



Minireview

Microsaccades: Small steps on a long way

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ABSTRACT

Contrary to common wisdom, fixations are a dynamically rich behavior, composed of continual, miniature eye movements, of which microsaccades are the most salient component. Over the last few years, interest in these small movements has risen dramatically, driven by both neurophysiological and psychophysical results and by advances in techniques, analysis, and modeling of eye movements. The field has a long history but a significant portion of the earlier work has gone missing in the current literature, in part, as a result of the collapse of the field in the 1980s that followed a series of discouraging results. The present review compiles 60 years of work demonstrating the unique contribution of microsaccades to visual and oculomotor function. Specifically, the review covers the contribution of microsaccades to (1) the control of fixation position, (2) the reduction of perceptual fading and the continuity of perception, (3) the generation of synchronized visual transients, (4) visual acuity, (5) scanning of small spatial regions, (6) shifts of spatial attention, (7) resolving perceptual ambiguities in the face of multistable perception, as well as several other functions. The accumulated evidence demonstrates that microsaccades serve both perceptual and oculomotor goals and although in some cases their contribution is neither necessary nor unique, microsaccades are a malleable tool conveniently employed by the visual system.

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1. Introduction

Human behavior unfolds simultaneously on a large number of spatial and temporal scales. In some cases, action on larger and longer scales is achieved by an accumulation of smaller and shorter constituents, just as walking is accomplished by putting one foot before the other in a coordinated fashion. In other cases, however, larger movements enable acting on a smaller scale. Tactile perception, for instance, relies on reaching movements, bringing the receptor (the finger tips, the tongue, the toes, etc.) to a surface that is to be sensed. If we try to feel the texture of a surface, we will aim for and touch it. Interestingly, as can be easily experienced, tactile perception is strongly facilitated if we move our fingers slightly across a small area of the surface or if we place our finger repeatedly at (possibly different parts of) the texture. In fact, such movements enable blind persons to read *Braille*.

Vision, like touch, has variable resolution depending on where a stimulus falls on the sensory surface. In vision, the highest resolution is achieved in the fovea, the locus on the retina with the high-

est receptor density. Acute vision depends heavily on the ability to align the eyes with a visual target. Indeed, eye-movement behavior is highly optimized to satisfy these needs; most of the time the eyes scan visual scenes in sequences of saccades and fixations. Saccades (rapid eye movements), on the one hand, aim for visual information currently outside the fovea. Fixations, on the other hand, keep a target relatively stable with respect to the photoreceptors on the retina. Notably, our eyes move continuously even during fixation. Rather than holding steady, they will drift slowly with respect to the scene and once or twice per second, involuntary microsaccades will occur. In contrast to moving our fingers across a surface, however, we do not perform these fixational eye movements (FEyeM) voluntarily. And although we are generally not aware of their existence, engrossing visual illusions demonstrate their fundamental role in visual perception (see Fig. 1; for particularly remarkable examples see also Ginsborg & Maurice, 1959; Murakami, 2003, 2006; Murakami & Cavanagh, 1998; Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008b; Zanker & Walker, 2004).

Research has long recognized the dependence of visual perception on retinal image motion per se, but there have been lively debates concerning the contributions of the different components constituting FEyeM to this function. Specifically, microsaccades have generated controversies among visual scientists from the late

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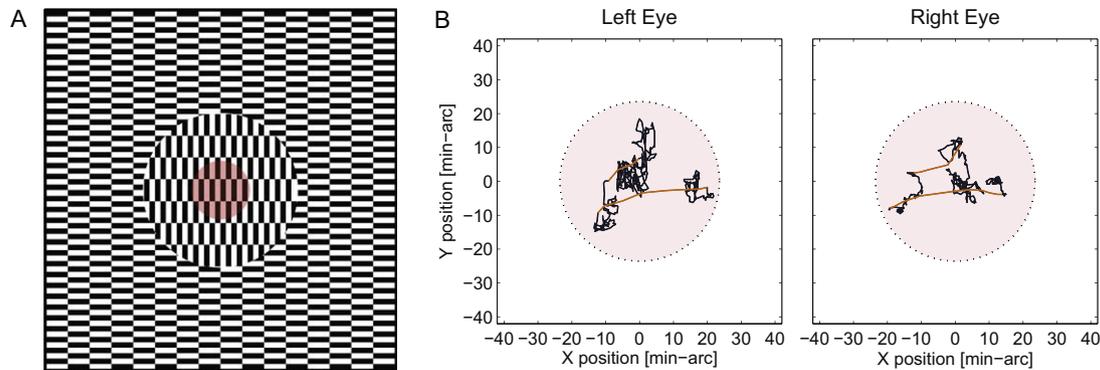


Fig. 1. Fixational eye movements. (A) Static motion illusion by Ouchi (1977), mediated by slip of the retinal image (Ölveczky et al., 2003). The central disk appears to move erratically relative to the checkered background. This is best appreciated if the figure is viewed at a distance of about 10 times the width of the figure as you have it in front of you. For this case, the red area has a diameter of 50 min-arc (as fixation dot in panel B). (B) Trajectory of the two eyes during 1 s of fixation on a black spot on a neutral background (highlighted by red dotted circle). Slow drift movements are displayed in dark color while rapid jerk-like microsaccades are highlighted in orange.

1950s to the 1980s. A look at the publication record of the field in Fig. 2 makes clear that by 1980, researchers faced the seemingly unsolvable problem of finding a specific function for microsaccades in visual processing. By 1987, the field had died completely. Indeed, this period of research on microsaccades ended ingloriously as testified by papers with titles like “Small saccades serve no useful purpose” (Kowler & Steinman, 1980) or “Miniature saccades: Eye movements that do not count” (Kowler & Steinman, 1979). Winterson and Collewijn (1976) found themselves “left with a dilemma” (p. 1390), since they had to conclude that microsaccades’ “significance during fixation remains obscure” (p. 1390). Similarly, according to Bridgeman and Palca (1980), “[t]he function of microsaccades is unknown” (p. 817). Kowler and Steinman (1979) brought the discussion to a temporary end, summarizing their research on the function of microsaccades with the words “Why human beings have the skill to make tiny high velocity eye movements remains a mystery” (p. 108).

Since the late 1990s, interest in the purpose of microsaccades has returned and reached new levels. Fig. 2 shows a stream graph that highlights this prodigious development by showing the number of all publications in this field along with their scientific impact across time.¹ This revival was a result of a remarkably interdisciplinary effort, including: (1) the development of increasingly precise, non-invasive eye-movement-recording devices allowing for larger samples of (naïve) participants being tested, (2) substantial advances in the field of neurophysiology allowing for the recording of single-neuron activity in awake and behaving monkeys, (3) the employment of computational processing power in the analysis of dynamically rich behavior, (4) the progressive application of mathematical modeling as a research tool in psychology and the neurosciences, and (5) novel data-analytic tools adopted, e.g., from statistical physics.

Yet in many cases the full history of the field is only scarcely considered in the present literature. In fact, many of today’s most promising lines of research were launched decades ago without ever finding their way in any publication on the topic. Of course, we must be aware of the foundations built in the past to draw valid conclusions from present investigations, especially, when both earlier and current results are conflicting or even incompatible. Here, I deliver a summary of the research on the purpose of microsaccades that I deem balanced and is, to my knowledge, exhaustive. This

work complements and extends earlier overviews that focussed on the dynamic and kinematic properties of microsaccades (Engbert, 2006b), the differences in FEyeM across species (Martinez-Conde & Macknik, 2008) and in normal versus pathological vision (Martinez-Conde, 2006), as well as the physiological correlates of FEyeM in animal models relevant for the understanding of the role of FEyeM in perception (Martinez-Conde, Macknik, & Hubel, 2004). Although these issues will clearly be raised here, the present manuscript takes a historical perspective and compiles evidence concerning the function of microsaccades in human vision and oculomotor control, which has been collected—with a decaying interest between 1980 and 1995—for about 60 years now (see Fig. 2).

1.1. Discovery of fixational eye movements

It is not clear, when the first observation of FEyeM was reported (Wade & Tatler, 2005). Various early authors noted that the eyes are never at rest. A first example can be found in a treatise by du Laurens (1599), the chief court physician of King Henry IV of France. When discussing the anatomy of the eye, he reported that “the eye standeth not still but moveth incessantly” (pp. 28–29). Another hint was documented some time later, when the French physicist Edme Mariotte engaged in a dispute about where visual perception begins—in the choroid (the vascular layer of the eyeball) or in the retina. Mariotte held that the choroid is the seat of vision, since the eye’s blind spot is covered by the retina, but not by the choroid membrane. In a letter exchange with his contemporary Perault, who argued that the blood vessels in the choroidea would hinder vision, Mariotte (1683) countered that “the Eyes are always in motion and very hard to be fixt in one place, tho it were desired” (p. 266, original italics). We do not know, however, whether these authors were really referring to the eye movements during fixation.

The first author who definitely proposed that eye movements persist even during attempted fixation was Jurin (1738). He based his claim on the following observation: to be able to distinguish two separate marks they must have a distance greater than that needed to perceive a jump of a single mark between the two locations. Jurin suggested that the eyes “tremble”, causing two separate marks to merge into a single mark’s percept. The first empirical evidence for the fact that the eyes move even during fixation was afforded by the English physician Robert Waring Darwin (the father of Charles Darwin) who studied afterimages of colored stimuli (see Fig. 3, for a demonstration). Darwin (1786) noticed that while he was trying to fixate a colored circle, a lucid edge was seen to liberate to the white-paper background. He concluded

¹ This graph calls attention to the evolution of microsaccade research and is not referenced against the development of the fields of vision and/or eye movements in general. In fact, these superordinate areas have grown similarly rapidly over the last six decades. However, they lack the pronounced drop in publication rate in the 1980s and 1990s and, thus, the revival.

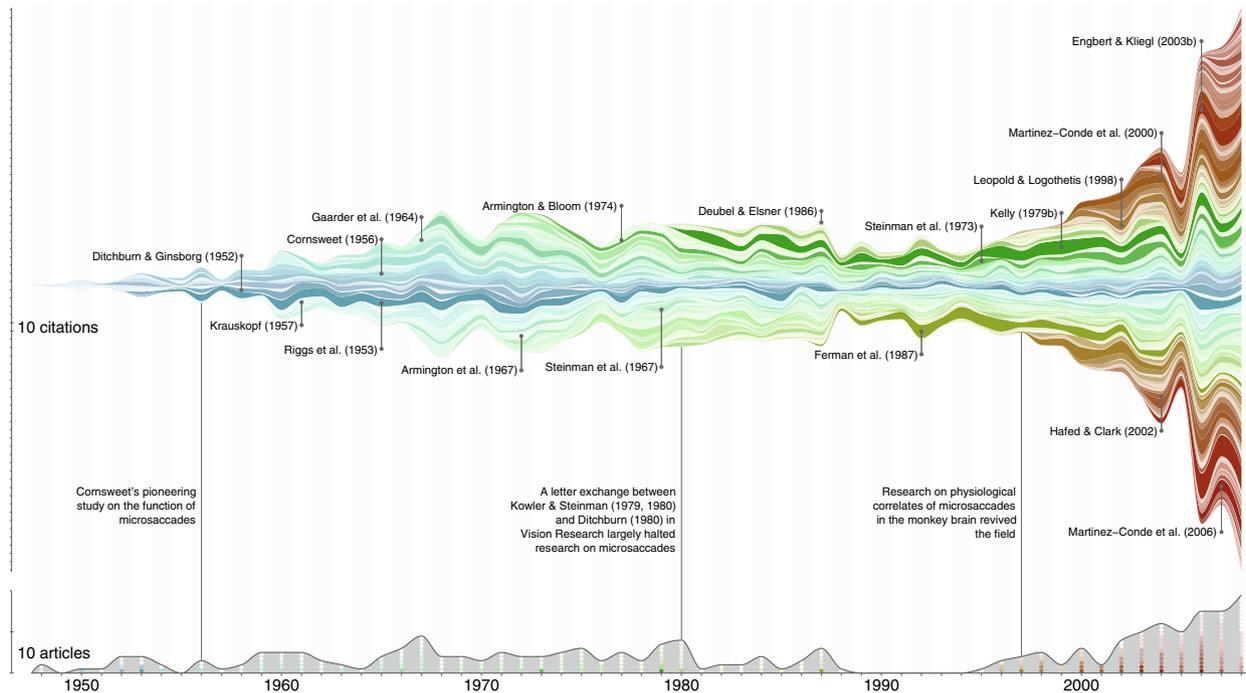


Fig. 2. Impact of research on microsaccades. The stacked graph at the top shows the impact of articles related to the function of microsaccades across time, from 1948 to 2008. Each stripe represents one of 253 articles for which data were available at the Web of Science. The height of the stripe shows the number of references to this article in a given year. Hence, the silhouette of the graph shows the overall impact of the field (685 citations in 2008). Stripe colors encode two dimensions: the age of an article (the warmer, the more recent) and its normalized impact (citations per year; the more saturated, the higher the impact; full saturation for >12 citations per year). The wiggle for each single stripe in the graph is minimized following the procedure proposed by Byron and Wattenberg (2008), ensuring best legibility. As time progresses, newer publications were evenly added at the rims, resulting in an inside-out (rather than bottom-to-top) layout and making the old literature the core of the graph. Labels highlight a selection of original articles, both most cited and most neglected ones. The histogram at the bottom shows the number of items published in a given year; each dot is one article (same color as in top panel).

that “as by the unsteadiness of the eye a part of the fatigued retina falls on the white paper” (p. 341).² Eighty years later, Hermann von Helmholtz (1924, German original published in 1866) wrote that “it requires extraordinary effort and attention to focus the gaze perfectly sharply on a definite point of the visual field even for 10 or 20 seconds” (p. 266). He called this phenomenon the “wandering of the gaze” (p. 266) and proposed that the function of this motion would be to prevent retinal fatigue. As will be seen below, this proposal has been strongly substantiated since then. At those times, however, the accurate measurement of these miniature eye movements was technically impossible. Nevertheless, it was understood by early vision scientists, such as Ewald Hering (1899), to include the role of miniature eye movements in their considerations.

1.2. Three types of fixational eye movements

Objective measurements of FEyeM were made from the end of the 19th century on. For instance, Huey (1900) analyzed fixation durations in reading. He reported that the eyes moved even during “steady fixation”. Further early studies confirmed the existence of FEyeM (Dodge, 1907; McAllister, 1905), soon providing more detailed descriptions of eye movements during attempted fixation (Adler & Fliegelman, 1934; Lord & Wright, 1948; Marx & Trendelenburg, 1911). Today it is generally accepted, that FEyeM are composed of three different types of movement: *drift*, *tremor*, and

microsaccades (see Martinez-Conde et al., 2004, for a recent review).³ In the early 1950s, researchers in the field agreed on this typology (Barlow, 1952; Ditchburn & Ginsborg, 1953; Ratliff & Riggs, 1950), when the technical equipment of eye-movement recording had been improved so far as to accurately visualize tremor, the smallest component of FEyeM.

1.2.1. Drift

The trajectory of FEyeM is erratic and characterized mainly by a low-velocity component, the so called drift movements (dark parts of the eye-movement trace in Fig. 1B). By definition, drift occurs during the inter-saccadic intervals and can be described as a random walk (Cornsweet, 1956; Engbert & Kliegl, 2004; Findlay, 1971, 1974; Matin, Matin, & Pearce, 1970). During prolonged fixation, drift carries the retinal image by about 1–8 min-arc at a speed (mostly well) below 30 min-arc/s. During natural, intersaccadic fixation, somewhat higher velocities are commonly observed, in part as a consequence of ocular lens overshoots during saccadic eye movements (Deubel & Bridgeman, 1995).

The question of whether or not drift movements are correlated between the eyes has been addressed by several articles. Some studies found no correlation of drift movements in the two eyes (Krauskopf, Cornsweet, & Riggs, 1960; Yarus, 1967); other studies found that drift movements are in general binocularly synchronized (Riggs & Ratliff, 1951). Ditchburn and Ginsborg (1953) reported conjugacy for both the vertical and horizontal components of drift; the direction of these movements changing at random times. Moreover, the authors found intervals of

² Probably, this work had been started by Robert Waring's father Erasmus Darwin. On January 24, 1774, he wrote in a letter to Benjamin Franklin: “I have another very curious Paper containing Experiments on the Colours seen in the closed Eye after having gazed some Time on luminous Objects, which is not quite transcribed, but which I will also send you, if you think it is likely to be acceptable to the Society at this Time, but will otherwise let it lie by me another year” (Hussakof, 1916). Both Darwin and Franklin were members of the Royal Society at the time.

³ This pattern of FEyeM is commonly observed during attentive fixation. Fixation behavior during inattention may have fairly different characteristics (Gaarder, 1966a).

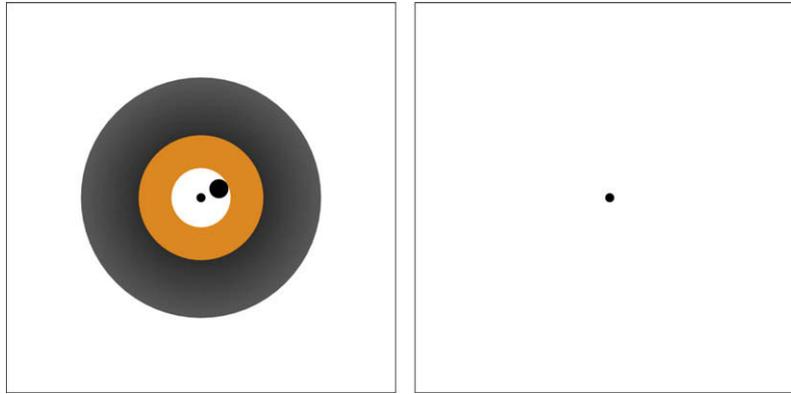


Fig. 3. Afterimage illustration of fixational eye movements. One's own fixational eye movements can be observed by inducing after images (Verheijen, 1961). Put the image at a distance of 20 cm in front of you. Fixate the spot at the center of the left image for about 30 s. Soon you may notice unstable contours flickering at the outer rim of the colored ring. If you now look at the spot in the white field to the right, you will perceive an afterimage of the picture, which has the appearance of an eye. The afterimage constantly follows your eye movements. Note that the eye is never perfectly motionless, even when you try to hold it as still as possible. You will also see the afterimage fade spontaneously, especially if you try to reduce your eye movements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

convergence and divergence, respectively, for the horizontal components. According to Ditchburn and Ginsborg (1953), however, this effect could be attributed to accommodation. More recently, binocular coherence of drift (and tremor) was also proposed by Spauschus, Marsden, Halliday, Rosenberg, and Brown (1999), see description of tremor). Finally, Thiel, Romano, Kurths, Rolfs, and Kliegl (2008) used a sophisticated surrogate data method (see also Thiel, Romano, Kurths, Rolfs, and Kliegl, 2006) to demonstrate significant phase synchronization of FEyeM, mainly consisting of drift, between the two eyes but not between vertical and horizontal components of one eye (see also Moshel et al., 2005, 2008). The authors proposed that motor neurons as the final common pathway of neural control of eye movements are candidates for the synchronization of fixational movements of both eyes. Note, that coherence and synchronization do not distinguish between conjugacy, convergence, and divergence. Rather, these terms refer to a coordinated behavior of drift in both eyes including velocity, acceleration, and, thus, also changes in movement direction.

1.2.2. Tremor

Tremor (also microtremor or physiological nystagmus) is an irregular, wave-like motion superimposed on the drift movements described before. Tremor was first reported by Adler and Fliegelman (1934), but then questioned by some authors (e.g. Hartridge and Thomson, 1948; Lord and Wright, 1948). Special high-resolution equipment is needed to record tremor (Bengi and Thomas, 1968; Yarus, 1967); it is not resolved in the trajectories in Fig. 1B. Tremor has a high frequency and a small extent. The reported frequency and amplitude values, however, deviate across various studies, although the variation can be attributed to individual differences (Barlow, 1952; Ratliff and Riggs, 1950) and recording methods differing between laboratories (Ditchburn and Ginsborg, 1953; Simon, Schulz, Rassow, and Haase, 1984). Reported frequencies in the early studies varied between 30 and 100 Hz with movement cycles having amplitudes of 0.1–0.5 min-arc (e.g., Adler and Fliegelman, 1934; Higgins and Stultz, 1953; Ratliff and Riggs, 1950). In a recent sample of 105 normal participants, frequencies ranged from 70 to 103 Hz with an average of 84 Hz (Bolger, Bojanic, Sheahan, Coakley, and Malone, 1999).

As with drift, binocular studies of FEyeM have revealed different patterns of results. Early binocular examinations did not find a binocular correlation of tremor (Ditchburn and Ginsborg, 1953; Riggs and Ratliff, 1951). More recently, however, evidence for a coherence of tremor movements in the two eyes emerged. Spauschus

et al. (1999) examined frequency components of ocular drift movements and tremor in both eyes simultaneously. After a correction for head movements, the authors found coherence of the eyes' accelerations in both low- (up to 25 Hz) and high- (60–90 Hz) frequency ranges. The authors suggested that these FEyeM might be related to the patterning of low-level but central drives to the extra-ocular muscle motor units. Concerning the high-frequency movements, this is in agreement with clinical studies showing a reduction or abolition of tremor in disease of the brain system (Michalik, 1987) and in comatose patients (Shakhnovich and Thomas, 1977), respectively.

1.2.3. Microsaccades

A couple of times per second, the slow drift movements of the eyes during fixation are interrupted by small rapid shifts in eye position (orange parts of the eye-movement trace in Fig. 1B). These jerk-like movements were first discovered by Dodge (1907). In most of the recent studies, they were called microsaccades, a term introduced by Zuber, Crider, and Stark (1964).⁴ It should be noted, however, that various terms can be found in the literature, including small, miniature, or fixational saccades, minisaccades, jerks, flicks, jumps, and so forth.⁵ Microsaccades clearly differ from drift movements by their high velocity, a fact used to detect these events in a stream of FEyeM data (e.g., Engbert and Kliegl, 2003b). Although monocular microsaccades were observed in some data sets (Engbert and Kliegl, 2003a, 2003b), their existence has been questioned (Collewijn and Kowler, 2008), and they are generally considered binocular movements (Boyce, 1967; Ditchburn and Foley-Fisher, 1967; Krauskopf et al., 1960; Møller, Laursen, Tygesen, and Sjølie, 2002). Moreover, microsaccades show a clear preference for horizontal and vertical directions, the latter being less frequent in humans. Ob-

⁴ It is a remarkable fact that Bert L. Zuber introduced three of the now most common terms in eye movement research in two subsequent papers (Zuber et al., 1964; Zuber, Stark, and Cook, 1965): microsaccade, saccadic suppression, and main sequence.

⁵ Another label was added in recent work that aimed to subdivide several saccade-saccade and saccade-drift combinations during fixation (Abadi and Gowen, 2004; Gowen and Abadi, 2005; Gowen, Abadi, and Poliakoff, 2005, 2007). To sum up these different fixation behaviors, these authors used the generic term *saccadic intrusions*. This term originates in the clinical literature and describes non-repetitive saccadic interruptions of fixation in patients with ocular instabilities. It is often used synonymously with its most frequent sub-category, *square-wave jerks*, paired saccades away from and back to a target separated by some 200 ms (Ciuffreda and Tannen, 1995). In terms of the definition of microsaccades adopted in the present work, such instances would be treated as two separate movements.

lique directions are observed rather exceptionally (Engbert, 2006b). Note, however, that biases in microsaccade directions may depend on the characteristics of a given task (see Gaarder, 1960, 1967, for particularly early findings).

