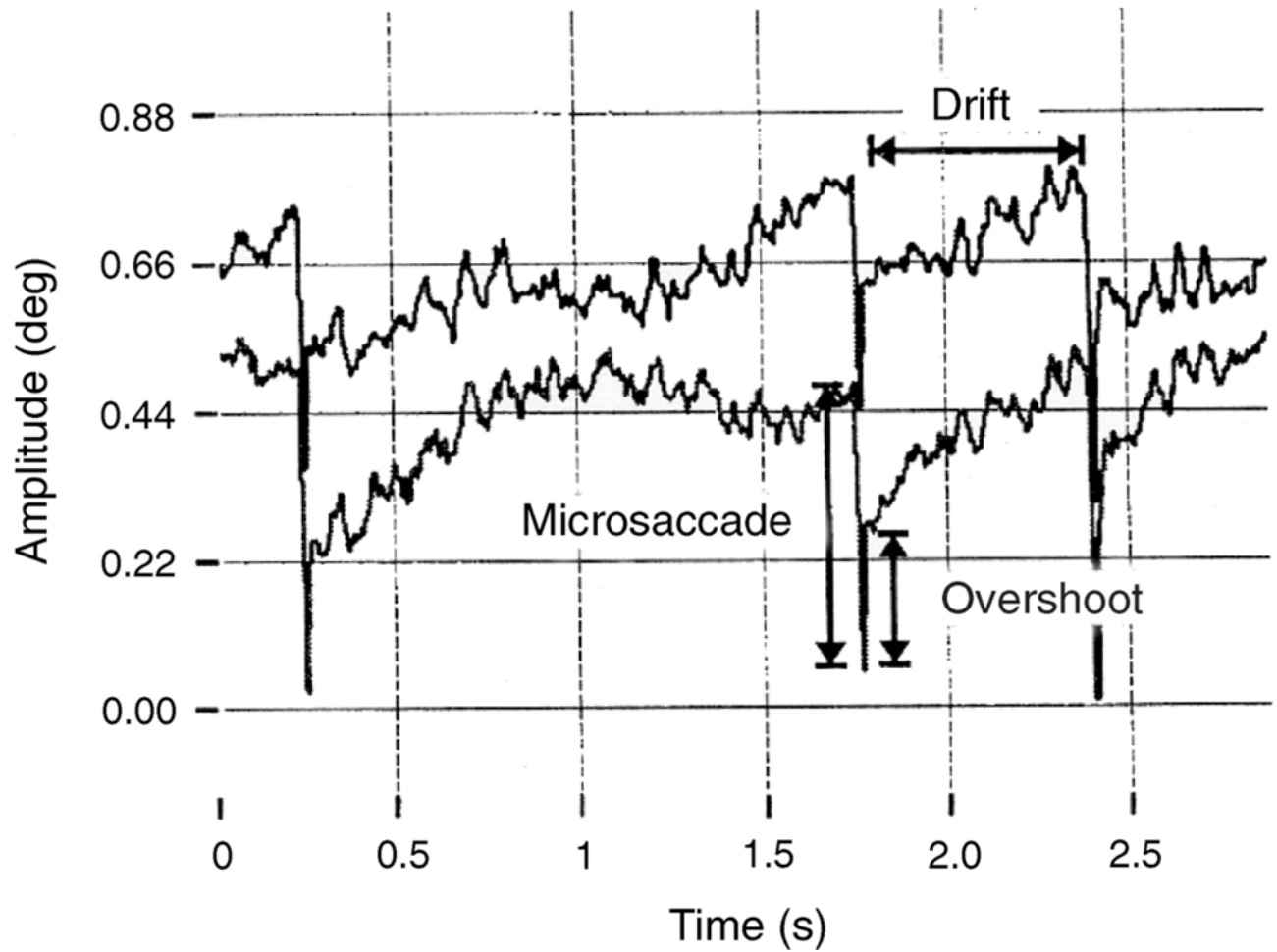
**Figure 6.**

The relative distribution (%) of the sizes of all saccades made during a natural task (sequential fixation or finger-tapping of real physical targets in which subjects could freely move their heads and arm. Figures taken from Malinov et al. (2000), *Vision Research*, 40, 2083–2090. Reproduced with permission; all saccades from 4 subjects pooled. (A) Overall size distribution for all saccades (horizontal and vertical components shown each for the two tasks). (B) Distribution of size for all saccades smaller than 5 deg. (C) Distribution of size (2-D vector) of size for all saccades smaller than 1 deg. Total number of saccades is given each panel. Notice the virtual absence of real microsaccades (<12 min arc). (Instrument noise is constant at bit-noise of  $\pm 1$  min arc).



**Figure 7.**

Sample records of horizontal and vertical eye movements taken from the same subject during fixation of a small stationary cross. Top records were made using a Dual Purkinje Image Tracker while the subject's head was stabilized by a bite-board. Bottom records were made with an Eyelink 1000 mounted on a table while the head was stabilized by a chin and forehead rest. Green traces (top traces of each graph) show vertical movements, blue (bottom traces of each) show horizontal (Kowler, unpublished recordings).



**Figure 8.** Sample recordings of eye movements during fixation (from Møller et al., 2002, *Graefe's Archive for Clinical and Experimental Ophthalmology*, 240, 765–770). Reproduced with permission.