All types of saccades (including most microsaccades) share important characteristics: They are conjugated binocular high-velocity movements with a distinct correlation of peak velocity and movement amplitude (the so-called main sequence; Zuber et al., 1965), suggesting a common generator (Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, and Martinez-Conde, 2008; Rolfs, Laubrock, and Kliegl, 2006, 2008b; Rolfs, Kliegl, and Engbert, 2008a; Zuber et al., 1965). Telling apart microsaccades from other saccades is, therefore, a matter of definition and depends both on the laboratory and on the species under examination (reviewed in Martinez-Conde and Macknik, 2008; Martinez-Conde et al., 2004). Some authors apply a stringent amplitude criterion (e.g., <15 min-arc, Collewijn and Kowler, 2008; Malinov, Epelboim, Herst, and Steinman, 2000; Steinman, Pizlo, Forofonova, and Epelboim, 2003), based on assembled data from the early literature on the topic (Boyce, 1967; Ditchburn and Foley-Fisher, 1967; Krauskopf et al., 1960). Indeed, being eye movements *during* fixation, the overlap of the retinal image on the fovea before and after a microsaccade should be substantial. It is quite clear, however, that microsaccades cannot be defined solely on the basis of amplitude, since saccades with amplitudes of less than 5.7 min-arc can be performed voluntarily in the presence of a stationary fixation target (Haddad and Steinman, 1973). In line with the definition of microsaccades in the earliest studies, I refer to microsaccades as involuntary saccades that occur spontaneously during intended fixation. In fact, although many labs use upper bounds of 1° or even 2° to distinguish microsaccades from saccades, the majority of microsaccades observed in a variety of tasks have amplitudes smaller than 30 min-arc anyway (see, e.g., Engbert, 2006b; Otero-Millan et al., 2008). The upper bounds aim to capture the tail of the amplitude distribution of microsaccades observed during prolonged fixation.⁶ However, a distinction between microsaccades and large saccades becomes more difficult when fixation is not explicitly required, e.g., in free-viewing tasks. Under these circumstances, a pragmatic working definition will have to rely on an amplitude criterion, derived either from data collected in fixation tasks in the same subjects (Otero-Millan et al., 2008) or from a bimodality in the saccade amplitude distribution, unfortunately a rare phenomenon, which may however be boosted by alternating free-viewing and simple fixation tasks (Konstantin Mergenthaler & Ralf Engbert, personal communication).

2. Finding the purpose of microsaccades

As soon as micromovements of the eye were an established phenomenon, several groups developed clever optical techniques

⁶ Clearly, the video-based eye tracking systems now commonly used in the study of microsaccades do not achieve the excellent spatial resolution of some of the more sophisticated techniques used in earlier studies. Therefore, very small microsaccades might go undetected in studies employing off-the-shelf equipment (Collewijn and Kowler, 2008). However, it remains unclear why early and current studies differ with respect to the largest observed microsaccades. Differences in experimental settings (e.g., means of head fixation, such as bite boards) and visual stimulation (e.g., the popular use of computer screens) are likely candidates. In addition, an underestimation of amplitudes in many early studies followed from recordings of eye movements in only one dimension. However, I speculate that a main cause for the increase in microsaccade amplitude across the decades is the inclusion of naïve observers in recent studies. Whereas a careful application of the sophisticated procedures of eye-movement recording in the early studies required the use of experienced and highly trained observers (most often the authors), naïve observers normally have no prior training in experimental fixation tasks. Indeed, a study reviving the optical-lever technique, a method with highest spatial resolution, reported an amplitude range of 3–50 min-arc in naïve observers (Schulz, 1984).

to counteract any retinal image motion—FEyeM were effectively switched off. These studies brought to light an amazing discovery: when the visual environment becomes completely static on our retinae, it rapidly fades from visual perception (Ditchburn and Ginsborg, 1952; Riggs and Ratliff, 1952; Riggs, Ratliff, Cornsweet, and Cornsweet, 1953; Yarbus, 1957a, 1957b). These results have ever since influenced our thinking about the basis of visual perception.

As another consequence of these findings, a second question arose: If seemingly irregular eye movements are inevitable (or even necessary) during fixation, why do we not lose track of a target? Subsequent research tried to sort out which types of FEyeM contribute to these fundamental perceptual and oculomotor functions. In particular, the role of microsaccades triggered long-lasting scientific debates. It was Cornsweet (1956) who first approached the purpose of microsaccades empirically.

2.1. In the beginning there was Cornsweet

In his seminal study, Cornsweet (1956) examined which conditions evoked drift and microsaccades during fixation. At that time, various proposals had been circulating. First, it had been suggested that FEyeM are stimulated directly by retinal fading (Ditchburn and Ginsborg, 1952; Ginsborg, 1953). Second, various authors had argued that displacement of the fixation target from the optimal location could result in corrective drift or microsaccades or both (Adler and Fliegelman, 1934; Ditchburn, 1955; Ditchburn and Ginsborg, 1953; Ginsborg, 1953; Ratliff and Riggs, 1950; Doesschate, 1954). Third, it had been proposed that oculomotor instability might be generated independently of visual signals (Ratliff and Riggs, 1950).

To test these ideas directly, Cornsweet (1956) flickered a small bar stimulus at different frequencies presented either stabilized with respect to the retina or under normal viewing conditions. Low flicker rates improved visibility of the stabilized stimulus; high flicker rates resulted in increased disappearance times that were comparable to those observed for static stabilized images. To test whether drift movements were triggered by disappearance, the author correlated disappearance-time fractions obtained for a whole range of flicker-frequencies with the rate of drift movements. No positive correlations were observed. In fact, drift rates were lower for normal viewing than they were in the stabilized condition. Thus, drift was not directly related to disappearance and did not correct for displacement of the fixation target that must have resulted from normal viewing conditions. Finally, the author found that fixation errors increased over intervals of drift. It was concluded that drift is not under direct visual control.

Microsaccade rates were not correlated with disappearance-time fractions either. However, they were clearly related to fixation displacement. First, fewer microsaccades were observed in the retinal-stabilization condition. Second, the probability of microsaccade occurrence increased with the distance of the viewing point from the mean eye position over a 45 s trial. Third, this microsaccade then went most probably in the direction of the fixation stimulus—the probability being highly correlated with the amount of displacement. Finally, the amplitude of microsaccades depended on the magnitude of displacement. Larger displacements were associated with larger microsaccades. However, since the minimum saccade amplitude was found to be 3 min-arc, microsaccades tended to overshoot the point of minimum error after small displacements. Cornsweet (1956) concluded that while the instability of the oculomotor system results in drift, taking the eye (on average) farther and farther away from some optimal locus, microsaccades serve the role of returning the eyes on a fixated target.

Thus, Cornsweet's results were surprisingly clear and straightforward. His conclusions, however, turned out to be premature, mainly because his setup could only record (and correct for) the movements of one eye, and only in the horizontal plane. In what follows, I will describe the aftermath of Cornsweet's studies on visual and oculomotor functions of microsaccades. Although, subsequent work focused for a long time on the control of fixation position and prevention of perceptual fading, the scope of the potential functions of microsaccades broadened considerably in later research.

2.2. Control of fixation position

Cornsweet's (1956) observations triggered much dispute on the role of microsaccades in fixation control and not all of the subsequent studies could replicate his findings. In one of the first studies employing binocular eye-movement measurements, Krauskopf et al. (1960) found that while drift movements were not correlated between the two eyes, microsaccade directions and amplitudes were. This finding challenged Cornsweet's model, because microsaccades should produce fixation errors in one eye at least. Thus, Krauskopf and his colleagues modified Cornsweet's model, suggesting that both eyes independently correct for their individual fixation errors when a certain amount of error had accumulated. In addition, a central mechanism was assumed, triggering a microsaccade in both eyes at the same time. However, while microsaccade direction was highly correlated between the two eyes, the amplitude in the "passive" eye was proposed to be smaller, resulting in a correction of fixation errors in both eyes on average. Indeed, for Krauskopf's participants, microsaccade amplitudes were reliably smaller in one eye than in the other. A subsequent study by St. Cur and Fender (1969) lend further support to this conclusion, showing that microsaccades significantly reduce disparity between the two eyes.

An even stronger challenge to Cornsweet's conclusions was a study by Nachmias (1959), who examined FEyeM along eight meridians to arrive at a better estimate of the interactions between microsaccades and drift. He discovered that the distribution of microsaccade directions is highly idiosyncratic, i.e., they vary considerably between observers. In Nachmias's participants, microsaccades indeed compensated for fixation errors, however, the time since the last microsaccade was a better predictor for the occurrence of a microsaccade than the amount of displacement from some optimal locus. Moreover, the author demonstrated that some compensation was achieved by drift, especially along those meridians where compensation by microsaccades was poor. Two years later, Nachmias (1961) published another study, on the determinants of drift movements during fixation. He replicated the most important findings of his earlier study. First, microsaccade occurrence did not depend on the drift rate. Second, like microsaccades, drift could also correct for errors produced by other drift along certain meridians. Third, as compared to fixation error, again, the time since the last microsaccade was a better predictor for the observation of another microsaccade. In addition, the author demonstrated that drift could at least indirectly be influenced by visual factors, showing that drift rates and directions depended on the viewing distance of fixation targets. Specifically, drift was more pronounced when observers fixated a stimulus at a distance of 30 cm than at optical infinity.

The finding that drift might contribute to the maintenance of fixation on a target has been replicated by other authors, though correction by drift was not necessarily as effective as correction by microsaccades (de Bie and van den Brink, 1984; Fiorentini and Ercoles, 1966; Schulz, 1984; St. Cur and Fender, 1969). Boyce (1967) as well as Beeler (1965, as cited in St. Cur and Fender, 1969) found that only 30%, or less, of the microsaccades observed

in their participants were correcting for previous drift. Also Proskuryakova and Shakhnovich (1967) and Glezer (1959) found no evidence for an inverse relationship between drift and microsaccade direction. It is important to note that due to the technical complexity of eye-movement recording decades ago, most of the early studies used highly-trained observers (the authors, in most cases). However, using naïve participants, Møller, Laursen, and Sjølie (2006) recently reported similar findings. On the basis of these findings, a case was made that both microsaccades and drift may be error-correcting and -producing as well (Nachmias, 1961; Steinman, Haddad, Skavenski, and Wyman, 1973).

These findings fueled the idea that microsaccades do not serve a particular purpose, but rather represent "busy work" of the oculomotor system while it is forced to fixate over unnaturally long periods of time (Kowler and Steinman, 1980; Steinman et al., 1973). In addition, it was discovered at that time that just by a simple change in the instruction (from "fixate" to "hold the eyes still"), participants were capable of reducing their microsaccade rates significantly, usually to about 0.5 Hz. This important finding was first noticed by Fiorentini and Ercoles (1966) and afterwards documented in some more detail by Steinman, Cunitz, Timberlake, and Herman (1967). Voluntary inhibition of microsaccades has been replicated frequently, in normal humans (Gowen et al., 2005; Haddad and Steinman, 1973; Haddad and Winterson, 1975; Kowler and Steinman, 1977, 1979; Murphy, Haddad, and Steinman, 1974; Puckett and Steinman, 1969; Steinman, Skavenski, and Sansbury, 1969; Winterson and Collewijn, 1976) as well as in patients with amblyopia (Ciuffreda, Kenyon, and Stark, 1979; Schor and Hallmark, 1978), a disorder of the eye associated with high rates of drift movements (Ciuffreda, Kenyon, and Stark, 1980).

Several authors emphasized that the variability of fixation position was not enhanced when microsaccades were suppressed (Murphy et al., 1974; Puckett and Steinman, 1969; Steinman et al., 1967, 1973; Winterson and Collewijn, 1976). As a consequence, these authors stressed the argument that microsaccades are not necessary for the control of fixation position. Rather, the process of *slow control*, i.e., drift movements that keep the eyes on a target, was proposed to serve that purpose. Winterson and Collewijn (1976) as well as Steinman et al. (1973) found that the slow control system is not equally effective in all observers. Steinman et al. (1973), however, argued that even their participant with the least effective slow control of fixation position, exceeded natural fixation durations by the factor of ten successively maintaining a fixation target within the foveal area. Slow-control mechanisms have since been observed in preschool children (Kowler and Martins, 1982) and in several vertebrates, including cats (Winterson and Robinson, 1975), rabbits (Collewijn and van der Mark, 1972), and monkeys (Skavenski, Robinson, Steinman, and Timberlake, 1975; Snodderly, 1987). Kowler and Steinman (1980) summarized the literature, finding that 85% of the participants in all studies showed effective slow control in the absence of microsaccades. They concluded that microsaccades could not have evolved to control fixation position in a subset of normal humans as small as 15%. Further research, primarily by Steinman and colleagues, focussed on the origin of the signal used to establish slow control mechanisms (Matin et al., 1970; Murphy et al., 1974; Sansbury, Skavenski, Haddad, and Steinman, 1973; Skavenski, 1971, 1972; Skavenski and Steinman, 1970; Steinman, 1965, 1976).

Thus, the findings concerning the role of microsaccades and drift movements in the control of fixation position are inconsistent and partially conflicting. Both microsaccades and drifts may enhance or decrease the deviation between the desired gaze position and the line of sight. Moreover, if microsaccades are suppressed, drift alone slowly controls for emerging fixation errors. Differences between observers, stimuli, analyses, and even in the definition of

a “correcting” movement may account for a part of these inconsistencies (St. Cur and Fender, 1969).

There is the chance that new analytic tools shed light on these controversies. In a recent paper, Engbert and Kliegl (2004) described FEyeM in terms of the statistics of a random walk. Using a standard deviation analysis (see Fig. 4), the authors showed that FEyeM, recorded during the fixation of a small dot, systematically deviate from Brownian motion, i.e., purely random movement; FEyeM were best described by a subdivision in two different time scales. Over short periods of time (2–20 ms), the eyes tended to keep going in one direction (persistent behavior), effectively increasing the variance in spatial displacement beyond what was expected on the basis of Brownian motion, possibly to enhance the amount of retinal image motion. On longer time scales (100 ms, or more), in contrast, a control mechanism set in, decreasing variance in displacement below what is observed in Brownian motion (anti-persistent behavior) and ensuring that fixation errors as well as binocular disparity were reduced. Cutting out microsaccades from the time series and repeating their analysis with pure drift segments, the authors found that these correlations disappeared. They concluded that a considerable part of both tendencies increasing variance and fixation control was due to microsaccades. These results have since been validated (Liang et al., 2005; Moshel et al., 2008) and replicated (Mergenthaler and Engbert, 2007), using different analysis techniques to analyze the time-scale behavior. As shown in a modeling study by Mergenthaler and Engbert (2007), drift alone may also result in a separation of two time scales, although microsaccades would still contribute to this behavior. The contribution of microsaccades appeared to be particularly evident in the horizontal dimension (Liang et al., 2005; Moshel et al., 2008). In addition, a study by Rolfs, Engbert, and Kliegl (2004b) supported the ecological validity of Engbert and Kliegl’s findings. Both the separation in two time scales and a significant contribution of microsaccades to this behavior was evident not only when participants sat in a chair with their head positioned on a chin rest, but also if the chin rest was removed and if participants were standing upright. The different behavior on two temporal scales offer an explanation for the controversial results of earlier studies.

A general major challenge for the study of control properties of FEyeM is that they have to be studied during fixation of a stationary target, making any changes in the visual input unfeasible. For the proper experimental study of a control system, however,

changes in the input are a basic requirement. de Bie and van den Brink (1984, see also de Bie, 1986) highlighted this problem in an interesting study that went largely unnoticed in the literature on the topic. Their approach was to displace a fixation target by 2.5 min-arc, that is, so slightly that it still fell in the area of normal gaze position variation during fixation. The authors observed a very lawful behavior in response to these target shifts. The induced biases in fixation position resulted either in drift or of small saccades that both, on average, reduced the target error by an amount linearly increasing with the distance between the eyes and the fixation target just before the correction. The authors then examined microsaccades and drifts occurring when the same amounts of displacement were observed during fixation on a stationary target. Exactly the same relationships applied. These results accommodated the differences of earlier findings and showed that an isotropic error-correction mechanism may apply for microsaccadic behavior. If the distance between gaze and the fixation goal exceeds a threshold, a microsaccade is generated. It is important to note, however, that individual microsaccades were not very precisely hitting the fixation goal, a high degree of accuracy was found only when saccade lengths were averaged across many instances of microsaccades.

Thus, both slow control and microsaccadic correction contribute to fixation stability. Recent behavioral and neurophysiological data lead us to suggest that both mechanisms may have a common neurophysiological implementation. A key node in the control of saccades, fixations, and smooth pursuit is the superior colliculus (SC), a layered brainstem structure in the dorsal part of the mesencephalon. The intermediate and deeper layers of this structure are arranged in a topographic map. Recent evidence suggests that this map encodes behavioral goal locations that gaze direction will act on, independent of the behavioral strategy chosen to reach that goal (fixation, saccades, or smooth pursuit), and independent of visual input at this goal location (Hafed, Goffart, and Krauzlis, 2008; Hafed and Krauzlis, 2008). The goal to fixate is encoded in the very rostral end of the SC, activity in more caudal parts of the SC signal a discrepancy between the desired and the current gaze position. Rolfs et al. (2008a) have shown that several lines of evidence converge on the idea that microsaccades are generated in the rostral pole of the SC (see also Rolfs et al., 2006, Rolfs, Laubrock, and Kliegl, 2008b). Extracellular recordings of neurons in the monkey SC have now revealed causal evidence for this hypothesis (Hafed, Goffart, and Krauzlis, 2009). Cells in the rostral SC exhibited a remarkable

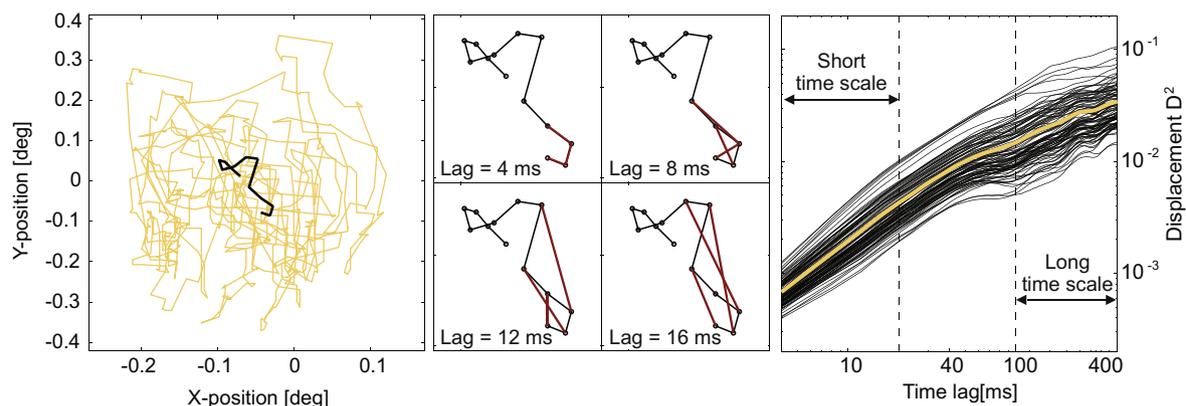


Fig. 4. Standard deviation analysis of fixation control. Engbert and Kliegl (2004) used a standard deviation analysis to determine the dynamic properties of eye position control during fixation. The left panel shows the gaze position data of a sample trial. The mean square displacements were computed for all possible time lags, which are constrained by the sampling rate of the eye tracker (here 250 Hz) on the lower end and the duration of the trial on the upper end. The middle panel shows for four different time lags how displacements were determined (red lines). For reasons of clarity, only the first three cases of the black part of the eye-movement trace in the left-hand panel are shown. The panel on the right plots the observed mean square displacement as a function of time lag in a log–log plot. Data from single trials are shown in black; the average is shown in orange. The slope of this function corresponds to the scaling exponent. On the short time scale, slopes were greater than 1, indicating persistent behavior; on the long time scale, slopes were smaller than 1, indicating anti-persistent behavior (see text). (Figure from Rolfs et al., 2004b.)

selectivity for microsaccades of certain amplitudes and directions. This result strongly suggests that microsaccades are not just random motor noise, but originate from coordinated neural activity. Interestingly, activity of neurons in this part of the SC map were shown to correlate with smooth pursuit eye movements (Basso, Krauzlis, and Wurtz, 2000; Krauzlis, Basso, and Wurtz, 1997, 2000). It has been argued repeatedly that drift is essentially smooth pursuit of a target with zero velocity (de Bie and van den Brink, 1984; Nachmias, 1961; Murphy, Kowler, and Steinman, 1975). Following this idea, goal locations represented in the SC may also result in systematic drift movements in the presence of a stationary target (Rolfs, 2009).

I conclude that a contribution of microsaccades is not a necessity for accurate fixation when observers try to hold their eyes as still as possible, however, they are clearly a significant source of position correction during visual fixation. Based on several lines of evidence I argue that microsaccades and drift serve the same behavioral goal, potentially implemented by a common neurophysiological machinery.

2.3. Prevention of perceptual fading

2.3.1. Perceptual fading

In the early 1950s of the last century, scientists developed clever techniques to largely counteract image motion with respect to the eye. The results of these studies were striking, showing that the visual world fades from view within a few seconds (Ditchburn and Ginsborg, 1952; Pritchard, 1961; Pritchard, Heron, and Hebb, 1960; Riggs and Ratliff, 1952; Riggs et al., 1953; Yarbus, 1957a, 1957b; Heckenmueller, 1965, extensively reviews these early findings). The disappearance times reported in these early studies, however, have to be interpreted with caution, since the stabilization methods used may have been faulty to some extent (cf., Barlow, 1963), e.g., due to slippage of the contact lens.⁷ Later studies used retinal stabilization techniques that made entoptic structures visible to the viewer (Campbell and Robson, 1961; Sharpe, 1971). These structures are part of the eye itself, hence, virtually perfectly stabilized with respect to the retina. In one of the first of these efforts, Ditchburn, Fender, Mayne, and Pritchard (1956) produced a stabilized retinal image of the retina itself. Ratliff (1958) proposed to take advantage of the phenomenon of “Haidinger’s Brushes”, entoptic images that can be seen by simply looking through a polarizer at a field of blue light. Interestingly, the perception of these brushes is transient as it would be expected from retinal stabilization studies. The same is true for Maxwell’s spot and a visual phenomenon reported by Shurcliff (1959), which he called the “greenish-yellow blotch”. Shurcliff (1959) had 110 observers viewing a uniformly colored field. Ninety-five of them reported that the perception of the field suddenly becomes broken up into blotchy areas of two very different colors—mostly in the range between yellow and green. After a few seconds, this pattern disappears, supposedly, because its position is stable with respect to the perceptual system (Alpern, 1972).

⁷ Barlow (1963) originally raised the debate about the quality of retinal stabilization using different techniques mainly because some authors reported that faded images reappear again after a few seconds, then to fade repeatedly (Barlow, 1963; Ditchburn, 1955; Ditchburn and Fender, 1955; Ditchburn, Fender, and Mayne, 1959; Ditchburn and Ginsborg, 1952; Ditchburn and Pritchard, 1956; Pritchard, 1961; Pritchard et al., 1960; Riggs and Ratliff, 1952; Riggs et al., 1953). Barlow (1963) argued that this effect may be caused by slippage of the contact lens attached to the eye. The author showed that under thorough control reappearance effects were much weaker and images did never reappear in all detail. The debate has not been settled (e.g., Arend and Timberlake, 1986; Ditchburn, 1987; Evans, 1965), first of all, because authors using suction caps to secure a strong attachment of the contact lens to the eye did not report reappearance of disappeared images (Gerrits, de Haan, and Vendrik, 1966; Yarbus, 1957a, 1957b), while afterimages of light flashes (which are most certainly fixed with respect to the retina) were observed to reappear after disappearance (e.g., Bennet-Clark and Evans, 1963).

Other authors used the shadow of blood vessels of the retina as visual stimuli, replicating the phenomenon of visual fading (von Helmholtz, 1924; Campbell and Robson, 1961; Drysdale, 1975; Sharpe, 1972). Again, the image faded over intervals of several seconds. Finally, using a very sophisticated illumination technique, Coppola and Purves (1996) demonstrated more recently that entoptic images of the finest blood capillaries disappeared in less than 80 ms on average, indicating that an active mechanism of image erasure and creation might be the basis of normal visual processing. Converging evidence for rapid image fading was contributed by Rucci and Desbordes (2003) who had observers judge the orientation of low-contrast bar stimuli embedded in noise that were presented for half a second through an optical-electronic device, coupling a Dual-Purkinje eye tracker and a stimulus deflector to achieve retinal stabilization. Although observers probably never experienced subjective disappearance of these short-lived stimuli, a substantial drop in performance was still observed. These retinal stabilization studies reinforce the idea that our nervous system has evolved to optimally detect changes in our environment. As a consequence, unchanging aspects of the visual field fade from view. To counteract this, our retinas have to move with respect to the visual surrounding. This strongly suggests that eye movements are essential to sustain visual perception during fixation.

All of the studies reported above, however, took place under typical, rather artificial laboratory conditions, which were arguably ecologically invalid. Movements of the head and the torso were minimized by use of chin rests, bite boards, cheek pads, and so forth, and subjects were usually required to maintain fixation for the entire duration of the stabilization procedure. This raised doubts in the significance of their results in understanding the maintenance of visual perception in natural situations (Kowler and Steinman, 1980; Steinman, 2003; Steinman et al., 1973). Therefore, Skavenski, Hansen, Steinman, and Winterson (1979) examined retinal image motion under conditions of small natural and artificial body rotations. The authors reported substantial motion of the retinal image. A good deal of the body and head rotations was compensated for by eye movements (up to 90%), however, considerable retinal image motion remained—clearly more than under conditions of head fixation. Skavenski et al. (1979) argued that these additional movements could be sufficient to prevent any retinal fatigue. Indeed, earlier studies had shown that if the effect of FEyeM on retinal image motion was optically amplified by a factor of two, virtually no perceptual fading of visual stimuli could be observed (Riggs et al., 1953) and small differences in contrast were detectable as under unconstrained viewing conditions (Clowes, 1961). In fact, van Nes (1968) found improved image visibility when regular motion was added to the naturally occurring eye movements during fixation. The results by Skavenski and his colleagues were confirmed under even more natural conditions—during active head rotations (Ferman, Collewijn, Jansen, and van den Berg, 1987; Steinman and Collewijn, 1980; see also Steinman and Collewijn, 1978) and when participants were involved in an active motor task (Epelboim, 1998).

Clearly, these papers were of outstanding interest to the field, since they first examined image visibility under more realistic conditions. The important conclusion to be drawn from these is that oculomotor compensation for body and head rotations does not aim to achieve retinal image stabilization; rather it appears to adjust retinal image motion so as to be optimal for continuous visual processing under the range of natural body movements. The reported results, however, are not entirely conclusive with regard to the purpose of FEyeM, since these still took place in these studies. To date no systematic study (known to the author) eliminated FEyeM but provided an image to the retina that followed the motions of the head, a condition that may disentangle the importance of both eye and head movements in the maintenance of visual per-

ception. However, two anecdotal findings bear directly on the question. First, in his venturesome experiments on visual perception during muscular paralysis, Stevens et al. (1976) experienced perceptual fading when the whole body was paralyzed, but not, if only the eyes were paralyzed with a local anesthetic. The most straightforward explanation of this difference is that residual motion of the retinal image due to direct or indirect movement of the head prevented retinal adaptation. Second, in subject AI who was born without the ability to move her eyes, Gilchrist, Brown, and Findlay (1997) have found that saccade-like movements of the head emerged as her strategy to scan visual scenes. Indeed, eye-movement recordings revealed only very constrained drift, but during fixation, continuous drifts of the head were observed (Gilchrist et al., 1997, Gilchrist, Brown, Findlay, and Clarke, 1998). In fact, in visually-mediated action tasks (e.g., making a cup of tea), AI let her eyes drift over an object at speeds up to 30°/s, presumably, because of the effort associated with head saccades and, certainly, at the cost of visual resolution (Land, Furneaux, and Gilchrist, 2002). Based on these findings, it appears that saccades (and microsaccades) are the preferred sampling strategy of the visual system (Otero-Millan et al., 2008). Drift movement of the head or the eyes, however, may suffice to prevent perceptual fading.

2.3.2. Contribution of different types of FEyeM

Assuming that FEyeM help to counteract retinal adaptation, it remains to be known which part of the motion contributes to this function. Ratliff and Riggs (1950) computed the amount of image motion, FEyeM produce with respect to the photoreceptors on the retina. They found that drift movements cover up to a dozen photoreceptors. Equally, microsaccades carry the retinal image over a dozen or more receptor cells, depending on the movement amplitude. Tremor, in contrast, rarely exceeds amplitudes that correspond to one retinal photoreceptor. Thus, while drift and microsaccades produce retinal image motion that might have a sensible effect on visibility, the importance of tremor in this regard appeared unlikely (Ditchburn, 1955; Krauskopf, 1957; Sharpe, 1972; Tulunay-Keeseey and Riggs, 1962), unless it exceeded amplitudes of 0.3 min-arc and there is a summation of eye movements over the whole frequency spectrum (Ditchburn et al., 1959). In addition to these spatial aspects, tremor's temporal characteristics—its frequency is far above the flicker-fusion frequency of the human visual system—have raised further doubts in the significance of this motion for visibility (Ditchburn, 1955; Gerrits and Vendrik, 1970; Yarbus, 1967). Recently, however, Greschner, Bongard, Rujan, and Ammermüller (2002) reported that ganglion cells in the turtle retina were most effectively synchronized with imposed periodic low-amplitude motion similar to tremor (but at a much lower frequency). Moreover, synchronization of cell-firing was shown to improve the estimation of the spatial frequency of stimuli. The authors concluded that periodic motion could advance stimulus feature estimation by the brain. In monkeys, Martinez-Conde, Macknik, and Hubel (2002) incidentally noticed that the activity of cells in the lateral geniculate nucleus, an early stage in the visual processing pathway of the brain, followed the refresh frequency of the monitor used for stimulus presentation (74 Hz). Thus, at early stages in human visual processing even tremor might play a role (cf., Martinez-Conde et al., 2004). Indeed, an increasing amount of psychophysical, neurophysiological, and modeling studies seem to support this view (Funke, Kerscher, and Wörgötter, 2007; Hennig, Kerscher, Funke, and Wörgötter, 2002; Hennig and Wörgötter, 2004; Segev, Schneidman, Goodhouse, and Berry, 2007; Wallis, 2006). Here, I will focus on the role of drift and microsaccades in the maintenance of perception.

One method to examine the importance of different types of FEyeM for visibility is to eliminate them by means of retinal stabilization and then impose controlled movements with certain char-

acteristics. To my knowledge, the first manuscript describing this approach was published by Krauskopf in 1957.⁸ It was soon commonly used in a number of studies. The findings revealed, however, were partially controversial.

Under conditions of retinal stabilization, Krauskopf (1957) introduced vibrational sinusoidal movements with amplitudes of 0.5–4 min-arc to the retinal image and varied their temporal frequencies. He found that movement frequencies of 1, 2, and 5 Hz decreased contrast thresholds when the movement amplitude was at least 1 min-arc; thus, these movements were beneficial for vision. In contrast, higher frequencies (10, 20, and 50 Hz) were detrimental for perception when compared to an image stabilized on the retina. He speculated that both drift and microsaccades could contribute to image visibility, but conceded that the motion induced in his study was largely artificial.

Subsequent studies corroborated Krauskopf's general findings. Tulunay-Keeseey and Riggs (1962) imposed oscillatory motion of different frequencies and amplitudes to an image otherwise stabilized with respect to the retina. Imposed motion was effective in increasing visibility times of their Mach-band stimuli, but only if it had a low frequency (about 3 cycles/s) and a large amplitude (greater than 1 min-arc/s). In a setup by Yarbus (1959), a glass capillary was mounted onto a suction cap attached to the eye ball. Opaque fluids carrying an air bubble were moved through this capillary at different speeds. Yarbus (1959) showed that velocities of down to 3–5 min-arc/s prevented stimuli from disappearing, which under conditions of retinal stabilization had faded from perception. Similar conclusions could be drawn from a study by Fiorentini and Ercoles (1957), who imposed oscillatory motion to Mach band stimuli without making use of retinal stabilization, but controlling for FEyeM statistically.

Ditchburn et al. (1959) studied image visibility while imposing motion imitating drift, microsaccades, and tremor, respectively, on an otherwise stabilized image. Visibility of faded images was not improved when imposing drift motion or tremor by themselves. In contrast, simulated microsaccades strongly regenerated faded images to a very sharp percept which then faded again. It was concluded that microsaccades play a role in the maintenance of vision, but that the system cannot rely on these movements alone. At the time, Ditchburn's proposal was supported by several findings. For instance, Clowes (1962) showed that microsaccade rates were greatly increased in an effort to counteract fusion of equiluminant colors presented side by side at foveal vision (see also McCree, 1960). In turn, microsaccades were found to be infrequent when no stimulus was presented (Cornsweet, 1956; Matin et al., 1970; Nachmias, 1961; Otero-Millan et al., 2008; Skavenski and Steinman, 1970), but see (Fiorentini and Ercoles, 1966; Skavenski and Steinman, 1970).⁹

Therefore, in a later study, Ditchburn, Drysdale, and Drysdale (1977a) investigated effects of step and pulse movements on the visibility of stimuli stabilized with respect to the retina. Step movements displaced the target abruptly to a new position, where it then remained. These movements clearly resulted in a sudden reappearance of a faded stimulus. The gain in visibility was a function of movement amplitude, with largest movements (24 min-arc) increasing visibility of the target most effectively and over long periods of time (up to 70 s). Pulse movements, also displaced the retinal image to a new position, however, returned it to the ini-

⁸ Krauskopf (1957) acknowledges an earlier paper delivered by T.N. Cornsweet and L.A. Riggs at the Eastern Psychological Association Meeting in 1954. According to Krauskopf (1957), the results of these authors were in good agreement with his own.

⁹ Note, however, that there are also some observers exhibiting higher rates of microsaccades in the dark (Fiorentini and Ercoles, 1966; Skavenski and Steinman, 1970), which may be attributed to differences in individual drift rates and a corresponding need to redirect gaze to its initial position (Skavenski and Steinman, 1970).

tial position after a variable delay. Pulses did not notably enhance perception when return times were below 8 ms. The authors argued that at such short times, the signal must be completely temporally integrated on the level of photochemical processes in the receptors. The integration time appeared to be directly determined by neural processes accumulating just sufficient information to extract a signal from a background of photon noise. In a second paper, the consequences of oscillatory movements imposing sinusoidal, square-wave and triangular-wave motion of different frequencies and magnitudes were examined (Ditchburn, Drysdale, and Drysdale, 1977b). Imposed movement had two opposite effects on the visibility of stimuli. First, visibility was increased due to fluctuations caused by the movement. Second, it was decreased by blurring stimulus boundaries. The parameters of the movement that optimally enhanced visibility depended on the characteristics of the stimulus, in detail, its contrast and the sharpness of its boundaries. Appreciable enhancement of perception was achieved with movement amplitudes of about 20 min-arc and frequencies of around 5 Hz. Movement of a small extent and with temporal frequencies below 0.5 Hz was found to be detrimental to perception, as were frequencies well above the flicker-fusion frequency. The authors concluded that all three components of FEyeM microsaccades, drift, and tremor probably contribute to the maintenance of perception during fixation. In a natural visual scene which includes contrasts of all levels and different types of gradings at boundaries, however, drift and tremor might not suffice to provide a basis for good vision. Microsaccades may, first of all, ensure that stimuli with low contrast or graded boundaries are continually restored.

The findings of Ditchburn and his colleagues were partially challenged by the work of Gerrits and Vendrik (1970, 1974). In their experiments, an object was mounted in the rotor of a small electric motor, directly attached to the eye by means of a cap sucked onto the cornea. In this way, stimuli could be presented that followed a predefined movement paths. The first of these two studies used regular rotational movements to simulate fixational drift, microsaccades, and high-frequency tremor. This study revealed that only continuous, drift-like motion effectively restored vision of a faded object (Gerrits and Vendrik, 1970). These findings were extended using a more flexible stimulation method (Gerrits and Vendrik, 1974). Now, stimuli could be controlled to an extent that imposed movements were very similar to real microsaccades and drifts, which are neither regular nor rotational. Moreover, not only foveal but also parafoveal vision could be examined. Normal continuous vision was found only when the stimulus moved continuously and irregularly, i.e., if movement direction continuously changed. Since only ocular drift possesses both these characteristics, it was concluded that these movements account for most of the effectiveness of FEyeM in the maintenance of visual perception. If at all, microsaccadic movements would help to improve perception of stimulus features in parafoveal and peripheral areas (Gerrits and Vendrik, 1974). Gerrit and Vendrik's results were corroborated by a series of experiments by Kelly and his colleagues, carefully studying the effects of retinal image motion on contrast thresholds (Kelly, 1979a, 1979b, 1981; Kelly and Burbeck, 1980). Using the method of adjustment with indefinite viewing time, contrast thresholds for luminance gratings stabilized on the retina were increased to about a 30-fold; for chromatic gratings detection was impossible even at the highest contrast, meaning an >45-fold increase in color contrast thresholds (Kelly, 1981). Contrast sensitivity was restored when continuous retinal image motion in the velocity range of fixation drift movements was artificially imposed (Kelly, 1979b, 1981). Microsaccade rates had previously been shown to increase when observers viewed luminance defined stimuli close to foveal threshold (Steinman and Cunitz, 1968) or chromatic bipartite fields under condi-

tions of retinal stabilization (Clowes, 1962). Based on Kelly's and Gerrits and Vendrik's results, however, drift was now thought to play the most significant role in the continuous maintenance of visual perception during fixation. As a consequence of these accumulated data, the results of Ditchburn et al. (1959, 1977a, 1977b) emphasizing that microsaccades can restore visibility in case of perceptual fading, were eclipsed.

Additional doubts regarding the significance of microsaccades for visual perception emerged for at least three reasons. First, microsaccades (as all saccades) may cause saccadic suppression, i.e., they are accompanied by a strong elevation of the perceptual threshold. This was first noted by Ditchburn (1955) and later examined in more detail (Beeler, 1967; Zuber et al., 1964; Zuber and Stark, 1966).¹⁰ Second, foveal vision of stimuli did not deteriorate notably in situations where microsaccades were effectively inhibited (Steinman et al., 1967). Rather, microsaccades were suppressed if high foveal acuity was required to perform accurately in observational (Bridgeman and Palca, 1980) and finely-guided visuo-motor tasks (Winterson and Collewijn, 1976). Third, there was evidence that the occurrence of a microsaccade is not locked to the disappearance of a stabilized image (Cornsweet, 1956, recently replicated and extended in a so far unpublished study by Poletti and Rucci, 2007). Finally, as mentioned above, it had become very clear that in natural vision there is no lack of retinal image motion (see Collewijn and Kowler, 2008, for a recent review).

How can we integrate the large body of evidence reviewed in this section? Human visual perception relies upon constantly changing input. Preventing such changes results in rapid fading of the image falling onto the retina. According to one view, fading of peripheral vision may be desirable in tasks requiring continuous fixation of a foveal object to prevent distraction from peripheral vision (Collewijn and Kowler, 2008). Alternatively, the absence of changes in static parts of a visual scene, must be compensated for by eye movements taking place during fixation. Evidence accumulates that both drift and microsaccades are necessary to achieve continual perception during fixation. The efficacy of different types of FEyeM in the preservation of a stable percept depends on the location and the characteristics of the stimulus content in the visual scenery. Recently, it has been shown that drift movements causing low retinal image slip precede a higher rate of microsaccades (Engbert and Mergenthaler, 2006), clearly increasing variance in the visual input signal. Thus, the dynamic interactions of drift movements and microsaccades might constitute the basis for sustained visual perception during fixation. This finding may account for the strong interindividual variability found in fixational eye-movement patterns, i.e., microsaccade and drift rates. Future studies will have to examine whether changes in the visual input result in less effort of the eyes to move during fixation, which would be predicted if the need for a changing retinal image drives FEyeM. The strong inhibition of microsaccades following perceptual events (e.g., Engbert and Kliegl, 2003b, see also section 2.7 below) may well be a fingerprint of the interplay between active and passive stimulation. In addition, there is substantial retinal image slip provided by head and body movements, but its unique contribution to perception is yet to be shown. Receptive fields in the visual periphery are considerably larger than those in the fovea. When head and body movements are less prominent, only microsaccades will be able to produce noticeable effects and sustain per-

¹⁰ Krauskopf, Graf, and Gaarder (1966) found no difference comparing detection thresholds during and 50 ms after microsaccades, however, according to the experiments by Zuber and Stark (1966) and Beeler (1967) saccadic suppression may still be strong at that time. For one participant, Krauskopf et al. (1966) compared thresholds directly after the microsaccade and 200 ms later. The observed numerical difference between thresholds in the two time windows was not statistically reliable. Thus, in face of the conflicting positive evidence, this null-result is subject to appeal.

ception in these regions, whereas drift movements might generate sufficient image motion to restore vision in the fovea (as might microsaccades in the absence of drift, [Martinez-Conde et al., 2004](#)).

2.4. Generation of visual transients

There is more to microsaccades than just adding to the image motion on the retina. Microsaccades change the retinal image abruptly, producing a sudden transient in the visual input stream. Indeed, transient visual stimulation has been used heavily in the visual sciences and its strong impact on visual perception is undoubted. However, such flashes of light rarely occur in the natural environment. [Armington \(1977\)](#) acknowledged this imbalance between scientific practice and nature. He emphasized, however, that transients certainly occur as a result of eye movements that translate the retinal image several times per second. Thus, microsaccades may implement a mechanism to provide the visual system with transient stimulation and, therefore, play a significant role in visual perception.

2.4.1. Physiological concomitants

In a pioneering study using the combined measurement of eye movements and electroencephalograms (EEG), [Gaarder, Krauskopf, Graf, Kropfl, and Armington \(1964\)](#) showed that the retinal image shifts accompanying microsaccades induce strong visual responses in the human brain. Subjects continuously fixated foveally presented stimuli of varying luminance contrast. Microsaccades elicited strong visual responses on occipital electrodes, composed of a negative wave followed by a positive one. These responses were clearly visual (and not the result of the motor processes involved in microsaccade generation), because their amplitude increased with stimulus contrast while the latency of the initial negative component decreased. The authors realized that changes in the visual input are necessary to evoke visual responses in the human brain and proposed that vision is based on discontinuous bursts of activity in the nervous system. These results anticipated much of the literature published in the 1990s and 2000s on microsaccade-related visual responses in the monkey brain (see below). Yet, neither this work nor the follow-up studies by [Gaarder and his colleagues \(Armington, Gaarder, and Schick, 1967; Armington and Bloom, 1974\)](#) have ever been considered in the literature on the purpose of microsaccades.

Building up on these findings, [Armington et al. \(1967\)](#) presented their observers with striped patterns and recorded occipital EEG and electroretinograms (ERG) in response to microsaccadic eye movements. Based on amplitude values of microsaccades reported in the literature (amplitudes could not be distilled in their own measurements) and their correspondence to the grid stimuli used in their study, the authors argued that the retinal image shift induced by microsaccades accounts well for their effects. Direct evidence for this idea was reported in a follow-up study, using the setup shown in [Fig. 5](#) to simultaneously record eye movements, ERG, and EEG. [Armington and Bloom \(1974\)](#) had participants fixate the center of a large circular stimulus consisting of a stripe pattern (see [Fig. 5A](#)). Spatial frequencies of the stripes ranged from 0.47 to 4.55 cycles per degree (cpd). In general, as shown in [Fig. 5B](#), responses in the ERG were of larger amplitude than those in the EEG measurements, but both linearly increased with the amplitude of triggering microsaccade. In addition, larger responses were observed for patterns of fine stripes, i.e., high spatial frequencies, if microsaccade amplitude was controlled for. These results indicate that larger changes of the retinal input across a saccade result in stronger neuronal responses. Following this idea, microsaccades shifting the retinal image by a grating's full cycle should hardly produce a change in the stimulus and, thus, a minor response.

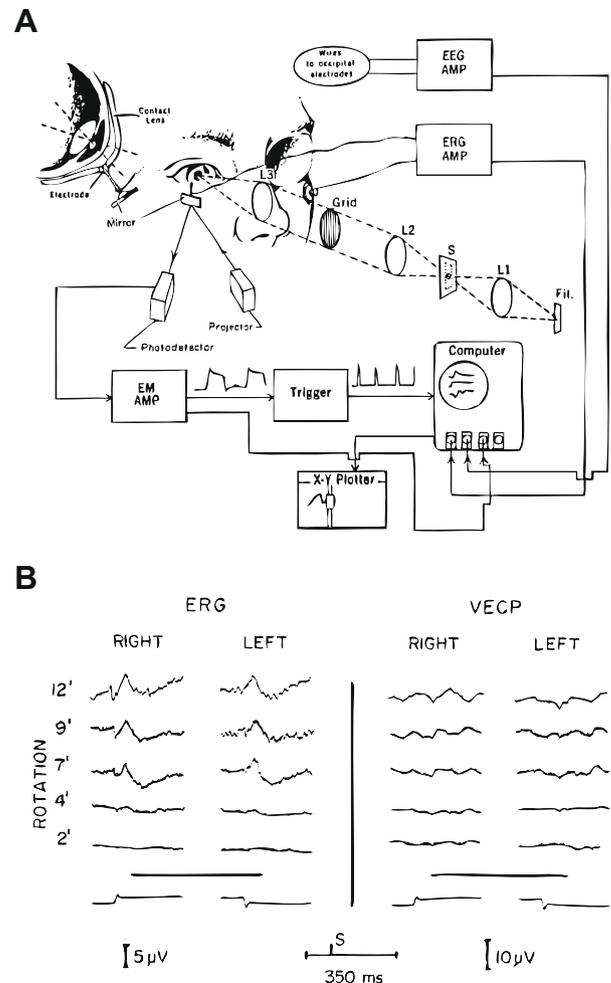


Fig. 5. Microsaccade-evoked brain potentials. (A) Setup used by [Armington and Bloom \(1974\)](#) to record FEyeM, ERG, and EEG simultaneously. (From [Armington, 1977](#).) (B) Average ERG and EEG activity following microsaccades of different amplitudes (labeled eye rotation). Data were analyzed separately for microsaccades to the left and to the right. The EEG data are entitled VECP (visually evoked cortical potential). (From [Armington and Bloom, 1974](#).)

However, too few large saccades were observed in their sample to test this hypothesis.

The findings of [Gaarder, Armington, and colleagues](#) have been replicated and extended to other stimulus configurations in more recent EEG ([Dimigen, Valsecchi, Sommer, and Kliegl, in press](#)) and functional magnetic resonance imaging studies ([Tse, Baumgartner, and Greenlee, 2007, 2009](#), see also, [Greenlee and Tse, 2008](#)). [Dimigen et al. \(in press\)](#) emphasized implications for the interpretation of human physiological data, which are usually collected under the assumption that all eye movements are precluded by the instruction to fixate. In combination with the fact that the occurrence of microsaccades is strongly influenced by a broad range of experimental factors, microsaccade-triggered EEG components may systematically alter results obtained with these methods. A similar problem has been identified by [Yuval-Greenberg, Tomer, Nelken, and Deouell \(2008\)](#), who showed that the broadband induced gamma-band response in the EEG, which has been linked to many aspects of cognitive processing (attention, memory, object recognition, etc.), is a reflection of muscle spikes that reliably accompany microsaccades in the EEG signal. Since systematic variations in microsaccade statistics are commonly observed in many experimental situations (see [Section 2.7](#)) and may exhibit fairly different time courses depending on stimulus properties

(e.g., Rolfs et al., 2008a, see Fig. 8B in Section 2.7) and the task (e.g., Valsecchi, Betta, and Turatto, 2007), microsaccadic spike potentials will have affected previous reports of induced gamma-band responses in the EEG (Yuval-Greenberg et al., 2008; Fries, Scheeringa, and Oostenveld, 2008). These results have set off an avalanche of bewilderment in the EEG community as exemplified by a large number of online comments at the journal's website and a heated discussion of the findings in the current literature (e.g., Melloni, Schwiedrzik, Wibral, Rodriguez, and Singer, 2009b; Yuval-Greenberg, Keren, Nelken, and Deouell, 2009). Certainly, this community will benefit from the existing body of literature on microsaccades, as will the study of microsaccades from the necessity to record FEyeM in future human brain imaging studies.

Strong support for microsaccade-related genuine brain activity in the visual cortex has been obtained in electrophysiological studies of the monkey brain. Indeed, these findings contributed strongly to the revival of the study of microsaccades several years ago (see Fig. 2). Monkeys are an ideal model for investigating the impact of FEyeM in the human brain, since their fixation behavior is very similar to that of human observers (Motter and Poggio, 1984; Skavenski et al., 1975; Snodderly, 1987; Snodderly and Kurtz, 1985; overview in Martinez-Conde et al., 2004). It is known that the erratic motion of the retinal image that is caused by FEyeM contributes to the variability of cortical activity, which can be attributed to the movement of cortical receptive fields with respect to the visual world (Gur and Snodderly, 1987; Gur and Snodderly, 1997; Snodderly, Kagan, and Gur, 2001). In particular, microsaccades raise responsiveness to visual stimulation in a number of brain areas involved in visual information processing, as revealed by single-cell recordings in monkeys. These areas include the lateral geniculate nucleus (Martinez-Conde et al., 2002), V1 (Kagan, Gur, and Snodderly, 2008; Martinez-Conde, Macknik, and Hubel, 2000, 2002; Martinez-Conde, 2006; Snodderly et al., 2001 but see Leopold and Logothetis, 1998), V2 (Leopold and Logothetis, 1998), V4 (Leopold and Logothetis, 1998), and MT (Bair and O'Keefe, 1998). No microsaccade-related modulation of neural activity was observed in area IT (Leopold and Logothetis, 1998). In addition, several studies suggested microsaccade-related extraretinal influences on neural activity in V1, i.e., a change in firing rate unrelated to visual input (e.g., in the dark) (Leopold and Logothetis, 1998; Snodderly et al., 2001; Kagan et al., 2008).

Neural activity has also been related to the slow components of FEyeM. Snodderly et al. (2001) monitored firing rates during periods not containing any microsaccades, that is, when the eye is slowly drifting; other studies used these intervals simply as a baseline reference. Based on their measurements, Snodderly et al. (2001) proposed the subdivision of V1 neurons into cells that are driven by (a) saccades sweeping a stimulus onto, off, or across their receptive field (saccade cells), (b) receptive field position over the stimulus or drift movements (position/drift cells), or (c) all of these (mixed cells). It was argued that these distinct firing behaviors of cells could implement different functional purposes of the visual system, such as the coding of spatial details and saccadic suppression. Thus, there might be a continuum of neural activity in the visual cortex associated with FEyeM. To examine responses in drift periods and the amount of extraretinal signals conveyed by microsaccades in more detail, the same group recently examined a large sample of V1 neurons in an elaborate follow-up study (Kagan et al., 2008). Again, three types of cells were distinguished: saccade cells, drift/position cells and mixed cells. Saccade cells showed transient bursts of activity after microsaccades but no response to drift. Indeed, these transient responses were qualitatively comparable to those after the presentation of flash stimuli or stimuli moving at a high speed. In about 1/3 of their saccade cells, extraretinal modulations were observed, consisting of a weak initial suppression and a strong subsequent enhancement. This result may account

for discrepancies between earlier reports (Leopold and Logothetis, 1998; Martinez-Conde et al., 2002). Kagan et al. (2008) also compared responses to microsaccades to those after voluntary saccades. Very similar results were obtained for both. Position/drift cells, in turn, did not increase firing rates after saccades. Instead, they showed sustained responses during drift periods, had often smaller receptive fields and were sign-of-contrast selective. The responses of these cells to drift were very similar to those to slow continuous stimulus motion. Mixed cells, finally, showed both response patterns, transient bursts after saccades and sustained discharges during drift. These results suggest that motion-dependent neuronal responses in V1 can be explained in a single framework, irrespective of whether it was generated by FEyeM or imposed by external movement. Based on their results the authors conclude that microsaccades and saccades have the same consequences for visual processing. In addition, drift provides sustained responses in a sub-population of V1 neurons. In combination, drift and saccades ensure continuous visual experience.

In a series of prominently published, but little-noticed articles, Kenneth Gaarder put forward an explicit model proposing what information microsaccade-related brain activity contains. He proposed that the transfer of edge information in the visual system is mediated by microsaccades (for an overview see Gaarder, 1967). In an early study, Gaarder (1960) observed that microsaccades are systematically altered by the currently viewed image (see Fig. 6A), anticipating many of the more recent results in the field. This finding was subsequently replicated and extended with more participants and experimental conditions (Gaarder, 1967). Based on these results, Gaarder (1966b) proposed a model according to which discontinuous input of edge information is achieved by microsaccades. Specifically, due to the net change of the retinal activation pattern, each microsaccade establishes a unique set of edge information, mainly based on its direction, but also on its magnitude. The general idea is illustrated in Fig. 6B and C. Gaarder's finding that microsaccades generate strong transient responses in the occipital cortex (Armington et al., 1967; Gaarder et al., 1964) suggested a physiological mechanism implementing the transmission of this information in the visual system and supported the idea of the discontinuous nature of these processes. In an extension of his model, Gaarder (1967) proposed that the retinal activity bursts generated by microsaccades are stored as templates and cycled in short-term memory. These templates would be very similar for a given fixation, but sufficiently unique to complement each other, to finally organize a percept. It was proposed that the cycling of templates is related to the occipital alpha rhythm (Gaarder, Koresko, and Kropfl, 1966). Combining behavioral and physiological data acquired in an ahead-of-the-time setup for simultaneous recordings of eye movements and EEG, Gaarder's and Armington's work on the purpose of microsaccades is intriguing and notable for its theoretical specificity. Their work should take a prominent place in the literature on microsaccades.

More recently, several other mechanisms have been put forward, how sensory processing may benefit from microsaccade-related transient responses in the visual system. MacEvoy, Hanks, and Paradiso (2008) proposed that both saccadic suppression and post-saccadic enhancement assist the effort of the visual system to maintain perceptual stability across saccades, the first by filtering retinal smear during the saccade, the latter by emphasizing sources of reliable information.¹¹ In neurons in the LGN and the primary visual cortex Martinez-Conde et al. (2000, 2002) found that microsaccades were better correlated with bursts of spikes than with single spikes or the instantaneous firing rate of neurons. Similar bursts of activity have

¹¹ This proposal was made in a study of large saccades, but also applies to microsaccades.

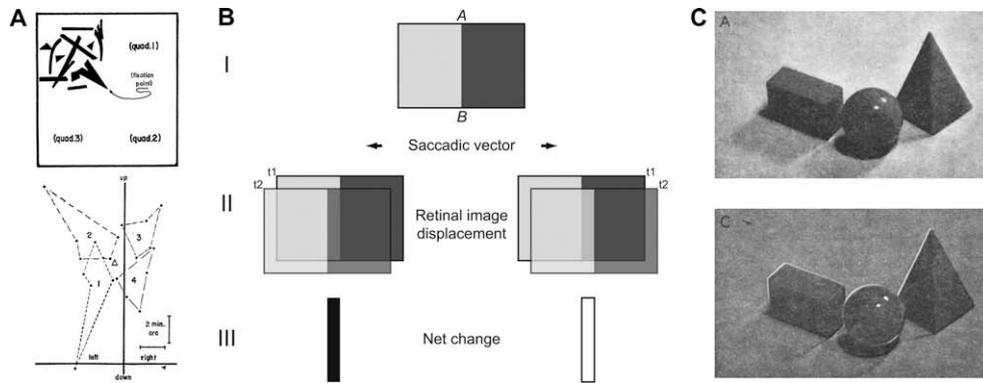


Fig. 6. *Microsaccades and edge processing.* (A) A stimulus used by Gaarder (1960) is shown in quadrant 4 of the upper diagram. The lower panel shows the distribution of mean saccade vectors in response to stimuli presented in either of the four quadrants. Microsaccades varied systematically as a function of visual display. (From Gaarder, 1960.) (B) (I) Diagram of a segment of an edge (between A and B) falling on the retina. (II) Displacement of the edge by a saccadic vector occurring between time t_1 and time t_2 . (III) Net change produced by the microsaccade. (Reproduced from Gaarder, 1966b.) (C) Simulation of retinal image edge generation by microsaccades. The upper picture shows the stimulus. The lower picture highlights the net changes at the object contours. The arrow represents the direction of the microsaccade. (From Gaarder, 1966b.)

been found in V1 single-cell studies in freely viewing monkeys (Livingstone, Freeman, and Hubel, 1996; Martinez-Conde, 2006). Martinez-Conde et al. (2000, 2002) proposed that bursts of spikes might be most reliable as neural signals for visibility, allowing microsaccades to provide a reinforcing signal of the stationary input.

Based on their results of enhanced responses of neurons throughout areas in the visual cortex, Leopold and Logothetis (1998) discussed that microsaccades may affect the synchronization of activity across these areas (see also Purpura, Kalik, and Schiff, 2003; Sobotka, Nowicka, and Ringo, 1997). In their study, early visual areas were most strongly affected by microsaccades, whereas higher visual areas (like IT) disregarded microsaccades and thus matched perception. Martinez-Conde et al. (2000) extended the synchronization idea and proposed that, due to the synchronization within a level of the processing hierarchy, spatial and temporal summation is facilitated after each microsaccade and then propagated to the next level of processing. These ideas suggest that transients induced by microsaccades may first of all affect the perception of stimuli, for which spatial summation is more likely to be a valuable mechanism (e.g., low-contrast stimuli).

A study presented last year at the COSYNE conference showed that microsaccades indeed relate to synchronization of neural firing across populations of neurons in areas V1 and V4 of the macaque visual cortex. Bosman, Womelsdorf, Desimone, and Fries (2008, 2009) studied local field potentials recorded simultaneously from up to eight electrodes and correlated oscillatory neural synchronization in the Gamma band to the occurrence of microsaccades. In both areas (V1 and V4), strong synchronization followed microsaccades. In addition, synchronization in V4 neurons preceded microsaccades. These results point to the validity of the speculations outlined above and open doors for identifying the role of microsaccades in the generation of neuronal coherence (see Melloni, Schwiedrzik, Rodriguez, and Singer, 2009a, for a discussion of this idea), which might be fundamental for neuronal communication (Fries, 2005).

2.4.2. Perceptual impact

The finding of increased and possibly synchronized neuronal activity in response to FEyeM may provide a physiological mechanism for these eye movements to act on visual processing. However, by itself, it does not bear on their functional role in visual perception. On the contrary, I have reviewed evidence that microsaccades were neither necessary nor sufficient to sustain perception in many cases. Also, microsaccades are not part of a feedback circuit that triggers their generation based on perceptual fading.

In 1986, however, two under-recognized articles by Deubel and Elsner aimed to improve the reputation of microsaccades and argued in favor of their significance for vision. In the task of Deubel and Elsner (1986) participants had to detect low-contrast sine-wave gratings under unconstrained viewing conditions. They found that the detection of low-spatial-frequency gratings (0.5 cpd) was frequently preceded by a microsaccade (see Fig. 7A), indicating the dependence of detection thresholds on the occurrence of involuntary saccades. In fact, as shown in Fig. 7B, microsaccades preceding detection of these gratings by 1000–600 ms had an amplitude distribution centered around 1° of visual angle, i.e., these microsaccades displaced the retinal image by half a phase of the stimulus, applying retinal contrast inversion. In another experiment observers had to report the disappearance of a grating that was initially presented at a high contrast but faded out slowly. In this task, microsaccade amplitudes adapted to the visual stimulus. That is, for 0.5 cpd gratings, microsaccade amplitudes consistently formed a peak at 1° of visual angle (Fig. 7C). Taken together, these results supported the view that microsaccades are an important tool for the visual system to enhance performance in near-threshold detection tasks. Deubel and Elsner agreed with Steinman et al. (1973) that microsaccades indeed can be suppressed in observational tasks without deterioration of the visual capacities; however, if viewers are not explicitly required to do so, microsaccades form a considerable part of their oculomotor activity in such tasks (see also Clowes, 1962).

To examine the plausibility of their psychophysical findings, Elsner and Deubel (1986) created a filter model implementing well-known properties of the visual sensory system. In this model, the effect of saccades on perception was simulated by sharp offsets and—after the duration of the saccade—displaced onsets of the visual scene, reproducing a period of saccadic suppression. The model predicted that saccadic eye movements enhance detection performance of near-threshold patterns. Moreover, the detection performance predicted by the model depended on the congruency of the pattern to be detected and the amplitude of the saccade. Thus, the model's predictions were completely in line with the empirical results by Deubel and Elsner (1986). It is noteworthy that the effect of saccadic suppression—which was previously thought to be detrimental for vision—predicts better perception in this framework, because of the emphasized transient stimulation. These results were consistent with earlier proposals (Ditchburn et al., 1959; Nachmias, 1961) and other empirical findings in detection tasks. For instance, King-Smith and Riggs (1978) reported facilitation effects of a saccade-like square-wave motion (10–

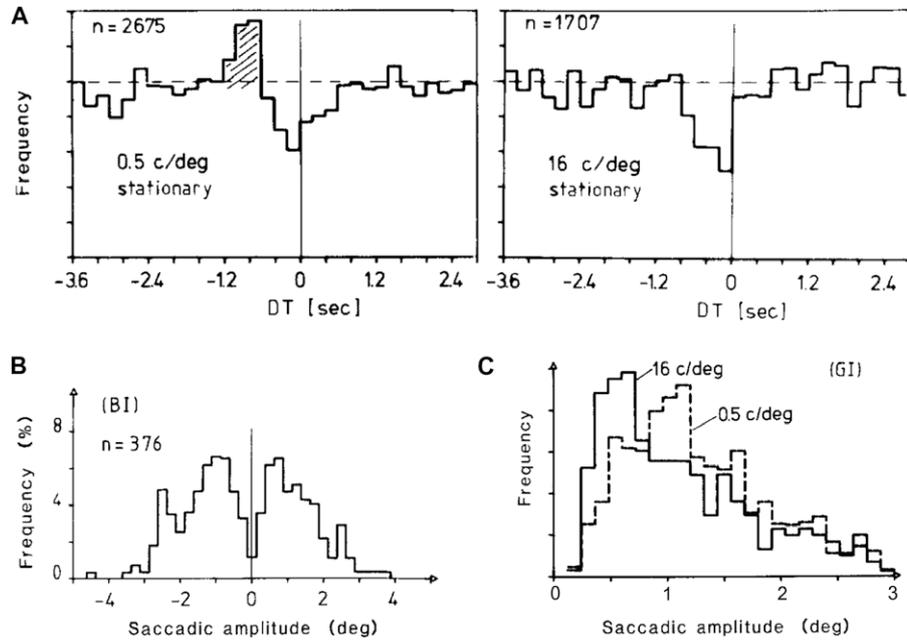


Fig. 7. Microsaccades and the detection of low-contrast gratings. (A) Relative microsaccade frequency locked to the detection of low-contrast gratings of two different spatial frequencies. DT is time relative to the manual response. (B) Amplitude distribution of microsaccades preceding the detection of 0.5 cpd gratings for one exemplary observer. (C) Amplitude distributions of microsaccades on 0.5 cpd and 16 cpd gratings, respectively (see text for details). (From Deubel and Elsner, 1986.)

100 min-arc) in the detection of low-contrast stimuli stabilized with respect to the retina. Moreover, contrast-sensitivity was increased if exaggerated eye movements occurred in detection tasks using high-frequency gratings flickering with high temporal frequencies (Kulikowski, 1971).

Deubel and Elsner (1986) argued that the role of microsaccades might have been obscured in earlier studies, when observation took place under constrained viewing conditions. This consideration might also account for very different contrast threshold functions that were determined in similar tasks by Kelly (1979b) and Koenderink and van Doorn (1979), respectively, the latter study using an unstabilized viewing condition. In fact, several studies had pointed out earlier that a strong increase in contrast thresholds, as those observed by Kelly, can only be observed if contrast judgements are made in the steady state of image stabilization (after long periods of visual fixation). Much weaker or no effects of image stabilization were found if test stimuli had sharp onsets transients (Breitmeyer and Julesz, 1975; Tulunay-Keeseey and Bennis, 1979) and were presented for a 6 ms to 10 s rather than an indefinite period (Tulunay-Keeseey and Bennis, 1979; Tulunay-Keeseey and Jones, 1976).

In addition, various authors raised the proposal that microsaccades might, first of all, enhance perception of stimuli in the visual periphery and parafoveal region (Ditchburn, 1980; Gerrits and Vendrik, 1974; Martinez-Conde et al., 2000, 2004; Snodderly, 1987). This idea would be in agreement with the finding that simulated saccadic displacements greater than 10 min-arc reliably enhance the probability of stimulus reappearance in the Troxler illusion (Clarke and Belcher, 1962), i.e., the disappearance of low-contrast stimuli during normal fixation (Troxler, 1804). To finally test this idea directly, Martinez-Conde, Macknik, Troncoso, and Dyar (2006) studied the relationship between microsaccades and reappearance in the Troxler illusion (see also the comment by Engbert, 2006a). The authors suggested a causal role of microsaccadic activity in the fading and reappearance of Troxler stimuli. Specifically, a higher rate of microsaccades preceded onsets of perceptual visibility. Moreover, the average microsaccade rate prior to an intensifying percept was higher and microsaccade amplitudes ex-

ceeded their average magnitude. In contrast, the average microsaccade rate prior to a fading percept was lower and microsaccade amplitudes fell short of their average magnitude. This potential perceptual function of microsaccades could be demonstrated for various eccentricities, ranging from 3° to 9°, the magnitude of the effects increasing with eccentricity. These effects were replicated under conditions where the head was free to move, i.e., not restrained by a chin rest (Martinez-Conde et al., 2006, experiment 3), contradicting earlier objections that microsaccades do not aid vision in more natural viewing conditions (Kowler and Steinman, 1980; Malinov et al., 2000; Skavenski et al., 1979; Steinman et al., 1973; Steinman and Collewijn, 1980, 2003; Steinman et al., 2003). In a follow-up, Troncoso, Macknik, and Martinez-Conde (2008a) correlated the occurrence of microsaccades to the counteraction of perceptual filling-in of artificial scotomas, implemented by small gray areas embedded in dynamic noise. In this display the gray area is at times visible and at other times perceived to be filled with the background noise. The authors found that the probability of microsaccades was significantly lower just before a perceptual transition to filling-in and much higher before the unfilled region reappeared. These results demonstrate that microsaccades contribute to the visibility of second-order stimuli. Finally, a recent study by Hsieh and Tse (2009) found decreases in microsaccade rate prior to motion-induced blindness, the subjective disappearance of salient visual stimuli embedded in a motion field. Reappearance of these stimuli, in turn, followed significantly increased microsaccade rates.

To sum up, I have argued that microsaccades contribute uniquely to visual processing by creating strong transients in the visual input stream. I have reviewed physiological and psychophysical findings supporting this idea and discussed several theoretical claims arguing for functional significance of these transients. In particular, microsaccades may structure the visual input in an organized fashion if activity across areas is synchronized as a result of each flick of the eye. Psychophysical evidence suggests that a coordinated transient onset may be particularly effective for the detection of stimuli that require summation of signal across space (peripheral input and low-contrast stimuli). These consider-

ations do also provide a framework for understanding the impact of microsaccades in multistable perception, reviewed in Section 2.8. I conclude that microsaccades are a flexible tool in the repertoire of the visual system that contributes to the perception of the visual world, albeit uniquely so only for a share of it.

2.5. Visual acuity

Very early on, it was recognized that motion of the retinal image necessarily has an impact on visual acuity (e.g., Hering, 1899; Jurin, 1738; von Helmholtz, 1924), at least if the motion is greater in extent than the anatomically determined spatial resolution of the retina. In fact, however, humans exhibit extraordinary performance in visual-acuity tasks, far better than predicted by a static mosaic of retinal cones. This characteristic of human vision has been termed hyperacuity. Dynamic theories of hyperacuity in the first half of the 20th century assumed that eye movements during fixation aid visual performance (e.g., Averill and Weymouth, 1925; Adler and Fliegelman, 1934; Marshall and Talbot, 1942). Inspired by these theories, Riggs, Armington, and Ratliff (1954) determined the amount of retinal image motion during fixation. For exposure durations of up to 10 ms the image was found to be virtually stable with respect to the photoreceptors of the retina (motion only rarely exceeded 10 sec-arc). A 100 ms were needed to shift the image over 25 sec-arc, i.e., the diameter of a foveal cone. In 1 s, the eye moved the image by some 3 min-arc. In an overview of the early findings on the relation between FEyeM and visual acuity, Riggs (1965, pp. 341–345) argued that because threshold for visual acuity do not improve for exposure durations longer than 200 ms, visual acuity should hardly be affected by FEyeM.

One method used to test the effect of FEyeM on visual acuity was to vary exposure times of stimuli in high acuity tasks while measuring the extent of retinal motion taking place in these intervals. Ratliff (1952) presented a test stimulus consisting of parallel lines for 75 ms. The tilt of this grating varied across trials and observers had to judge its orientation. Large drift movements and tremor were shown to hinder the judgement. However, Ratliff (1952) admitted that FEyeM could still aid other perceptual acuity tasks, such as the evaluation of straightness of lines, the recognition of simple borders, or the detection of grainy structures. Moreover, the author argued that FEyeM could come into play when longer stimulus exposure durations are needed for perceptual judgments.

A second method used to test the effect of FEyeM on visual acuity was to manipulate their effect on retinal image motion, either counteracting or exaggerating it. Riggs et al. (1953) showed that the counteraction of FEyeM in a retinal stabilization paradigm did not affect visual acuity with exposure durations of up to 110 ms. Rather, there was a slight tendency for better performance in the no-motion condition. As reported above, however, FEyeM were necessary to prevent the image from fading when longer presentation times were applied. These results were followed up in a study by Tulunay-Keeseey (1960). Detection, resolution, and localization tasks (using fine lines, gratings, and vernier offsets, respectively) were performed with different exposure times. Visual acuity was not affected by the exclusion of retinal image motion in any of these tasks. Moreover, exposure times longer than 200 ms did not increase acuity. Thus, retinal motion was neither detrimental nor beneficial for visual-acuity performance in this study. Further, it was concluded that visual fading was too slow to impair visual acuity. In stereoscopic vision, Shortess and Krauskopf (1961) confirmed that FEyeM did not affect visual acuity for exposure durations between 20 ms and 1 s. It appeared that in the visual system FEyeM are implemented such that visual acuity is good while retinal adaptation is properly prevented.

The general impact of FEyeM on visual acuity was continually discussed over several decades and modern approaches again emphasize the role of FEyeM in visual information processing, linking back to the early dynamic theories (e.g., Ahissar and Arieli, 2001; Pitkow, Sompolinsky, and Meister, 2008; Rucci and Casile, 2005). It is beyond the scope of the present work to review the whole body of literature on that topic. Thoughtful resumés of the earlier studies have been drawn elsewhere (e.g., Steinman and Levinson, 1990). A conclusive recent finding, however, should be reported. Using a new and very flexible method of retinal image stabilization (Santini, Redner, Iovin, and Rucci, 2007), Rucci, Iovin, Poletti, and Santini (2007) were able to selectively stabilize the retinal image during fixation and, thus, to study the effect of FEyeM on vision in their natural context, i.e., subsequent to (non-stabilized) saccades. Observers made saccades to a peripheral cue that was then replaced for 1 s by a grating stimulus embedded in noise. In a two-alternative forced-choice task, observers had to judge the tilt of the grating. Comparing stabilized and normal viewing conditions, the authors found that FEyeM improved the detectability of high-spatial-frequency gratings embedded in low-pass filtered noise, but not for low-spatial-frequency grating embedded in high-pass-filtered noise. These results were explained by the fact that FEyeM improve the signal-to-noise ratio for the former, but not for the latter condition. In another experiment, only one component of image motion was stabilized, either that orthogonal to the grating or the one parallel to it. Image motion did only improve performance, if it moved the stimulus perpendicular to the grating. In a control experiment, the passive replay of FEyeM (recorded in previous trials) on an otherwise stabilized retinal image was sufficient to achieve discriminability similar to that during normal vision. Both these results provided strong evidence for their explanation. Unfortunately, however, this study did not examine the different contributions of different types of FEyeM. Although microsaccades did occur in their study and were shown to improve discrimination performance in a precursor study (Rucci and Desbordes, 2003), they may not have been necessary to improve discriminability. Their subject AR, for instance, hardly produced any microsaccades but still showed the perceptual benefit of FEyeM. In the remainder, therefore, I would like to highlight those studies that directly assessed the relation between microsaccades and visual acuity.

Rattle and Foley-Fisher (1968) were the first to report a correlation between microsaccades and visual function. They showed that inter-microsaccade-intervals were directly correlated with performance in a vernier-acuity task. Few microsaccades predicted better performance. The authors suggested that microsaccades put an end to integration periods necessary to resolve fine spatial detail. Obviously then, microsaccades were not beneficial in Rattle's paradigm.

Winterson and Collewijn (1976) assessed the role of microsaccades in finely guided visuomotor tasks. Their participants aimed and shot a rifle or threaded a sewing needle while eye movements were recorded. It was observed, that the frequency of microsaccades decreased strongly during the task as compared to a normal fixation condition. Bridgeman and Palca (1980) studied microsaccades in a purely observational high-acuity localization paradigm, modeled after the needle-threading task. In their task, a vertical line moved along a linear horizontal trajectory towards a horizontal line. The end of the moving trajectory was hidden behind a vertical bar. While fixating the tip of the horizontal line, observers had to judge whether the tip of the vertical line would have ended above or below the horizontal line. Bridgeman and Palca (1980) confirmed the decrease in microsaccade frequency before the judgement and concluded that microsaccades were neither important nor essential in high-acuity tasks. These findings fitted well with the picture of the assumed uselessness of microsaccades, that built up when it was shown that these FEyeM can be suppressed volun-

tarily without noticeable deterioration of visual performance in observational tasks (see above).

This reasoning, however, is by no means compulsory and was subject to several objections. First, *de Bie (1986)* found a small but significant increase in microsaccade rate in two perceptual high-acuity tasks (vernier offset and Landolt C discrimination). The authors were confused about the discrepancy of their result with the earlier findings. They noted that in both studies (*Bridgeman and Palca, 1980; Winterson and Collewyn, 1976*) the task culminated in an expected event (a motor act or the moment of a perceptual event). Therefore, the authors performed a small experiment in which a fixation target was slightly displaced either at a predictable point (3 s after the start of a trial) in time or at random intervals. *de Bie (1986)* found a strong decrease in microsaccade prior to the target step if it was temporally predictable, but a stable rate of microsaccades when the target was displaced at random intervals (see also *Findlay, 1974*). Therefore, the earlier studies might have confounded expectation effects with an active suppression of microsaccades in a high acuity task. Additional concerns with the conclusions drawn from the studies by *Winterson and Collewyn (1976)* and *Bridgeman and Palca (1980)* were raised in a presentation by *Ko, Poletti, and Rucci (2009)* at this year's Meeting of the Vision Sciences Society in Naples, Florida. In a design very similar to that by *Bridgeman and Palca*, the authors showed that microsaccade rates were indeed lower in the virtual threading task than during prolonged fixation, but still much higher than during free viewing. In addition, the rate of microsaccades increased as the needle approached the thread, and microsaccade amplitudes decreased significantly to match the distance between the two objects. This is the opposite of what the earlier studies had reported. Control experiments revealed that this difference to the results by *Bridgeman and Palca (1980)* and *Winterson and Collewyn (1976)* is due to the requirement to fixate and the engagement in an active motor task, respectively, both of which result in a decrease of microsaccade rate (and amplitude) as the needle approaches the thread. Finally, as *Donner and Hemilä (2007)* recently argued, it is crucial in the high-acuity tasks employed by *Winterson and Collewyn (1976)* or *Bridgeman and Palca (1980)* to anchor the percept to a fixed spatial reference frame (see also *Ahissar and Arieli, 2001*). Microsaccades may rather play a role in the localization or discrimination of stimuli if an external reference frame is not required. Indeed, *Donner and Hemilä (2007)* demonstrated in a model study of retinal ganglion-cell responses that microsaccades are ideal candidates for enhancing the spatial resolution of the visual system.

I conclude that the role of microsaccades in high acuity tasks is debatable and carefully designed studies should address the issue in more detail. Flexible retinal stabilization methods have recently been developed (*Santini et al., 2007*) and successfully applied (*Rucci et al., 2007*). These methods can be used in thoroughly controlled experiments with naïve participants and have the potential to disentangle the contributions of different types of eye movements to the changes in performance in high-acuity and other visual tasks.

2.6. Scanning of small regions

The question whether microsaccades play a role in visual acuity is closely related to the proposal that this type of miniature eye movements might resemble attentional shifts scanning confined spatial regions near the target being fixated (*Cunitz and Steinman, 1969; Steinman et al., 1973*). That is, microsaccades might serve the same function as large saccades, namely visual search. For instance, as shown by *Kowler and Anton (1987)*, observers strongly decreased their mean saccade amplitudes when they had to read twisted text. The hypothesis that microsaccades serve the purpose of visual search could also account for fixation errors produced by

microsaccades; remember that microsaccades did not always correct for previous drift movements (*Boyce, 1967*) and if they did, the correction was frequently associated with large errors (*Boyce, 1967; Cornsweet, 1956; Nachmias, 1961; de Bie and van den Brink, 1984*).

Taking a first step to examine the possibility that microsaccades generally obey the same principles as large saccades, *Cunitz and Steinman (1969)* examined frequencies of microsaccades in simple fixation tasks and in reading. Inter-saccade-interval distributions of microsaccades during fixation of a T-shaped stimulus were very similar to those found for reading saccades. Microsaccades, defined by amplitudes smaller than 11.6 min-arc in this study, occurred very rarely during reading fixations (in 2–5%), in these cases doubling fixation durations. That is, microsaccades occurred after and were followed by intervals of a typical reading-fixation duration, implicating that they were observed only in very long fixations. *Cunitz and Steinman (1969)* speculated that both microsaccades and large saccades are controlled by a single system, anticipating later results (*Hafed et al., 2009; Otero-Millan et al., 2008; Rolfs et al., 2006, 2008a, 2008b*). In addition, the authors suggested that both types of movements serve to scan the visual scene, though on different spatial scales.

Some more facts may be worth noting. *Wyman and Steinman (1973)* demonstrated that position errors, which were produced by target steps as small as 3.4 min-arc, can be reduced by small voluntary saccades, suggesting once more that both microsaccades and normal scanning saccades differ only in amplitude, but not in their purpose (see also *de Bie and van den Brink, 1984; Timberlake, Wyman, Skavenski, and Steinman, 1972*). Also *Haddad and Steinman (1973)* emphasized that saccades as small as fixational microsaccades can be triggered voluntarily. In their study, involuntary saccades still occurred, most of the time correcting for preceding drift movements of the eyes. However, observers were aware of having made these microsaccades. It was argued, that tiny saccades serve visual search.

Finally, *Kowler and Steinman (1977)* directly examined the role of small saccades in a scanning task: counting of visually presented items. A variable number of parallel bright bars was presented in a small display. The number of bars ranged from 10 to 19; they were presented for 7.6 s and reports were given immediately after the offset of the display. The authors themselves participated and tried either to suppress saccades or to use saccades to their convenience during the task. Counting of the repetitive bar patterns did not require saccades. The number of correct reports did not differ as a function of instruction. In a second experiment, the authors showed that saccades may indeed improve counting accuracy, if perceptual confusion is reduced. This time, the items in a display had odd shapes and were haphazardly arranged. Under the instruction to suppress all saccades, counting accuracy was fair (somewhat more than 60% correct), however, if microsaccades (mainly below 30 min-arc in amplitude) were not avoided, accuracy nearly reached the ceiling. *Kowler and Steinman (1977)* tried to determine why saccades yielded a benefit in counting accuracy, but a clear answer could not be given in their study. In a follow-up experiment, however, *Kowler and Steinman (1979)* showed that saccades were not beneficial if the counting display spanned half a degree of diameter only. In this case, their counting accuracy with and without saccades could not be distinguished. The authors argued that saccades might only be generated as a consequence of attention shifts within the display; this is more likely to occur if the display spans a larger area (see also *Kowler and Steinman, 1977*). It was concluded that very small saccades (15 min-arc, or less) do not serve a purpose in a counting task.

Another explanation why saccades may be beneficial in a counting task is that they repeatedly generate new onsets in the visual system. *Kowler and Sperling (1980)* rejected this hypothesis as un-

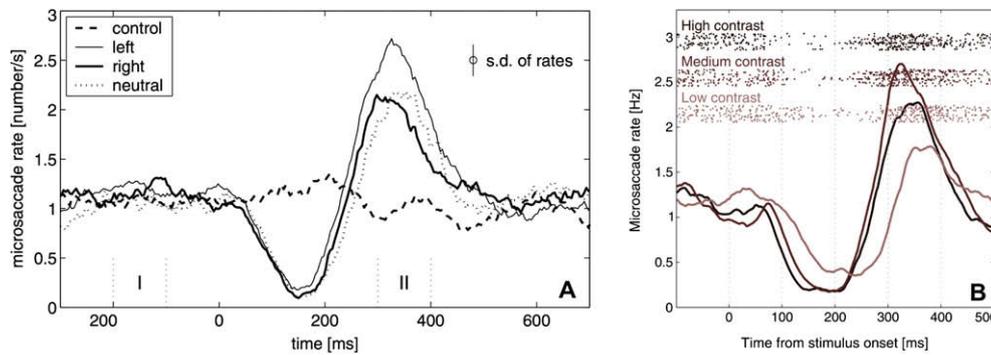


Fig. 8. *Microsaccade rate signature.* Perceptual transients produce dynamic changes in microsaccade rate, typically consisting of a fast inhibition and a subsequent rebound phase. (A) Microsaccade rate signature in response to arrow cues in an attentional cuing task. (From Engbert and Kliegl, 2003b) (B) The time course, shape and duration of the rate signature is sensitive to stimulus variables, here luminance contrast. (From Rolfs et al., 2008a.)

likely. In their visual search task, participants searched a numeral contained in an array of letters and reported its identity. In one condition, the search display set on and was then presented continuously throughout a trial. In another condition, the display was shortly flashed at the beginning of a trial and flashed again in the midpoint of a dark interval, resulting in an additional onset. Search performance was better if the array was shown continuously across a trial, that is, when no second onset was induced. However, these conditions differed not only in the number of onset transients of the display, but also with respect to the total presentation times of the stimulus (see also the follow-up study Kowler and Sperling, 1983). Therefore, a conclusive interpretation of the role of microsaccades in visual-search or the impact of resulting transients on visual performance is hard to envision, as one would have to assume that vision is based only on the transient following a saccade and not on the whole period of fixation. In addition, these approaches neglect that the visual system may have knowledge about (or even be in control of) the time of occurrence of microsaccades (Martinez-Conde et al., 2000), which is clearly not the case for externally generated visual transients.¹²

There is no doubt that large saccades are used to scan a visual scene, bringing potentially interesting regions onto the foveae. Brockmann and Geisel (2000) confirmed that saccades freely inspecting a static visual scene show statistics of an optimal random-search process, minimizing the time needed to scan a whole scene. Microsaccades during continual fixation of a small dot, however, do not show such properties, as Engbert (2006b) reported. Thus, it could not be supported by these analyses that microsaccades serve the purpose of (optimal) visual search on a smaller scale. This study, however, was based on data acquired during the fixation of a small bright dot on an otherwise dark computer screen, a task that may not be optimal to examine visual-search behavior in microsaccades. An arguably more ecologically valid task was used in a recent study by (Otero-Millan et al., 2008), who studied microsaccades and saccades in different free-viewing, visual search and exploration tasks. They found that the use of microsaccades and saccades was considerably higher when observers explored or searched images showing natural visual scenes rather than a blank field. In particular, microsaccades were most frequent, when a target was found in a search array. These findings highlight that microsaccades are among the standard repertoire of the visual and oculomotor system. Several other studies (see above) reported strong benefits associated with the generation of small saccades. One possibility is that these are a consequence of

attentional shifts in the foveated region. A link between microsaccades and covert attention has been well established as we will see in the next section.

2.7. Shifts of attention

Movements of gaze may also be referred to as *overt* shifts of visual attention. In contrast, we use the term *covert* when attention is allocated to the visual periphery without moving the eyes to that location. Recently, much progress has been made in understanding the behavior of microsaccades during shifts of covert attention. Engbert and Kliegl (2003b) examined microsaccade statistics in an attentional cuing paradigm comparable to that originally introduced by Posner (1980). The authors analyzed the evolution of microsaccade statistics in response to shifts of endogenous spatial attention (leftward or rightward) instructed by centrally presented arrow or color cues. Cues were followed by a target stimulus either at the cued (80% of trials) or the uncued (20%) location, which had to be detected as quickly as possible. Microsaccade rate (occurrences per second) evolved in a characteristic fashion in this task (see Fig. 8A). Initially, microsaccades occurred at normal frequency (about 1 microsaccade per second on average). After cue presentation, a conspicuous drop in the rate of microsaccades was observed (see de Bie, 1986, for the earliest report of this effect); this inhibition reached a minimum at about 150 ms after cue onset and was then followed by a strong enhancement in microsaccade rate. Subsequently, microsaccade rate reached a maximum at 350 ms after cue onset, before it finally resettled at the baseline level (500 ms after cue onset). The general shape of this *microsaccade rate signature* turned out to be very common in response to any sudden visual (Betta and Turatto, 2006; Betta, Galfano, and Turatto, 2007; Clark, Hafed, and Jie, 2007; Galfano, Betta, and Turatto, 2004; Gowen, Abadi, Poliakoff, Hansen, and Miall, 2007; Laubrock, Engbert, and Kliegl, 2005; Laubrock, Engbert, Rolfs, and Kliegl, 2007; Laubrock, Engbert, and Kliegl, 2008; Rolfs, Engbert, and Kliegl, 2004a, Rolfs, Engbert, and Kliegl, 2005, 2006, 2008a, 2008b; Turatto, Valsecchi, Tamè, and Betta, 2007; Valsecchi and Turatto, 2007, 2009; Valsecchi et al., 2007; Valsecchi, Dimigen, Kliegl, Sommer, and Turatto, 2009) and auditory (Rolfs et al., 2005; Rolfs et al., 2008a; Valsecchi and Turatto, 2009; see also, Kanai, Muggleton, and Walsh, 2008) transients.¹³ However, the time course varies considerably across different paradigms and conditions. While the initial inhibi-

¹² In fact, based on that idea, Martinez-Conde et al. (2000) proposed that microsaccades can be used to disambiguate response latency from latency changes due to stimulus brightness.

¹³ The microsaccade rate signature was anticipated in an article by Findlay (1974), studying visual direction constancy across microsaccades. He noticed that microsaccades occur only in the first 100 ms of a 250 ms period between two stimuli. If this period was increased to 1 s, microsaccades were most frequent between 200 and 500 ms after the onset of the first stimulus.

tion is a very stereotypical response whose latency and magnitude depends mainly on sensory factors (Rolfs et al., 2008a, e.g., Fig. 8B), the later rebound effect is sensitive to cognitive variables (Engbert, 2006b), and may even be absent in certain conditions, e.g., after rare target stimuli in oddball tasks (Valsecchi and Turatto, 2007, 2009; Valsecchi et al., 2007, 2009).

More importantly, Engbert and Kliegl (2003b) showed that the direction of microsaccades clearly depended on the direction of the attentional shift induced by spatially informative cues. Before cue presentation, microsaccades went equally likely in one direction or the other in the horizontal plane. During the enhancement epoch, i.e., some 300 ms after cue presentation, distributions of microsaccade directions were clearly shifted towards the cued side. This finding confirmed earlier suggestions based on numerically compatible but non-significant results (Kohama and Usui, 2002).

Using a paradigm well established in the literature on attention, the study by Engbert and Kliegl (2003b) provided clear evidence for a distinct correlation between attentional cuing and microsaccade direction. Another study employing a slightly different and cleverly designed experimental paradigm, arrived at the same conclusions. Hafed and Clark (2002) had observers fixate a central dot, surrounded by four peripheral targets placed left, right, above, and below the fixation spot, creating an imaginary diamond. In every trial, a random sequence of cue stimuli, each presented for 1200 ms halfway between fixation and one of the peripheral targets, induced covert attention shifts to the corresponding location. After an unpredictable number of cues, the peripheral target that was most recently cued shortly changed its color to yellowish or greenish and observers had to make a judgment. By varying the cue-target interval between 150 and 1200 ms, the authors were able to investigate the time course of performance in the discrimination task. Having multiple cue periods without a discrimination target in each trial, sufficient data was collected to conduct analyses of the dynamics of microsaccadic behavior. Thus, Hafed and Clark were able to directly correlate the time course of microsaccadic behavior to that of behavioral performance in the discrimination task. The authors found an early bias of microsaccades in the direction of the cued target (from 170 to 340 ms after cue onset) and a later period with a bias for cue-opposing microsaccades (510–850 ms after cue onset). This later effect was interpreted as an attention shift back to the fixation spot. Indeed, discrimination performance was best in the first 300 ms after cue onset and then dropped to chance level. Hafed and Clark (2002) also ran a second condition, in which the cue validly indicated that the peripheral target on the mirror side of the stimulus arrangement was judged (anti-cue). In this task, microsaccades first moved towards the cue, i.e., away from the target, before being biased in the direction of the target. Performance was found to improve with increasing cue-target intervals. These results strongly suggested that microsaccades are reliable indicators of covert attention.

Two related studies provided similar results. In one study (Rolfs et al., 2004a, 2005), peripheral attentional cues were presented, indicating the likely location of a subsequently presented discrimination target. Again, after an initial, relatively small cue-directed bias in microsaccade direction, these authors found that microsaccades favored to move in the direction opposite the cued location. Combining the evidence from a recent study by Tse, Sheinberg, and Logothetis (2003) on the distribution of attention in response to peripheral flashes with the knowledge from previous studies on the correspondence of microsaccade direction and spatial attention (Engbert and Kliegl, 2003b; Hafed and Clark, 2002), it was concluded that microsaccades indicated the direction of covert attention shifts in both central and peripheral cuing tasks. It was argued that the attentional shift was in the direction opposite the cue to inhibit automatic saccadic responses to the salient stimulus. In a

change-blindness paradigm, Tse et al. had established that attention (defined by close-to-perfect change detection) in response to a peripheral flash (cue) extended along the cue-fixation axis in both directions—to the cued location and, in particular, to the opposite side. In their paradigm, however, a relation between FEyeM and shifts of attention was not evident (Tse, Sheinberg, and Logothetis, 2002, 2004). Rolfs et al. (2004a) argued that the very frequent display changes in Tse et al.'s experiments effectively eliminated directional effects.

In another study, Laubrock et al. (2005) mapped the time course of microsaccade dynamics, comparing central and peripheral cuing in spatial attention tasks. In an adaptation of a paradigm by Müller and Rabbitt (1989), these authors separated the effects of attention shifts from those related to the preparation of a response saccade. Central cues, although validly indicating the target position, triggered only weak cue-related effects in microsaccade direction emerging late in the cue-target interval. In contrast, valid peripheral flash cues, evoked a rapidly occurring microsaccade direction bias towards the cued location. Short time later, this behavior was replaced by a strong cue-opposing bias in microsaccade directions. Laubrock et al. (2005), however, offered a different explanation for the cue-opposing bias in microsaccade directions: Frequently, shifts of covert attention are perceived as actual eye movements (Deubel, Irwin, and Schneider, 1999). Thus, participants might have perceived their covert attention shift to the peripheral flash as an overt movement, which they correct for by microsaccades in the opposite direction.

Differential influences of attention on microsaccade statistics have been generalized and extended along several lines. First, Galfano et al. (2004) studied the influence of uninformative cues on microsaccade statistics in a simple detection task. Uninformative exogenous attentional cues usually result in inhibition of return, that is, a performance drop at the cued spatial location that rapidly follows an initial benefit (see Klein, 2000, for a review and explanations of this effect). Galfano et al. (2004) replicated both the rate signature and the cue opposing microsaccade-direction effect observed earlier (Hafed and Clark, 2002; Rolfs et al., 2004a). The authors concluded that inhibition of return is reflected in the patterns of microsaccade direction (see also Betta et al., 2007). In another study using irrelevant cues, Laubrock et al. (2008) replicated all results of earlier studies using informative cues, i.e., also an early cue-directed bias in microsaccade direction. Second, starting out from the literature on multisensory interactions in the control of attention and saccades, Rolfs et al. (2005) examined the impact of informative cues in auditory, visual, and intermodal spatial attention task. In all cuing conditions, i.e., also in the absence of any changes of the visual display, the microsaccade rate signature was observed. Primarily during the enhancement epoch of the rate signature, microsaccades were biased towards the direction opposite the cue as soon as visual attention got involved in the task (i.e., with visual cues or targets or both). In the purely auditory cuing condition, however, there was only a weak effect of the cue on microsaccades, i.e., for left cues, they were directed to the cued location. Rolfs et al. (2005) related these findings to hemispheric asymmetries processing of auditory stimuli and the control of spatial attention. They proposed to use microsaccades as a tool to study multisensory integration and the time course of saccade preparation during shifts of covert attention in different sensory modalities. Finally, results reported by Jie (2007, in parts published in Clark et al., 2007) indicate that the directions of microsaccades occurring in the steady state of smooth pursuit on a continuously moving target show systematic, short-lived deviations in the direction of peripheral flash stimuli.

The accumulated knowledge about microsaccadic behavior in spatial attention tasks and its sensitivity to specific parameters of the task offer a valuable tool to improve our understanding of

attentional processes. For instance, in a study of social attention, [Deaner and Platt \(2003\)](#) showed that monkeys and humans shift covert attention in response to non-informative eye-gaze cues. Microsaccade directions were significantly biased in the direction of unpredictable gaze cues, when these were followed by a detection target 400 or 800 ms later. In another study, [Turatto et al. \(2007\)](#) examined two different search tasks (feature detection vs. feature discrimination) in an identical visual array. Based on different distributions of microsaccade directions, they provided evidence for distinct local vs. global processing modes in attentional selection.

The studies reviewed above demonstrate that microsaccades are a reliable correlate of covert spatial attention, which can be exploited for the study of visual (and potentially multisensory) selective processing. However, the present review is concerned with the function of microsaccades. A priori, a causal connection between microsaccades and attention seems unlikely. Nevertheless, [Horowitz, Fine, Fencsik, Yurgenson, and Wolfe \(2007a\)](#) tested whether microsaccades or drift movements do necessarily result in attention shifts. Using again a simple attentional cuing paradigm (modeled after [Engbert and Kliegl, 2003b](#)), the authors reasoned that if microsaccade direction is a nearly perfect indicator of covert attention, it should more reliably predict response times than the attentional cue itself when cue and microsaccade direction were opposed. No evidence for this causal hypothesis was found, leading [Horowitz et al. \(2007a\)](#) to conclude that microsaccades are not an index of covert attention. [Laubrock et al. \(2007\)](#) pointed out that this is by far too strong a conclusion, since the demonstration of the absence of a causal link does not disqualify microsaccades as useful indicators (“correlates”) of spatial attention. In addition, microsaccade direction explains some of the residual variance in response times after statistical control of the cue effect. Note, however, that this effect is an order of magnitude smaller than the classical cuing benefit. It turns out that the interactions of microsaccades with response latencies depend on many experimental factors and in a more complex manner than predicted by a one-to-one relationship between spatial attention and microsaccade generation ([Kliegl, Rolfs, Laubrock, and Engbert, 2009](#)). First of all, long intervals between the occurrence of a microsaccade in a cue-target interval and the actual response camouflage potential effects of microsaccades on response times. This becomes a severe challenge if long cue-target intervals are studied or if responses are slow. In addition, several studies suggest an interaction of microsaccade generation with oculomotor ([Horowitz, Fine, Fencsik, Yurgenson, and Wolfe, 2007b; Kliegl et al., 2009; Laubrock et al., 2007; Montagnini and Chelazzi, 2009; Rolfs et al., 2006, 2008b](#)) or manual ([Betta and Turatto, 2006; Kliegl et al., 2009; Laubrock et al., 2007; Rolfs et al., 2008a](#)) response preparation.

Thus, it appears likely that microsaccades are not the cause of shifts of attention in the visual field. Given the strong correlation with attentional variables (e.g., attentional cues), other experimental paradigms may be developed to overcome the present challenges of relating microsaccades more directly to correlates of visual attention in performance (see, e.g., [Hafed and Clark, 2002](#)). In addition, it is still possible that microsaccades do serve a role in selective visual processes (e.g., sustaining the representation of attended objects). Clarifying this possibility will require further investigation.

2.8. Resolving perceptual ambiguities

As discussed earlier, microsaccades are related to alternations in bistable perceptual phenomena like the visibility of stimuli close to perceptual threshold ([Deubel and Elsner, 1986](#)), the Troxler illusion ([Martinez-Conde et al., 2006](#)), perceptual filling-in ([Troncoso et al., 2008a](#)), or motion-induced blindness ([Hsieh and Tse,](#)

[2009](#)). Bistability is also the hallmark of binocular rivalry phenomena. These occur when two dissimilar stimuli are dichoptically presented. Observers usually report seeing either one or the other object, but rarely both at a time. In this paradigm, [Levelt \(1967\)](#) found that dominance and suppression intervals of either eye can be described by a gamma distribution. This distribution can be the result of a discrete process. Reviving an old debate regarding the question whether rivalry is of central or peripheral origin (for an overview of the classical literature, see [Breese, 1899](#)), [Levelt](#) proposed that microsaccades may constitute this stream of discrete events. The summation of energy increments across several microsaccades were thought to gradually reduce the visual threshold of the suppressed eye and, thus, to result a flip in perceptual dominance. [Blake, Fox, and McIntyre \(1971\)](#) followed up on this proposal in a study of binocular rivalry between two afterimages of ring-disk stimuli. In line with earlier reports ([Ditchburn and Pritchard, 1960; Pritchard et al., 1960](#)), they showed that even with these perfectly stabilized retinal images, perceptual alternations still occurred. In addition, the distribution of dominance and suppression times was comparable to that previously described by [Levelt \(1967\)](#) and [Fox and Herrmann \(1967\)](#) for non-stabilized viewing conditions (see also [Brascamp, van Ee, Pestman, and van den Berg, 2005](#)). The authors admitted, however, that a gamma distribution may not be the best description of the data, since significant deviations were found. Still, [Blake et al. \(1971\)](#) could conclude that switching in binocular rivalry situations can not be critically dependent on peripheral factors such as miniature eye movements. Later, studies of binocular rivalry between differently oriented gratings ([Wade, 1974](#)) and single line stimuli ([Wade, 1975](#)) confirmed that the distribution of dominance periods generally has a similar shape for both real images and afterimages. In line with early reports, however, these studies reported that rivalry was slower in the case of afterimages, compatible with the idea that peripheral factors like eye movements contribute to the rivalry process.

Although many authors had previously correlated gaze position and perceptual dominance in a variety of different multistable stimuli (see [van Dam and van Ee, 2005](#), for an overview), [Sabrin and Kertesz \(1980\)](#) were the first to actually study the role of microsaccades. Their data corroborated [Levelt's](#) proposal that microsaccades are related to perceptual alternations: In a binocular rivalry situation, microsaccade rates increased by 50% as compared to normal viewing. In addition, the rate of microsaccades declined at the end of a suppression interval, indicating that the depth of suppression is not constant over a rivalry interval. In a follow up study, the stimulus presented to one eye was stabilized with respect to the retina, and simulated microsaccades were artificially superimposed on it ([Sabrin and Kertesz, 1983](#)). Imposed movements were most effective in increasing the visibility of the suppressed stimulus if their rate and amplitude were similar to that of naturally occurring microsaccades. In this study, rivalry could also be observed when no movement was imposed on the stabilized retinal image. [Sabrin and Kertesz \(1983\)](#) concluded that FEyeM were not mandatory for the occurrence of binocular rivalry phenomena, however, microsaccades most efficiently provoked them. [van Dam and van Ee \(2006a\)](#) extended these results by showing that alternations in bistable phenomena are due to the retinal image shifts induced by microsaccades, not by the eye movements per se. To this end, trials including microsaccades were divided into two classes, those in which microsaccades caused a strong change in the retinal image of the suppressed grating and those in which microsaccades changed the retinal image by a full cycle, thus, not leading to a dramatic change in retinal stimulation. Perceptual flips were shown to occur primarily after microsaccades causing significant changes on the retina.

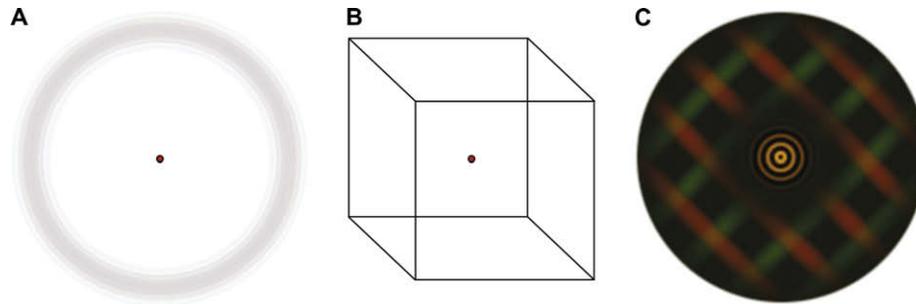


Fig. 9. Multistable stimuli. Three examples of multistable phenomena. (A) Troxler fading. After several seconds of fixation of the red dot, the outside ring will start to fade and reappear repeatedly. Microsaccades often precede reappearance; long periods without microsaccades often precede disappearance (Martinez-Conde et al., 2006). (B) Necker cube. This figure gives rise to alternative 3D interpretations. At times, perspective reverses spontaneously. These reversals might not be related to microsaccades (van Dam & van Ee, 2006b). (C) Monocular rivalry. During fixation at the center of this stimulus (designed for a study by Knapen et al., 2007), perceptual dominance of the two gratings (green vs. red) starts alternating. In addition, the stimulus appears to move erratically. A role of microsaccades in monocular rivalry is likely.

Similar results were obtained in the study of monocular rivalry (see example in Fig. 9C), for which a major role of retinal image shifts has been identified. Rivalry alternations occurred independently of whether the shift was caused by small voluntary saccades (Georgeson, 1984), imposed retinal image motion, or FEyeM (Bradley and Schor, 1988). Although in the latter study microsaccades occurred frequently during fixation of the stimulus (see their Fig. 3), their particular role in monocular rivalry remained unexplored.

A direct relationship between microsaccadic behavior and perceptual state was demonstrated by Laubrock et al. (2008) in another bistable stimulus, ambiguous apparent motion. In their experiments, observers saw a grid of dots presented through an aperture. By continuously cycling the position of the grid, an apparent motion is perceived. If the grid jumps by half a cycle in each frame, motion direction becomes ambiguous and leads to a bistable percept. In a first experiment, the authors found a strong correlation between the direction of microsaccades and subsequent reports of perceived movement direction. To examine the direction of this relationship more closely in a second experiment, the authors examined microsaccades before the stimulus actually started moving. It was observed that if microsaccades occurred before or around the time of the motion onset they strongly affected the perceived direction of the ambiguous stimulus. In a portion of trials, an irrelevant transient presented shortly at one side of the aperture was used to systematically bias microsaccade direction before the actual onset of the motion. In these trials, microsaccades were biased first towards and then away from the irrelevant transient. However, these microsaccades did not significantly influence the perceived direction of a subsequently presented ambiguous motion stimulus. Laubrock et al. (2008) concluded that microsaccades may indeed influence perceptual states in the face of ambiguous stimulation. This influence disappears, according to the authors, if microsaccade occurrence is attributable to an external source (i.e., the transient), potentially because voluntary efforts aiming at ignoring the transient also reset biases induced by microsaccades before motion onset.

A similar relationship between microsaccades and perception has recently been found for illusory motion, which is frequently observed in Op Art paintings like the *Enigma* created by Leviant (1982). Troncoso et al. (2008b) created a simplified version of such a stimulus, in which a gray band is embedded in an orthogonal grating of high spatial frequency. When viewed in the parafovea, illusory shadows appear to move quickly through the gray band. In their main experiment, observers were asked to judge the acceleration of this illusory motion. The authors found that reports of increases in perceived speed of illusory motion followed increases in microsaccade rate. In turn, reports of slowing or the absence of

motion followed a drop in microsaccade rate. The authors ran a control experiment on the same observers to examine whether these changes in microsaccade rate were in fact triggering the illusion or whether they were just the result of the changes in perception or the manual response to it. In this experiment, the observers reported changes in speed of small blobs moving physically through the gray band of their stimulus. In this experiment, microsaccade rates dropped off independently of the direction of change in motion speed (acceleration vs. deceleration). Response times collected in this control experiment were used to predict the time of perceptual alternations in the illusory motion experiment. Indeed, changes in microsaccade rates preceded changes in perception. Moreover, in a receiver-operating characteristic analysis, perceptual reports of physical motion could not be reliably predicted based on microsaccade rates preceding the event. However, changes in illusory motion were reliably predicted by microsaccade rates about 1000 ms before the perceptual change was reported, i.e., about 500 ms before the actual change in the percept. Therefore, as proposed earlier (Mon-Williams and Wann, 1996; Pritchard, 1958; Zanker, 2004; Zanker, Doyle, and Walker, 2003; Zanker and Walker, 2004), microsaccades appear to contribute to this type of illusory motion.

Finally, Cui, Wilke, Logothetis, Leopold, and Liang (2009) examined microsaccadic behavior under conditions of generalized flash suppression, in which a salient monocular stimulus may become invisible after the onset of a moving background pattern presented to both eyes (Wilke, Logothetis, and Leopold, 2003). They found that microsaccade rates decreased after the onset of the background pattern and remained low if the stimulus was not perceived, similar to when the stimulus was taken away simultaneously with the background onset. If the monkeys reported that the stimulus remained visible, microsaccade rate returned to baseline level within 250 ms after the minimum in microsaccade rate induced by background onset. An analysis of microsaccade directions revealed that microsaccades were biased (relative to a baseline) in the direction of the visible stimulus, in line with studies of microsaccade direction in endogenous cuing of spatial attention. This was not the case if the stimulus was invisible due to suppression or not present. Microsaccade amplitude, peak velocity, and duration did not depend on perceptual reports. In line with the ideas laid out in Section 2.4, continuous visibility of a stimulus (despite surround onset) could be interpreted as a manifestation of the efficiency of microsaccades in the post-surround-onset epoch. However, in their task, Cui et al. (2009) had observers report the visibility of the stimulus in an all-or-none fashion, any disappearance—even if short-lived—should result in a report of stimulus absence. Therefore, the authors speculated that their results may be a sign of a collaboration of perceptual and mo-

tor activities to achieve a meaningful interpretation of a multistable stimulus (see also Leopold and Logothetis, 1999). Consequently, the prolongation of the inhibition of microsaccades would be a strategy aiming at the prolongation of a perceptual state, namely invisibility of the stimulus. According to this hypothesis, microsaccades might contribute to refreshing retinal images and thus to stimulus visibility, once a stimulus percept was obtained. Altogether these results suggest that microsaccades are not the only cause to generate perceptual alternations during fixation. Rather they seem to be part of the repertoire of the visual system to solve ambiguities in the retinal input stream (see also Leopold and Logothetis, 1999).

A potential purpose of eye movements in general is the disambiguation of ambiguous stimuli (Hafed and Krauzlis, 2006). Literally, the change of eye position from glance to glance may let us see a challenging, or even multistable stimulus in different ways (Leopold and Logothetis, 1999). Microsaccades might not be related to all multistable perceptual phenomena (e.g., slant rivalry; van Dam and van Ee, 2005, see also Fig. 9B). The studies reviewed here, however, suggest that in many conditions of ambiguous visual stimulation microsaccades may in fact serve to generate different perceptual interpretations. A significant feature that microsaccades exhibit is the generation of visual transients, which—when imposed externally—have been shown to induce perceptual alternations in a number of ambiguous stimuli (Kanai, Moradi, Shimojo, and Verstraten, 2005). Combined with the fact that microsaccadic behavior adapts to some extent to current perceptual demands under conditions of perceptual uncertainty (e.g., Deubel and Elsner, 1986), microsaccades may reflect a process aiming for perceptual organization of a stimulus.

2.9. Further potential functions

So far I have discussed potential functions of microsaccades and other types of FEyeM that have been subject to intense study. Several others were proposed in the existing body of literature, which (as yet) received less attention. Certainly, they deserve a short review.

2.9.1. Image acquisition

In the field of computational vision, Kadyrov and Petrou (2004) presented a method for the reconstruction of missing parts of an image that integrates over a group of transformations of a spline grid used for interpolation. Applying this method, the authors achieved significantly better reconstructions of natural images and geometric structures than with any other simple interpolation approach tested; shape and accuracy were better preserved. Kadyrov and Petrou proposed that integration over a group of transformations may also be what the visual system does to transform the non-uniform input from the photoreceptors into clear and un-aliased images. Microsaccades may serve the purpose to provide the visual system with a number of simple image acquisitions to achieve an improved intake. Successive intakes may then be spatially aligned and averaged to obtain a clearer percept.

2.9.2. Mental imagery

In a study by Kowler and Steinman (1977) the task was to fixate on a small spot while answering questions like “How many windows are there on the second floor of your parents’ home?” Although the authors participated, the specific questions were unbeknownst to them before the test. The authors reasoned that answering such questions requires the scanning of a mental image using the mind’s eye. If saccades were necessary to correctly answer the questions, this could offer a hint at the purpose of microsaccades. However, visual imagery did not require saccades. Saccades were rarely made during the task and their number

was not different from a control condition, in which much less demanding questions had to be answered.

2.9.3. Decorrelation of natural image statistics and development of neural wiring

One of the most promising ideas concerning the function of retinal image motion was proposed by Michele Rucci and his coworkers. So far this work has focussed on FEyeM in general, without the investigation of the role of microsaccades, and only a short overview will be given (see Rucci, 2006; Rucci, 2008, for overviews). Rucci and colleagues promote the idea that FEyeM serve a critical role in the refinement and stabilization of cell-response characteristics during the development of early visual-information processing. Before eye opening, the wiring of neurons on the way from the LGN to the primary visual cortex relies on spontaneous activity that is correlated on a very small spatial scale. After eye opening, however, the visual input to the system is typically highly correlated over broad spatial ranges. In a series of modeling studies of retinal (Desbordes and Rucci, 2007; Poletti and Rucci, 2008), thalamic (Rucci, Edelman, and Wray, 2000; Rucci and Casile, 2004, 2005) and early cortical (Rucci and Casile, 2004) processing, it was recently shown that this statistical dependency may be strongly reduced in the presence of simulated FEyeM during the acquisition of visual information. Consequently, after eye opening, a regime of neural activity is established that is similar to that before visual input may affect the neural wiring between the early visual processing stages (Casile and Rucci, 2006; Rucci et al., 2000; Rucci and Casile, 2004). Thus, the refinement of receptive field organization in the primary cortex may rely on the same principles before and after eye opening. Moreover, the results of these studies suggest that FEyeM are crucial for structuring the visual input for further analysis in the course of visual information processing and, hence, for establishing efficient visual representations.

3. Summary and conclusions

Research on the purpose of microsaccades has come a long way. More than a hundred years ago, Dodge (1907) discovered these tiny flicks of the eye and half a century went by before Cornsweet (1956) started to examine their functions. Initially, research on the purpose of microsaccades focussed on the two obvious candidates: the prevention of perceptual fading and the control of gaze position over long periods of fixation. Later work increasingly widened the range of perceptual and cognitive functions that were related to microsaccades. In particular, we discussed their role in visual acuity, scanning of small spatial regions, attention, and multistable vision.

A major incentive that led me to write this article is a systematic unawareness of some of the early work on microsaccades in the present literature. This overview shows that some of the most promising ideas that are being developed and tested currently have their roots in earlier research on the topic. In fact, however, many articles, although describing discerning and intriguing research, did not even at their time find a way into the discussion of the purpose of microsaccades. I consider this an important factor why, by the time of 1980, research seemed to have arrived at a general consensus that microsaccades serve no useful purpose.

Several results led to the dismissal of any contribution of microsaccades to perceptual or oculomotor function and all of them have been carefully discussed. It appears that the strongest argument against a role of microsaccades in visual processing and fixation control is that other sources of eye position variation are sufficient to achieve the underlying behavioral and perceptual goals. Specifically, when microsaccades are actively inhibited by

holding the eyes as still as possible, a slow control mechanism sets in to correct for emerging fixation errors (Steinman et al., 1967). Similarly, as the work by Kelly and others shows, image motion similar to that of fixational drift is sufficient to restore vision when stabilized retinal images have faded. And as pointed out again recently, even in the absence of microsaccades, there is no lack of retinal image motion under most natural circumstances (Collewyn and Kowler, 2008). Indeed, as the accumulated evidence shows, drift plays a role in fixation control and, possibly together with head and body movements that generate retinal image motion, it appears to be a vital factor for perceptual processing. Moreover, microsaccades do not seem to be part of a closed-loop feedback system that automatically generates microsaccades when retinal image slip is low. That is, when the retinal image is artificially stabilized, microsaccades become less frequent (Cornsweet, 1956; Poletti and Rucci, 2007), although, under conditions of visual fixations, microsaccades are systematically preceded by periods of reduced drift (Engbert and Mergenthaler, 2006).

These results show that microsaccades are neither necessary nor a unique source for the prevention of perceptual fading and the control of fixation position. Rather, microsaccades and drift work hand in hand to implement these functions and, as discussed in Section 2.2, it is not unlikely that these different types of FEyeM have a common neurophysiological origin. But microsaccades have unique features that distinguish them from any other movements the eye undergoes during fixation. Microsaccades generate strong onset transients in the visual input stream. Physiological responses of the visual cortex in monkeys and humans in response to microsaccades lend strong support to this idea. In the framework of these ideas, saccadic suppression is functional not only by assisting trans-saccadic perception and weighing the visual input stream according to its reliability (putting emphasis on fixation), but also by promoting a stronger onset transient after the microsaccade. This is noteworthy since saccadic suppression, that is, a raised perceptual thresholds around the time of the eye movement, has been used as an argument to deny the function of microsaccades. In fact, referring to the elevation of the perceptual threshold (saccadic suppression) associated with microsaccades, Bridgeman and Palca (1980) stated: "A phenomenon which triples visual thresholds in normal humans for over an hour each day requires explanation" (p. 813). From the perspective taken here, saccadic suppression may be one of the clues to close the books on the purpose of microsaccades.

Following others, I argued that the transients associated with microsaccades come to the benefit of visual processing, as they generate a coordinated and synchronized input signal. Importantly, I have put forward the idea that microsaccades represent a flexible behavior that adapts to task demands and, thus, represents a malleable tool for the visual system. In fact, if fixation behavior is not experimentally altered by instruction, microsaccades are generated frequently in many tasks, first of all, if these tasks involve perceptually challenging or even ambiguous stimuli. A number of psychophysical and modeling studies have shown that transients indeed reliably alter perception, especially when stimuli are of low-contrast or ambiguous. Importantly, it shows that while retinal image motion may be achieved in many ways, microsaccades appear to be a convenient behavior in many situations. Not only do these results suggest an important purpose of microsaccades, they also pinpoint the variety of functions that saccades may have in general.

It is remarkable that although much evidence has accumulated only later, Ditchburn (1980) found a nice analogy to make these points clear. There is no better way to end this review than with his final paragraph of one of the last articles of the first era of microsaccade research.

"Some acrobats walk on their hands with amazing agility and most young people can learn to do this tolerably well. Certain tasks, such as following a line marked on the floor can be performed with reasonable accuracy. Yet no one suggests, from these facts, that it is mysterious that feet have evolved. Similarly the fact that many subjects can perform certain kinds of visual tasks in the absence of frequent [micro]saccades does not conflict with the view that [micro]saccades play an important and, indeed, essential part in normal vision." (p. 272).

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References

- Abadi, R. V., & Gowen, E. (2004). Characteristics of saccadic intrusions. *Vision Research*, 44, 2675–2690.
- Adler, F. H., & Fliegelman, M. (1934). Influence of fixation on the visual acuity. *Archives of Ophthalmology*, 12, 475–483.
- Ahissar, E., & Arieli, A. (2001). Figuring space by time. *Neuron*, 32, 185–201.
- Alpern, M. (1972). *Eye movements* (Vol. VII/4, pp. 304–331). Berlin: Springer.
- Arend, L. E., & Timberlake, G. T. (1986). What is psychophysically perfect image stabilization? Do perfectly stabilized images always disappear? *Journal of the Optical Society of America A*, 3, 235–241.
- Armington, J. C. (1977). Psychophysical applications of human electroretinography. *Journal of the Optical Society of America*, 67, 1458–1465.
- Armington, J. C., & Bloom, M. B. (1974). Relations between the amplitudes of spontaneous saccades and visual responses. *Journal of the Optical Society of America*, 64, 1263–1271.
- Armington, J. C., Gaarder, K., & Schick, A. M. L. (1967). Variation of spontaneous ocular and occipital responses with stimulus patterns. *Journal of the Optical Society of America*, 57, 1534–1539.
- Averill, H. L., & Weymouth, F. W. (1925). Visual perception and the retinal mosaic. II. The influence of eye movements on the displacement threshold. *Journal of Comparative Psychology*, 5, 147–176.
- Bair, W., & O'Keefe, L. P. (1998). The influence of fixational eye movements on the response of neurons in area MT of the macaque. *Visual Neuroscience*, 15, 779–786.
- Barlow, H. B. (1952). Eye movements during fixation. *Journal of Physiology*, 116, 290–306.
- Barlow, H. B. (1963). Slippage of contact lenses and other artefacts in relation to fading and regeneration of supposedly stable retinal images. *Quarterly Journal of Experimental Psychology*, 15, 36–51.
- Basso, M. A., Krauzlis, R. J., & Wurtz, R. H. (2000). Activation and inactivation of rostral superior colliculus neurons during smooth-pursuit eye movements in monkeys. *Journal of Neurophysiology*, 84, 892–908.
- Beeler, G. W. (1967). Visual threshold changes resulting from spontaneous saccadic eye movements. *Vision Research*, 7, 769–775.
- Bengi, H., & Thomas, J. G. (1968). Three electronic methods for recording ocular tremor. *Medical and Biological Engineering*, 6, 171–179.
- Bennet-Clark, H. C., & Evans, C. R. (1963). Fragmentation of patterned targets when viewed as prolonged after-images. *Nature*, 199, 1215–1216.
- Betta, E., Galfano, G., & Turatto, M. (2007). Microsaccadic response during inhibition of return in a target–target paradigm. *Vision Research*, 47, 428–436.
- Betta, E., & Turatto, M. (2006). Are you ready? I can tell by looking at your microsaccades. *Neuroreport*, 17, 1001–1004.
- Blake, R. R., Fox, R., & McIntyre, C. (1971). Stochastic properties of stabilized-image binocular rivalry alternations. *Journal of Experimental Psychology*, 88, 327–332.
- Bolger, C., Bojanic, S., Sheahan, N. F., Coakley, D., & Malone, J. F. (1999). Dominant frequency content of ocular microtremor from normal subjects. *Vision Research*, 39, 1911–1915.
- Bosman, C., Womelsdorf, T., Desimone, R., & Fries, P. (2008). Microsaccades dynamically modulate Gamma-band synchronization in macaque visual cortex. In *Computational and Systems Neuroscience (COSYNE)*. Salt Lake City.

- Bosman, C. A., Womelsdorf, T., Desimone, R., & Fries, P. (2009). A microsaccadic rhythm modulates gamma-band synchronization and behavior. *Journal of Neuroscience*, 29, 9471–9480.
- Boyce, P. R. (1967). Monocular fixation in human eye movement. *Proceedings of the Royal Society of London B*, 167, 293–315.
- Bradley, A., & Schor, C. (1988). The role of eye movements and masking in monocular rivalry. *Vision Research*, 28, 1129–1137.
- Brascamp, J. W., van Ee, R., Pestman, W. R., & van den Berg, A. V. (2005). Distributions of alternation rates in various forms of bistable perception. *Journal of Vision*, 5 (4), 1, 287–298.
- Breese, B. B. (1899). On inhibition. *Psychological monographs* (Vol. 3, pp. 1–65).
- Breitmeyer, B., & Julesz, B. (1975). The role of on and off transients in determining the psychophysical spatial frequency response. *Vision Research*, 15, 411–415.
- Bridgeman, B., & Palca, J. (1980). The role of microsaccades in high acuity observational tasks. *Vision Research*, 20, 813–817.
- Brockmann, D., & Geisel, T. (2000). The ecology of gaze shifts. *Neurocomputing*, 643–650.
- Byron, L., & Wattenberg, M. (2008). Stacked graphs – geometry & aesthetics. *IEEE Transactions on Visualization and Computer Graphics*, 14, 1245–1252.
- Campbell, F. W., & Robson, J. G. (1961). A fresh approach to stabilized retinal images. *Journal of Physiology*, 158, 11P–12P.
- Casile, A., & Rucci, M. (2006). A theoretical analysis of the influence of fixational instability on the development of thalamocortical connectivity. *Neural Computation*, 18, 569–590.
- Ciuffreda, K. J., Kenyon, R. V., & Stark, L. (1979). Suppression of fixational saccades in strabismic and anisometropic amblyopia. *Ophthalmological Research*, 11, 31–39.
- Ciuffreda, K. J., Kenyon, R. V., & Stark, L. (1980). Increased drift in amblyopic eyes. *British Journal of Ophthalmology*, 64, 7–14.
- Ciuffreda, K. J., & Tannen, B. (1995). *Eye movement basics for the clinician*. St. Louis: Mosby.
- Clarke, F. J. J., & Belcher, S. J. (1962). On the localization of Troxler's effect in the visual pathway. *Vision Research*, 2, 53–68.
- Clark, J. J., Hafed, Z. M., & Jie, L. (2007). Attention and action. In L. R. Harris & M. R. M. Jenkin (Eds.), *Computational vision in neural and machine systems* (pp. 129–148). Cambridge University Press.
- Clowes, M. B. (1961). Some factors in brightness discrimination with constraint of retinal image movement. *Optica Acta*, 8, 81–91.
- Clowes, M. B. (1962). A note on colour discrimination under conditions of retinal image constraint. *Optica Acta*, 9, 65–68.
- Collewijn, H., & Kowler, E. (2008). The significance of microsaccades for vision and oculomotor control. *Journal of Vision*, 8(14), 20, 1–21.
- Collewijn, H., & van der Mark, F. (1972). Ocular stability in variable feedback conditions in the rabbit. *Brain Research*, 36, 47–57.
- Coppola, D., & Purves, D. (1996). The extraordinarily rapid disappearance of entoptic images. *Proceedings of the National Academy of Sciences, USA*, 93, 8001–8004.
- Cornsweet, T. N. (1956). Determination of the stimuli for involuntary drifts and saccadic eye movements. *Journal of the Optical Society of America*, 46, 987–993.
- Cui, J., Wilke, M., Logothetis, N. K., Leopold, D. A., & Liang, H. (2009). Visibility states modulate microsaccade rate and direction. *Vision Research*, 49, 228–236.
- Cunitz, R. J., & Steinman, R. M. (1969). Comparison of saccadic eye movements during fixation and reading. *Vision Research*, 9, 683–693.
- Darwin, R. W. (1786). New experiments on the ocular spectra of light and colours. *Philosophical Transactions of the Royal Society*, 76, 313–348.
- Deaner, R. O., & Platt, M. L. (2003). Reflexive social attention in monkeys and humans. *Current Biology*, 13, 1609–1613.
- de Bie, J. (1986). The control properties of small eye movements. Ph.D. Thesis, Technische Universiteit, Delft.
- de Bie, J., & van den Brink, G. (1984). Small stimulus movements are necessary for the study of fixational eye movements. In A. G. Gale & F. Johnson (Eds.), *Theoretical and applied aspects of eye movement research* (pp. 63–70). North Holland: Elsevier.
- Desbordes, G., & Rucci, M. (2007). A model of the dynamics of retinal activity during natural visual fixation. *Visual Neuroscience*, 24, 217–230.
- Deubel, H., & Bridgeman, B. (1995). Perceptual consequences of ocular lens overshoot during saccadic eye movements. *Vision Research*, 35, 2897–2902.
- Deubel, H., & Elsner, T. (1986). Threshold perception and saccadic eye movements. *Biological Cybernetics*, 54, 351–358.
- Deubel, H., Irwin, D. E., & Schneider, W. X. (1999). The subjective direction of gaze shifts long before the saccade. In W. Becker, H. Deubel, & T. Mergner (Eds.), *Current oculomotor research: Physiological and psychological aspects* (pp. 65–70). New York: Plenum Press.
- Dimigen, O., Valsecchi, M., Sommer, W., & Kliegl, R. (in press). Human microsaccade-related visual brain responses. *Journal of Neuroscience*.
- Ditchburn, R. W. (1955). Eye-movements in relation to retinal action. *Optica Acta*, 1, 171–176.
- Ditchburn, R. W. (1980). The function of small saccades. *Vision Research*, 20, 271–272.
- Ditchburn, R. W. (1987). What is psychophysically perfect image stabilization? Do perfectly stabilized images always disappear?: Comment. *Journal of the Optical Society of America*, 4, 405–406.
- Ditchburn, R. W., Drysdale, F. R. S., & Drysdale, A. E. (1977a). The effect of retinal-image movements on vision. I. Step movements and pulse movements. *Proceedings of the Royal Society of London B*, 197, 131–144.
- Ditchburn, R. W., Drysdale, F. R. S., & Drysdale, A. E. (1977b). The effect of retinal-image movements on vision. II. Oscillatory movements. *Proceedings of the Royal Society of London B*, 197, 385–406.
- Ditchburn, R. W., & Fender, D. H. (1955). The stabilised retinal image. *Optica Acta*, 2, 128–133.
- Ditchburn, R. W., Fender, D. H., & Mayne, S. (1959). Vision with controlled movements of the retinal image. *Journal of Physiology*, 145, 98–107.
- Ditchburn, R. W., Fender, D. H., Mayne, S., & Pritchard, R. M. (1956). A stabilized retinal image of the iris. *Proceedings of the Physical Society B*, 69, 1165–1166.
- Ditchburn, R. W., & Foley-Fisher, J. A. (1967). Assembled data in eye movements. *Optica Acta*, 14, 113–118.
- Ditchburn, R. W., & Ginsborg, B. L. (1952). Vision with a stabilized retinal image. *Nature*, 170, 36–37.
- Ditchburn, R. W., & Ginsborg, B. L. (1953). Involuntary eye movements during fixation. *Journal of Physiology*, 119, 1–17.
- Ditchburn, R. W., & Pritchard, R. M. (1956). Stabilized interference fringes on the retina. *Nature*, 177, 434.
- Ditchburn, R. W., & Pritchard, R. M. (1960). Binocular vision with two stabilized retinal images. *Quarterly Journal of Experimental Psychology*, 12, 26–32.
- Dodge, R. (1907). An experimental study of visual fixation. *Psychological Review Monograph Supplements*, 8, 1–95.
- Donner, K., & Hemilä, S. (2007). Modelling the effect of microsaccades on retinal responses to stationary contrast patterns. *Vision Research*, 47, 1166–1177.
- Drysdale, A. E. (1975). The visibility of retinal blood vessels. *Vision Research*, 15, 813–818.
- du Laurens, A. (1599). *A discourse of the preservation of the sight: Of Melancholike disease; of Rheumes, and of old age, translated by R. Surphlet edition. The Shakespeare Association Facsimiles* (Vol. 15). London: Humphrey Milford/Oxford University Press.
- Elsner, T., & Deubel, H. (1986). The effect of saccades on threshold perception – A model study. *Biological Cybernetics*, 54, 359–366.
- Engbert, R. (2006a). Flick-induced flips in perception. *Neuron*, 49, 168–170.
- Engbert, R. (2006b). Microsaccades: A microcosm for research on oculomotor control, attention, and visual perception. *Progress in Brain Research*, 154, 177–192.
- Engbert, R., & Kliegl, R. (2003a). Binocular coordination in microsaccades. In J. Hyönä, R. Radach, & H. Deubel (Eds.), *The mind's eye: Cognitive and applied aspects of eye movements* (pp. 103–117). Amsterdam: Elsevier.
- Engbert, R., & Kliegl, R. (2003b). Microsaccades uncover the orientation of covert attention. *Vision Research*, 43, 1035–1045.
- Engbert, R., & Kliegl, R. (2004). Microsaccades keep the eyes' balance during fixation. *Psychological Science*, 15, 431–436.
- Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences, USA*, 103, 7192–7197.
- Epelboim, J. (1998). Gaze and retinal-image-stability in two kinds of sequential looking tasks. *Vision Research*, 38, 3773–3784.
- Evans, C. R. (1965). Some studies of pattern perception using a stabilized retinal image. *British Journal of Psychology*, 56, 121–133.
- Ferman, L., Collewijn, H., Jansen, T. C., & van den Berg, A. V. (1987). Human gaze stability in the horizontal, vertical and torsional direction during voluntary head movements, evaluated with a three-dimensional scleral induction coil technique. *Vision Research*, 27, 811–828.
- Findlay, J. M. (1971). Frequency analysis of human involuntary eye movement. *Kybernetik*, 8, 207–214.
- Findlay, J. M. (1974). Direction perception and human fixation eye movements. *Vision Research*, 14, 703–711.
- Fiorentini, A., & Ercoles, A. M. (1957). Vision of oscillating non-uniform fields. *Optica Acta*, 4, 150–157.
- Fiorentini, A., & Ercoles, A. M. (1966). Involuntary eye movements during attempted monocular fixation. *Atti della Fondazione Giorgio Ronchi*, 21, 199–217.
- Fox, R., & Herrmann, J. (1967). Stochastic properties of binocular rivalry alternations. *Perception & Psychophysics*, 2, 432–436.
- Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9, 474–480.
- Fries, P., Scheeringa, R., & Oostenveld, R. (2008). Finding gamma. *Neuron*, 58, 303–305.
- Funke, K., Kerscher, N. J., & Wörgötter, F. (2007). Noise-improved signal detection in cat primary visual cortex via a well-balanced stochastic resonance-like procedure. *European Journal of Neuroscience*, 26, 1322–1332.
- Gaarder, K. (1960). Relating a component of physiological nystagmus to visual display. *Science*, 132, 471–472.
- Gaarder, K. (1966a). Fine eye movements during inattention. *Nature*, 209, 83–84.
- Gaarder, K. (1966b). Transmission of edge information in the human visual system. *Nature*, 212, 321–323.
- Gaarder, K. (1967). Mechanisms in fixation saccadic eye movements. *British Journal of Physiological Optics*, 24, 28–44.
- Gaarder, K., Koresko, R., & Kropff, W. (1966). The phasic relation of a component of alpha rhythm to fixation saccadic eye movements. *Electroencephalography and Clinical Neurophysiology*, 21, 544–551.
- Gaarder, K., Krauskopf, J., Graf, V., Kropff, W., & Armington, J. C. (1964). Averaged brain activity following saccadic eye movement. *Science*, 146, 1481–1483.
- Galfano, G., Betta, E., & Turatto, M. (2004). Inhibition of return in microsaccades. *Experimental Brain Research*, 159, 400–404.
- Georgeson, M. A. (1984). Eye movements, afterimages and monocular rivalry. *Vision Research*, 24, 1311–1319.
- Gerrits, H. J. M., de Haan, B., & Vendrik, A. J. H. (1966). Experiments with retinal stabilized images. Relations between the observations and neural data. *Vision Research*, 6, 427–440.

- Gerrits, H. J. M., & Vendrik, A. J. H. (1970). Artificial movements of a stabilized image. *Vision Research*, 10, 1443–1456.
- Gerrits, H. J. M., & Vendrik, A. J. H. (1974). The influence of stimulus movements on perception in parafoveal stabilized vision. *Vision Research*, 14, 175–180.
- Gilchrist, I. D., Brown, V., & Findlay, J. M. (1997). Saccades without eye movements. *Nature*, 390, 130–131.
- Gilchrist, I. D., Brown, V., Findlay, J. M., & Clarke, M. P. (1998). Using the eye-movement system to control the head. *Proceedings of the Royal Society of London B*, 265, 1831–1836.
- Ginsborg, B. L. (1953). Small voluntary movements of the eye. *British Journal of Ophthalmology*, 37, 746–754.
- Ginsborg, B. L., & Maurice, D. M. (1959). Involuntary movements of the eye during fixation and blinking. *British Journal of Ophthalmology*, 43, 435–437.
- Glezer, V. D. (1959). The eye as a scanning system. *The Journal of Physiology of USSR*, 45, 271–279.
- Gowen, E., & Abadi, R. V. (2005). Saccadic instabilities and voluntary saccadic behaviour. *Experimental Brain Research*, 164, 29–40.
- Gowen, E., Abadi, R. V., & Poliakoff, E. (2005). Paying attention to saccadic intrusions. *Cognitive Brain Research*, 25, 810–825.
- Gowen, E., Abadi, R. V., Poliakoff, E., Hansen, P. C., & Miall, R. C. (2007). Modulation of saccadic intrusions by exogenous and endogenous attention. *Brain Research*, 1141, 154–167.
- Greenlee, M. W., & Tse, P. U. (2008). Functional neuroanatomy of the human visual system: A review of functional MRI studies. In B. Lorenz & F.-X. Borruat (Eds.), *Pediatric ophthalmology, neuro-ophthalmology, genetics*. Berlin, Heidelberg: Springer.
- Greschner, M., Bongard, M., Rujan, P., & Ammermüller, J. (2002). Retinal ganglion cell synchronization by fixation eye movements improves feature estimation. *Nature Neuroscience*, 5, 441–447.
- Gur, M., & Snodderly, D. M. (1987). Studying striate cortex neurons in behaving monkeys: Benefits of image stabilization. *Vision Research*, 27, 2081–2087.
- Gur, M., & Snodderly, D. M. (1997). Visual receptive fields of neurons in primary visual cortex (V1) move in space with the eye movements of fixation. *Vision Research*, 37, 257–265.
- Haddad, G. M., & Steinman, R. M. (1973). The smallest voluntary saccade: Implications for fixation. *Vision Research*, 13, 1075–1086.
- Haddad, G. M., & Winterson, B. J. (1975). Effect of flicker on oculomotor performance. In G. Lennerstrand & P. Bach-y-Rita (Eds.), *Basic mechanisms of ocular motility and their clinical implications* (pp. 489–493). Oxford: Pergamon Press.
- Hafed, Z. M., & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research*, 42, 2533–2545.
- Hafed, Z. M., Goffart, L., & Krauzlis, R. J. (2008). Superior colliculus inactivation causes stable offsets in eye position during tracking. *Journal of Neuroscience*, 28, 8124–8137.
- Hafed, Z. M., Goffart, L., & Krauzlis, R. J. (2009). A neural mechanism for microsaccade generation in the primate superior colliculus. *Science*, 323, 940–943.
- Hafed, Z. M., & Krauzlis, R. J. (2006). Ongoing eye movements constrain visual perception. *Nature Neuroscience*, 9, 1449–1457.
- Hafed, Z. M., & Krauzlis, R. J. (2008). Goal representations dominate superior colliculus activity during extrafoveal tracking. *Journal of Neuroscience*, 28, 9426–9439.
- Hartridge, H., & Thomson, L. C. (1948). Methods of investigating eye movements. *British Journal of Ophthalmology*, 32, 581–591.
- Heckenmueller, E. G. (1965). Stabilization of the retinal image: A review of method, effects, and theory. *Psychological Bulletin*, 63, 157–169.
- Hennig, M. H., Kerscher, N. J., Funke, K., & Wörgötter, F. (2002). Stochastic resonance in visual cortical neurons: Does the eye-tremor actually improve acuity? *Neurocomputing*, 115–120.
- Hennig, M. H., & Wörgötter, F. (2004). Eye micro-movements improve stimulus detection beyond the Nyquist limit in the peripheral retina. In S. Thrun, L. Saul, & B. Schölkopf (Eds.), *Advances in neural information processing systems (NIPS2003)* (Vol. 16). MIT Press.
- Hering, E. (1899). Über die Grenzen der Sehschärfe. In *Berichte der mathematisch-physischen Classe der Kgl. Sächs. Gesellschaft der Wissenschaften zu Leipzig* (pp. 16–24).
- Higgins, G. C., & Stultz, K. F. (1953). Frequency and amplitude of ocular tremor. *Journal of the Optical Society of America*, 43, 1136–1140.
- Horowitz, T. S., Fine, E. M., Fencsik, D. E., Yurgenson, S., & Wolfe, J. M. (2007a). Fixational eye movements are not an index of covert attention. *Psychological Science*, 18, 356–363.
- Horowitz, T. S., Fine, E. M., Fencsik, D. E., Yurgenson, S., & Wolfe, J. M. (2007b). Microsaccades and attention. Does a weak correlation make an index? Reply to Laubrock, Engbert, Rolfs, and Kliegl (2007). *Psychological Science*, 18, 367–368.
- Hsieh, P.-J., & Tse, P. U. (2009). Microsaccade rate varies with subjective visibility during motion-induced blindness. *PLoS One*, 4, e5163.
- Huey, E. B. (1900). On the psychology and physiology of reading. I. *American Journal of Psychology*, 11, 283–302.
- Hussakof, L. (1916). Benjamin Franklin and Erasmus Darwin: With some unpublished correspondence. *Science*, 43, 773–775.
- Jie, L. (2007). An eye movement dependent visual attention model and its applications. Ph.D. Thesis, McGill University, Montreal.
- Jurin, J. (1738). An essay on distinct and indistinct vision. In R. Smith (Ed.), *Complete system of optics in four books* (Vol. 2, pp. 115–171). Cambridge.
- Kadyrov, A., & Petrou, M. (2004). Reverse engineering the human vision system: A possible explanation for the role of microsaccades. In *Pattern recognition. Proceedings of the 17th international conference on pattern recognition* (pp. 64–67).
- Kagan, I., Gur, M., & Snodderly, D. M. (2008). Saccades and drifts differentially modulate neuronal activity in V1: Effects of retinal image motion, position, and extraretinal influences. *Journal of Vision*, 8(14), 19, 1–25.
- Kanai, R., Moradi, F., Shimojo, S., & Verstraten, F. A. (2005). Perceptual alternations induced by visual transients. *Perception*, 34, 803–822.
- Kanai, R., Muggleton, N. G., & Walsh, V. (2008). TMS over the intraparietal sulcus induces perceptual fading. *Journal of Neurophysiology*, 100, 3343–3350.
- Kelly, D. H. (1979a). Motion and vision. I. Stabilized images of stationary gratings. *Journal of the Optical Society of America*, 69, 1266–1274.
- Kelly, D. H. (1979b). Motion and vision. II. Stabilized spatio-temporal threshold surface. *Journal of the Optical Society of America*, 69, 1340–1349.
- Kelly, D. H. (1981). Disappearance of stabilized chromatic gratings. *Science*, 214, 1257–1258.
- Kelly, D. H., & Burbeck, C. A. (1980). Motion and vision. III. Stabilized pattern adaptation. *Journal of the Optical Society of America*, 70, 1283–1289.
- King-Smith, P. E., & Riggs, L. A. (1978). Visual sensitivity to controlled motion of a line or edge. *Vision Research*, 18, 1509–1520.
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, 4, 138–147.
- Kliegl, R., Rolfs, M., Laubrock, J., & Engbert, R. (2009). Microsaccadic modulation of response times in spatial attention tasks. *Psychological Research*, 73, 136–146.
- Knapen, T., Kanai, R., Brascamp, J. W., van Boxtel, J., & van Ee, R. (2007). Distance in feature space determines exclusivity in visual rivalry. *Vision Research*, 47, 3269–3275.
- Koenderink, J. J., & van Doorn, A. J. (1979). Spatiotemporal contrast detection threshold surface is bimodal. *Optics Letters*, 4, 32–34.
- Ko, H.-K., Poletti, M., & Rucci, M. (2009). *Eye movements in a high-acuity visual task*. Naples, FL: Vision Sciences Society.
- Kohama, T., & Usui, S. (2002). Attentional effects on microsaccadic eye movements. *Current Psychology of Cognition*, 21, 377–395.
- Kowler, E., & Anton, S. (1987). Reading twisted text: Implications for the role of saccades. *Vision Research*, 27, 45–60.
- Kowler, E., & Martins, A. J. (1982). Eye movements in preschool children. *Science*, 215, 997–999.
- Kowler, E., & Sperling, G. (1980). Transient stimulation does not aid visual search: Implications for the role of saccades. *Perception & Psychophysics*, 27, 1–10.
- Kowler, E., & Sperling, G. (1983). Abrupt onsets do not aid visual search. *Perception & Psychophysics*, 34, 307–313.
- Kowler, E., & Steinman, R. M. (1977). The roll of small saccades in counting. *Vision Research*, 17, 141–146.
- Kowler, E., & Steinman, R. M. (1979). Miniature saccades: Eye movements that do not count. *Vision Research*, 19, 105–108.
- Kowler, E., & Steinman, R. M. (1980). Small saccades serve no useful purpose: Reply to a letter by R.W. Ditchburn. *Vision Research*, 20, 273–276.
- Krauskopf, J. (1957). Effect of retinal image motion on contrast thresholds for maintained vision. *Journal of the Optical Society of America*, 47, 740–744.
- Krauskopf, J., Cornsweet, T. N., & Riggs, L. A. (1960). Analysis of eye movements during monocular and binocular fixation. *Journal of the Optical Society of America*, 50, 572–578.
- Krauskopf, J., Graf, V., & Gaarder, K. (1966). Lack of inhibition during involuntary saccades. *American Journal of Psychology*, 79, 73–81.
- Krauzlis, R. J., Basso, M. A., & Wurtz, R. H. (1997). Shared motor error for multiple eye movements. *Science*, 276, 1693–1695.
- Krauzlis, R. J., Basso, M. A., & Wurtz, R. H. (2000). Discharge properties of neurons in the rostral superior colliculus of the monkey during smooth-pursuit eye movements. *Journal of Neurophysiology*, 84, 876–891.
- Kulikowski, J. J. (1971). Effect of eye movements on the contrast sensitivity of spatio-temporal patterns. *Vision Research*, 11, 261–273.
- Land, M. F., Furneaux, S. M., & Gilchrist, I. D. (2002). The organization of visually mediated actions in a subject without eye movements. *Neurocase*, 8, 80–87.
- Laubrock, J., Engbert, R., & Kliegl, R. (2005). Microsaccade dynamics during covert attention. *Vision Research*, 45, 721–730.
- Laubrock, J., Engbert, R., & Kliegl, R. (2008). Fixational eye movements predict the perceived direction of ambiguous apparent motion. *Journal of Vision*, 8(14), 13, 1–17.
- Laubrock, J., Engbert, R., Rolfs, M., & Kliegl, R. (2007). Microsaccades are an index of covert attention. *Psychological Science*, 18, 364–366.
- Leopold, D. A., & Logothetis, N. K. (1998). Microsaccades differentially modulate neural activity in the striate and extrastriate visual cortex. *Experimental Brain Research*, 123, 341–345.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, 3, 254–264.
- Levitt, W. J. M. (1967). Note on the distribution of dominance times in binocular rivalry. *British Journal of Psychology*, 58, 143–145.
- Leviant, I. (1982). Illusory motion within still pictures: The L-effect. *Leonardo*, 15, 222–223.
- Liang, J.-R., Moshel, S., Zivotofsky, A. Z., Caspi, A., Engbert, R., Kliegl, R., et al. (2005). Scaling of horizontal and vertical fixational eye movements. *Physical Review E*, 71, 031909.
- Livingstone, M. S., Freeman, D. C., & Hubel, D. H. (1996). Visual responses in V1 of freely viewing monkeys. *Cold Spring Harbor Symposia On Quantitative Biology*, 61, 27–37.

- Lord, M. P., & Wright, W. D. (1948). Eye movements during monocular fixation. *Nature*, 162, 25–26.
- MacEvoy, S. P., Hanks, T. D., & Paradiso, M. A. (2008). Macaque V1 activity during natural vision: Effects of natural scenes and saccades. *Journal of Neurophysiology*, 99, 460–472.
- Malinow, I. V., Epelboim, J., Herst, A. N., & Steinman, R. M. (2000). Characteristics of saccades and vergence in two types of sequential looking tasks. *Vision Research*, 40, 2083–2090.
- Mariotte, E. (1683). An account of two letters of Mr. Perault and Mr. Mariotte concerning vision. *Philosophical Transactions of the Royal Society*, 13, 265–267.
- Marshall, W. H., & Talbot, S. A. (1942). Recent evidence for neural mechanisms in vision leading to a general theory of sensory acuity. *Biological Symposia*, 7, 117–164.
- Martinez-Conde, S. (2006). Fixational eye movements in normal and pathological vision. *Progress in Brain Research*, 154, 151–176.
- Martinez-Conde, S., & Macknik, S. L. (2008). Fixational eye movements across vertebrates: Comparative dynamics, physiology, and perception. *Journal of Vision*, 8(14), 28. 1–16.
- Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2000). Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. *Nature Neuroscience*, 3, 251–258.
- Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2002). The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *Proceedings of the National Academy of Sciences, USA*, 99, 13920–13925.
- Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews Neuroscience*, 5, 229–240.
- Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron*, 49, 297–305.
- Marx, E., & Trendelenburg, W. (1911). Über die Genauigkeit der Einstellung des Auges beim Fixieren. *Zeitschrift für Sinnesphysiologie*, 45, 87–102.
- Matin, L., Matin, E., & Pearce, D. G. (1970). Eye movements in the dark during the attempt to maintain a prior fixation position. *Vision Research*, 10, 837–857.
- McAllister, C. N. (1905). The fixation of points in the visual field. *Psychological Review Monograph Supplements*, 7, 17–53.
- McCree, K. J. (1960). Colour confusion produced by voluntary fixation. *Optica Acta*, 7, 281–290.
- Melloni, L., Schwiedrzik, C. M., Rodriguez, E., & Singer, W. (2009a). (Micro)Saccades, corollary activity and cortical oscillations. *Trends in Cognitive Sciences*, 13, 239–245.
- Melloni, L., Schwiedrzik, C. M., Wibrall, M., Rodriguez, E., & Singer, W. (2009b). Response to: Yuval-Greenberg et al., “Transient induced gamma-band response in EEG as a manifestation of miniature saccades”. *Neuron* 58, 429–441. *Neuron*, 62, 8–10.
- Mergenthaler, K., & Engbert, R. (2007). Modeling the control of fixational eye movements with neurophysiological delays. *Physical Review Letters*, 98(138104), 1–4.
- Michalik, M. (1987). Spektralanalysen des okulären Mikrotremors bei Hirnstammfunktionsstörungen. *Zeitschrift für Elektroenzephalographie und Elektromyographie*, 18, 20–26.
- Møller, F., Laursen, M. L., & Sjølie, A. K. (2006). The contribution of microsaccades and drifts in the maintenance of binocular steady fixation. *Graefes Archives for Clinical and Experimental Ophthalmology*, 244, 465–471.
- Møller, F., Laursen, M., Tygesen, J., & Sjølie, A. (2002). Binocular quantification and characterization of microsaccades. *Graefes Archives for Clinical and Experimental Ophthalmology*, 240(9), 765–770.
- Montagnini, A., & Chelazzi, L. (2009). Dynamic interaction between Go and Stop signals in the saccadic eye movement system: New evidence against the functional independence of the underlying neural mechanisms. *Vision Research*, 49, 1316–1328.
- Mon-Williams, M., & Wann, J. P. (1996). An illusion that avoids focus. *Proceedings of the Royal Society of London B*, 263, 573–578.
- Moshel, S., Liang, J.-R., Caspi, A., Engbert, R., Kliegl, R., Havlin, S., et al. (2005). Phase-synchronisation decay of fixational eye movements. *Annals of the New York Academy of Sciences*, 1039, 484–488.
- Moshel, S., Zivotofsky, A. Z., Liang, J.-R., Engbert, R., Kurths, J., Kliegl, R., et al. (2008). Persistence and phase synchronisation properties of fixational eye movements. *European Physical Journal Special Topics*, 161, 207–223.
- Motter, B. C., & Poggio, G. F. (1984). Binocular fixation in the rhesus monkey: Spatial and temporal characteristics. *Experimental Brain Research*, 54, 304–314.
- Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 315–330.
- Murakami, I. (2003). Illusory jitter in a static stimulus surrounded by a synchronously flickering pattern. *Vision Research*, 43, 957–969.
- Murakami, I. (2006). Fixational eye movements and motion perception. *Progress in Brain Research*, 154, 193–209.
- Murakami, I., & Cavanagh, P. (1998). A jitter after-effect reveals motion-based stabilization of vision. *Nature*, 395, 798–801.
- Murphy, B. J., Haddad, G. M., & Steinman, R. M. (1974). Simple forms and fluctuations of the line of sight: Implications for motor theories of form processing. *Perception & Psychophysics*, 16, 557–563.
- Murphy, B. J., Kowler, E., & Steinman, R. M. (1975). Slow oculomotor control in the presence of moving backgrounds. *Vision Research*, 15, 1263–1268.
- Nachmias, J. (1959). Two-dimensional motion of the retinal image during monocular fixation. *Journal of the Optical Society of America*, 49, 901–908.
- Nachmias, J. (1961). Determiners of the drift of the eye during monocular fixation. *Journal of the Optical Society of America*, 51, 761–766.
- Ölveczky, B. P., Baccus, S. A., & Meister, M. (2003). Segregation of object and background motion in the retina. *Nature*, 423, 401–408.
- Otero-Millan, J., Troncoso, X. G., Macknik, S. L., Serrano-Pedraza, I., & Martinez-Conde, S. (2008). Saccades and microsaccades during visual fixation, exploration and search: Foundations for a common saccadic generator. *Journal of Vision*, 8(14), 21. 1–18.
- Ouchi, H. (1977). *Japanese optical and geometrical art*. New York: Dover.
- Pitkow, X., Sompolinsky, H., & Meister, M. (2008). A neural computation for visual acuity in the presence of eye movements. *PLoS Biology*, 5, e331.
- Poletti, M., & Rucci, M. (2007). Dependence of fixational saccades on the visual task and image fading conditions. *Journal of Vision*, 7, 21a [Abstract].
- Poletti, M., & Rucci, M. (2008). Oculomotor synchronization of visual responses in modeled populations of retinal ganglion cells. *Journal of Vision*, 8(14), 4. 1–15.
- Posner, M. I. (1980). Orientation of attention. The VIIth Sir Frederic Bartlett lecture. *Quarterly Journal of Experimental Psychology*, 32A, 3–25.
- Pritchard, R. M. (1958). Visual illusions viewed as stabilized retinal images. *Quarterly Journal of Experimental Psychology*, 10, 77–81.
- Pritchard, R. M. (1961). Stabilized images on the retina. *Scientific American*, 204, 72–78.
- Pritchard, R. M., Heron, H., & Hebb, D. O. (1960). Visual perception approached by the method of stabilized images. *Canadian Journal of Psychology*, 14, 67–77.
- Proskuryakova, N. G., & Shakhnovich, A. R. (1967). Quantitative characteristics of fixation micromovements of the eye. *Biophysics*, 13, 117–126.
- Puckett, J. W., & Steinman, R. M. (1969). Tracking eye movements with and without saccadic correction. *Vision Research*, 9, 695–703.
- Purpura, K. P., Kalik, S. F., & Schiff, N. D. (2003). Analysis of perisaccadic field potentials in the occipitotemporal pathway during active vision. *Journal of Neurophysiology*, 90, 3455–3478.
- Ratliff, F. (1952). The role of physiological nystagmus in monocular acuity. *Journal of Experimental Psychology*, 43, 163–172.
- Ratliff, F. (1958). Stationary retinal image requiring no attachments to the eye. *Journal of the Optical Society of America*, 48, 274–275.
- Ratliff, F., & Riggs, L. A. (1950). Involuntary motions of the eye during monocular fixation. *Journal of Experimental Psychology*, 40, 687–701.
- Rattle, J. D., & Foley-Fisher, J. A. (1968). A relationship between vernier acuity and intersaccadic interval. *Optica Acta*, 15, 617–620.
- Riggs, L. A. (1965). Visual acuity. In *Vision and visual perception* (pp. 321–349). New York: Wiley.
- Riggs, L. A., Armitage, J. C., & Ratliff, F. (1954). Motions of the retinal image during fixation. *Journal of the Optical Society of America*, 44, 315–321.
- Riggs, L. A., & Ratliff, F. (1951). Visual acuity and the normal tremor of the eyes. *Science*, 114, 17–18.
- Riggs, L. A., & Ratliff, F. (1952). The effects of counteracting the normal movements of the eye. *Journal of the Optical Society of America*, 42, 872–873.
- Riggs, L. A., Ratliff, F., Cornsweet, J. C., & Cornsweet, T. N. (1953). The disappearance of steadily fixated visual test objects. *Journal of the Optical Society of America*, 43, 495–501.
- Rolfs, M. (2009). A neural mechanism for fixation instability. *Science* (E Letter, 2 June 2009). <<http://www.sciencemag.org/cgi/eletters/323/5916/940>>.
- Rolfs, M., Engbert, R., & Kliegl, R. (2004a). Microsaccade orientation supports attentional enhancement opposite a peripheral cue. *Psychological Science*, 15, 705–707.
- Rolfs, M., Engbert, R., & Kliegl, R. (2004b). Perception and motor control: The link between fixational eye movements and postural sway. *Perception*, 33(Suppl. S), 136.
- Rolfs, M., Engbert, R., & Kliegl, R. (2005). Crossmodal coupling of oculomotor control and spatial attention in vision and audition. *Experimental Brain Research*, 166, 427–439.
- Rolfs, M., Kliegl, R., & Engbert, R. (2008a). Toward a model of microsaccade generation: The case of microsaccadic inhibition. *Journal of Vision*, 8(11), 5. 1–23.
- Rolfs, M., Laubrock, J., & Kliegl, R. (2006). Shortening and prolongation of saccade latencies following microsaccades. *Experimental Brain Research*, 169, 369–376.
- Rolfs, M., Laubrock, J., & Kliegl, R. (2008b). Microsaccade-induced prolongation of saccade latencies depends on microsaccade amplitude. *Journal of Eye Movement Research*, 1(3), 1. 1–8.
- Rucci, M. (2006). Visual encoding with jittering eyes. In Y. Weiss, B. Scholkopf, & J. Platt (Eds.), *Advances in neural information processing system* (Vol. 18, pp. 1137–1144). Cambridge, MA: MIT Press.
- Rucci, M. (2008). Fixational eye movements, natural image statistics, and fine spatial vision. *Network: Computation in Neural Systems*, 19, 253–285.
- Rucci, M., & Casile, A. (2004). Decorrelation of neural activity during fixational instability: Possible implications for the refinement of V1 receptive fields. *Visual Neuroscience*, 21, 725–738.
- Rucci, M., & Casile, A. (2005). Fixational instability and natural image statistics: Implications for early visual representations. *Network: Computation in Neural Systems*, 16, 121–138.
- Rucci, M., & Desbordes, G. (2003). Contributions of fixational eye movements to the discrimination of briefly presented stimuli. *Journal of Vision*, 3, 852–864.
- Rucci, M., Edelman, G. M., & Wray, J. (2000). Modeling LGN responses during free-viewing: A possible role of microscopic eye movements in the refinement of cortical orientation selectivity. *Journal of Neuroscience*, 20, 4708–4720.
- Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine spatial detail. *Nature*, 447, 851–855.

- Sabrin, H. W., & Kertesz, A. E. (1980). Microsaccadic eye movements and binocular rivalry. *Perception & Psychophysics*, 28, 150–154.
- Sabrin, H. W., & Kertesz, A. E. (1983). The effect of imposed fixational eye movements on binocular rivalry. *Perception & Psychophysics*, 34, 155–157.
- Sansbury, R. V., Skavenski, A. A., Haddad, G. M., & Steinman, R. M. (1973). Normal fixation of eccentric targets. *Journal of the Optical Society of America*, 63, 612–614.
- Santini, F., Redner, G., Iovin, R., & Rucci, M. (2007). EyeRIS: A general-purpose system for eye movement contingent display control. *Behavior Research Methods*, 39, 350–364.
- Schor, C., & Hallmark, W. (1978). Slow control of eye position in strabismic amblyopia. *Investigative Ophthalmology*, 17, 577–581.
- Schulz, E. (1984). Binocular micromovements in normal persons. *Graefes Archives for Clinical and Experimental Ophthalmology*, 222, 95–100.
- Segev, R., Schneidman, E., Goodhouse, J., & Berry, M. J. II. (2007). Role of eye movements in the retinal code for a size discrimination task. *Journal of Neurophysiology*, 98, 1380–1391.
- Shakhnovich, A. R., & Thomas, J. G. (1977). Micro-tremor of the eyes of comatose patients. *Electroencephalography and Clinical Neurophysiology*, 42, 117–119.
- Sharpe, C. R. (1971). A fresh approach to stabilized retinal images. Part II. *Journal of Physiology*, 217, 9P–10P.
- Sharpe, C. R. (1972). The visibility and fading of thin lines visualized by their controlled movement across the retina. *Journal of Physiology*, 222, 113–134.
- Shortess, G. K., & Krauskopf, J. (1961). Role of involuntary eye movements in stereoscopic acuity. *Journal of the Optical Society of America*, 51, 555–559.
- Shurcliff, W. A. (1959). New visual phenomenon: The greenish-yellow blotch. *Journal of the Optical Society of America*, 49, 1041–1048.
- Simon, F., Schulz, E., Rassow, B., & Haase, W. (1984). Binocular micromovement recording of human eyes – Methods. *Graefes Archives for Clinical and Experimental Ophthalmology*, 221, 293–298.
- Skavenski, A. A. (1971). Extraretinal correction and memory for target position. *Vision Research*, 11, 743–746.
- Skavenski, A. A. (1972). Inflow as a source of extraretinal eye position information. *Vision Research*, 12, 221–229.
- Skavenski, A. A., Hansen, R. M., Steinman, R. M., & Winterson, B. J. (1979). Quality of retinal image stabilization during small natural and artificial body rotations in man. *Vision Research*, 19, 675–683.
- Skavenski, A. A., Robinson, D. A., Steinman, R. M., & Timberlake, G. T. (1975). Miniature eye movements of fixation in rhesus monkeys. *Vision Research*, 15, 1269–1273.
- Skavenski, A. A., & Steinman, R. M. (1970). Control of eye position in the dark. *Vision Research*, 10, 193–203.
- Snodderly, D. M. (1987). Effects of light and dark environments on macaque and human fixational eye movements. *Vision Research*, 27, 401–415.
- Snodderly, D. M., Kagan, I., & Gur, M. (2001). Selective activation of visual cortex neurons by fixational eye movements: Implications for neural coding. *Visual Neuroscience*, 18, 259–277.
- Snodderly, D. M., & Kurtz, D. (1985). Eye position during fixation tasks: Comparison of macaque and human. *Vision Research*, 25, 83–98.
- Sobotka, S., Nowicka, A., & Ringo, J. L. (1997). Activity linked to externally cued saccades in single units recorded from hippocampal, parahippocampal, and inferotemporal areas of macaques. *Journal of Neurophysiology*, 78, 2156–2163.
- Spauschus, A., Marsden, J., Halliday, D. M., Rosenberg, J. R., & Brown, P. (1999). The origin of ocular microtremor in man. *Experimental Brain Research*, 126, 556–562.
- St. Cur, G. J., & Fender, D. H. (1969). The interplay of drifts and flicks in binocular fixation. *Vision Research*, 9, 245–265.
- Steinman, R. M. (1965). Effect of target size, luminance, and color on monocular fixation. *Journal of the Optical Society of America*, 55, 1158–1165.
- Steinman, R. M. (1976). Role of eye movements in maintaining a phenomenally clear and stable world. In R. A. Monty & J. W. Senders (Eds.), *Eye movements and psychological processes* (pp. 121–149). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Steinman, R. M. (2003). Gaze control under natural conditions. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (Vol. 2, pp. 1339–1356). Cambridge: MIT Press.
- Steinman, R. M., & Collewijn, H. (1978). How our two eyes are held steady. *Journal of the Optical Society of America*, 68, 1359.
- Steinman, R. M., & Collewijn, H. (1980). Binocular retinal image motion during active head rotation. *Vision Research*, 20, 415–429.
- Steinman, R. M., & Cunitz, R. J. (1968). Fixation of targets near the absolute foveal threshold. *Vision Research*, 8, 277–286.
- Steinman, R. M., Cunitz, R. J., Timberlake, G. T., & Herman, M. (1967). Voluntary control of microsaccades during maintained monocular fixation. *Science*, 155, 1577–1579.
- Steinman, R. M., Haddad, G. M., Skavenski, A. A., & Wyman, D. (1973). Miniature eye movement. *Science*, 181, 810–819.
- Steinman, R. M., & Levinson, J. Z. (1990). The role of eye movement in the detection of contrast and spatial detail. In E. Kowler (Ed.), *Eye movements and their role in visual and cognitive processes* (pp. 115–212). New York: Elsevier.
- Steinman, R. M., Pizlo, Z., Foronova, T. I., & Epelboim, J. (2003). One fixates accurately in order to see clearly not because one sees clearly. *Spatial Vision*, 16, 225–241.
- Steinman, R. M., Skavenski, A. A., & Sansbury, R. V. (1969). Effect of lens accommodation on holding the eye in place without saccades. *Vision Research*, 9, 629–631.
- Stevens, J. K., Emerson, R. C., Gerstein, G. L., Kallos, T., Neufeld, G. R., Nichols, C. W., et al. (1976). Paralysis of the awake human: Visual perceptions. *Vision Research*, 16, 93–98.
- ten Doesschate, J. (1954). A new form of physiological nystagmus. *Ophthalmologica*, 127, 65–73.
- Thiel, M., Romano, M. C., Kurths, J., Rolfs, M., & Kliegl, R. (2006). Twin surrogates to test for complex synchronisation. *Europhysics Letters*, 75, 535–541.
- Thiel, M., Romano, M. C., Kurths, J., Rolfs, M., & Kliegl, R. (2008). Generating surrogates from recurrences. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 366, 345–367.
- Timberlake, G. T., Wyman, D., Skavenski, A. A., & Steinman, R. M. (1972). The oculomotor error signal in the fovea. *Vision Research*, 12, 1059–1064.
- Troncoso, X. G., Macknik, S. L., & Martinez-Conde, S. (2008a). Microsaccades counteract perceptual filling-in. *Journal of Vision*, 8(14), 15, 1–9.
- Troncoso, X. G., Macknik, S. L., Otero-Millan, J., & Martinez-Conde, S. (2008b). Microsaccades drive illusory motion in the enigma illusion. *Proceedings of the National Academy of Sciences, USA*, 105, 16033–16038.
- Troxler, I. P. V. (1804). Über das Verschwinden gegebener Gegenstände innerhalb unseres Gesichtskreises. *Ophthalmologische Bibliothek*, 2, 1–53.
- Tse, P. U., Baumgartner, F., & Greenlee, M. W. (2007). fMRI BOLD signal reveals neural correlates of microsaccades. *Journal of Vision*, 7, 318a [Abstract].
- Tse, P. U., Baumgartner, F. J., & Greenlee, M. W. (2009). Event-related functional MRI of cortical activity evoked by microsaccades, small visually-guided saccades, and eyeblinks in human visual cortex. *Neuroimage*, in press.
- Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2002). Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Research*, 42, 1663–1669.
- Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2003). Attentional enhancement opposite a peripheral flash revealed using change blindness. *Psychological Science*, 14, 91–99.
- Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2004). The distribution of microsaccade directions need not reveal the location of attention. *Psychological Science*, 15, 708–710.
- Tulunay-Keese, U. (1960). Effects of involuntary eye movements on visual acuity. *Journal of the Optical Society of America*, 50, 769–774.
- Tulunay-Keese, U., & Bennis, B. J. (1979). Effects of stimulus onset and image motion on contrast sensitivity. *Vision Research*, 19, 767–774.
- Tulunay-Keese, U., & Jones, R. M. (1976). The effect of micromovements of the eye and exposure duration on contrast sensitivity. *Vision Research*, 16, 481–488.
- Tulunay-Keese, U., & Riggs, L. A. (1962). Visibility of Mach bands with imposed motions of the retinal image. *Journal of the Optical Society of America*, 52, 719–720.
- Turatto, M., Valsecchi, M., Tamè, L., & Betta, E. (2007). Microsaccades distinguish between global and local visual processing. *Neuroreport*, 18, 1015–1018.
- Valsecchi, M., Betta, E., & Turatto, M. (2007). Visual oddballs induce prolonged microsaccadic inhibition. *Experimental Brain Research*, 177, 196–208.
- Valsecchi, M., Dimigen, O., Kliegl, R., Sommer, W., & Turatto, M. (2009). Microsaccadic inhibition and P300 enhancement in a visual oddball task. *Psychophysiology*, 46, 635–644.
- Valsecchi, M., & Turatto, M. (2007). Microsaccadic response to visual events that are invisible to the superior colliculus. *Behavioral Neuroscience*, 121, 786–793.
- Valsecchi, M., & Turatto, M. (2009). Microsaccadic responses in a bimodal oddball task. *Psychological Research*, 73, 23–33.
- van Dam, L. C. J., & van Ee, R. (2005). The role of (micro)saccades and blinks in perceptual bi-stability from slant rivalry. *Vision Research*, 45, 2417–2435.
- van Dam, L. C. J., & van Ee, R. (2006a). Retinal image shifts, but not eye movements per se, cause alternations in awareness during binocular rivalry. *Journal of Vision*, 6, 1172–1179.
- van Dam, L. C. J., & van Ee, R. (2006b). The role of saccades in exerting voluntary control in perceptual and binocular rivalry. *Vision Research*, 46, 787–799.
- van Nes, F. L. (1968). Enhanced visibility by regular motion of retinal images. *American Journal of Psychology*, 81, 367–374.
- Verheijen, F. J. (1961). A simple after image method demonstrating the involuntary multi-directional eye movements during fixation. *Optica Acta*, 8, 309–311.
- von Helmholtz, H. (1924). *Treatise on physiological optics* (Vol. 2). Menasha, Wisconsin: The Optical Society of America [Originally published as *Handbuch der physiologischen Optik* [1866; Leipzig: Voss].
- Wade, N. J. (1974). The effect of orientation in binocular contour rivalry of real images and afterimages. *Perception & Psychophysics*, 15, 227–232.
- Wade, N. J. (1975). Binocular rivalry between single lines viewed as real images and afterimages. *Perception & Psychophysics*, 17, 571–577.
- Wade, N. J., & Tatler, B. W. (2005). *The moving tablet of the eye*. Oxford: Oxford University Press.
- Wallis, G. (2006). The temporal and spatial limits of compensation for fixational eye movements. *Vision Research*, 46, 2848–2858.
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron*, 39, 1043–1052.
- Winterson, B. J., & Collewijn, H. (1976). Microsaccades during finely guided visuomotor tasks. *Vision Research*, 16, 1387–1390.
- Winterson, B. J., & Robinson, D. A. (1975). Fixation by the alert but solitary cat. *Vision Research*, 15, 1349–1352.
- Wyman, D., & Steinman, R. M. (1973). Small step tracking: Implications for the oculomotor “dead zone”. *Vision Research*, 13, 2165–2172.
- Yarbus, A. L. (1957a). A new method of studying the activity of various parts of the retina. *Biophysics*, 2, 165–167.

- Yarbus, A. L. (1957b). The perception of an image fixed with respect to the retina. *Biophysics*, 2, 683–690.
- Yarbus, A. L. (1959). The perception of images moving across the retina at a fixed speed. *Biophysics*, 4, 70–80.
- Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum Press.
- Yuval-Greenberg, S., Keren, A. S., Nelken, I., & Deouell, L. Y. (2009). Response to letter: Melloni et al., “Transient induced gamma-band response in EEG as a manifestation of miniature saccades”. *Neuron* 58, 429–441. *Neuron*, 62, 10–12.
- Yuval-Greenberg, S., Tomer, O., Nelken, I., & Deouell, L. Y. (2008). Transient induced gamma-band response in EEG as a manifestation of miniature saccades. *Neuron*, 58, 429–441.
- Zanker, J. M. (2004). Looking at Op Art from a computational viewpoint. *Spatial Vision*, 17, 75–94.
- Zanker, J. M., Doyle, M., & Walker, R. (2003). Gaze stability of observers watching Op Art pictures. *Perception*, 32, 1037–1049.
- Zanker, J. M., & Walker, R. (2004). A new look at Op art: Towards a simple explanation of illusory motion. *Naturwissenschaften*, 91, 149–156.
- Zuber, B. L., Crider, A., & Stark, L. (1964). Saccadic suppression associated with microsaccades. *Quarterly Progress Report*, 74, 244–249.
- Zuber, B. L., & Stark, L. (1966). Saccadic suppression: Elevation of visual threshold associated with saccadic eye movements. *Experimental Neurology*, 16, 65–79.
- Zuber, B. L., Stark, L., & Cook, G. (1965). Microsaccades and the velocity–amplitude relationship for saccadic eye movements. *Science*, 150, 1459–1460.