

Review



**Cite this article:** Martinez-Conde S, Macknik SL. 2017 Unchanging visions: the effects and limitations of ocular stillness. *Phil. Trans. R. Soc. B* **372:** 20160204. <http://dx.doi.org/10.1098/rstb.2016.0204>

Accepted: 19 December 2016

One contribution of 17 to a theme issue 'Movement suppression: brain mechanisms for stopping and stillness'.

**Subject Areas:**

neuroscience, physiology, behaviour, cognition

**Keywords:**

microsaccades, drift, tremor, fixational eye movements, fading, neural adaptation

**Author for correspondence:**

Susana Martinez-Conde  
e-mail: smart@neuralcorrelate.com

# Unchanging visions: the effects and limitations of ocular stillness

Susana Martinez-Conde and Stephen L. Macknik

Department of Ophthalmology, State University of New York (SUNY) Downstate Medical Center, 450 Clarkson Avenue, Brooklyn, NY 11203, USA

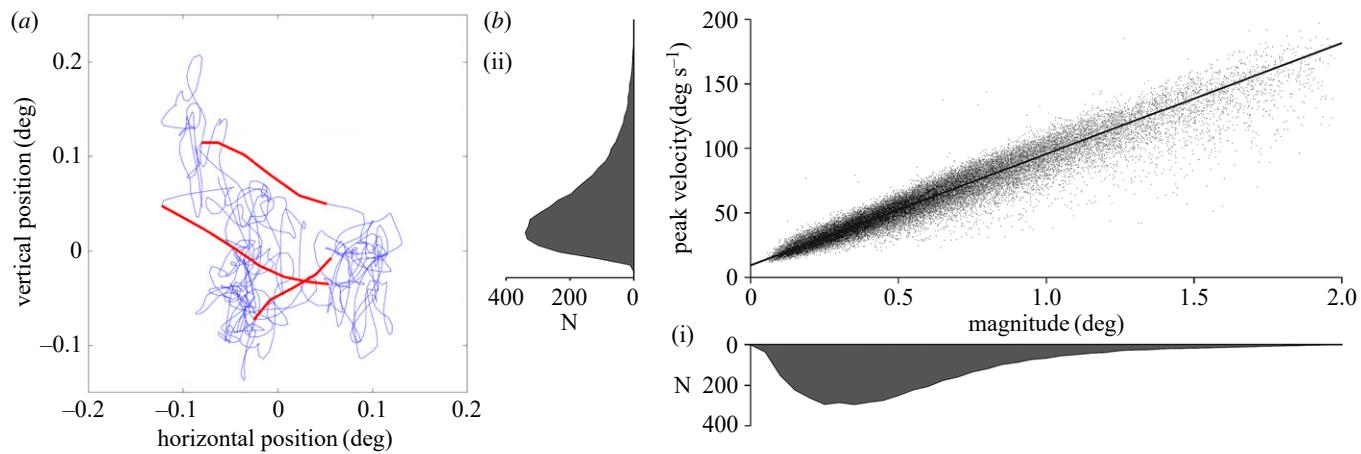
SM-C, 0000-0003-4600-9767

Scientists have pondered the perceptual effects of ocular motion, and those of its counterpart, ocular stillness, for over 200 years. The unremitting 'trembling of the eye' that occurs even during gaze fixation was first noted by Jurin in 1738. In 1794, Erasmus Darwin documented that gaze fixation produces perceptual fading, a phenomenon rediscovered in 1804 by Ignaz Paul Vital Troxler. Studies in the twentieth century established that Jurin's 'eye trembling' consisted of three main types of 'fixational' eye movements, now called microsaccades (or fixational saccades), drifts and tremor. Yet, owing to the constant and minute nature of these motions, the study of their perceptual and physiological consequences has met significant technological challenges. Studies starting in the 1950s and continuing in the present have attempted to study vision during retinal stabilization—a technique that consists on shifting any and all visual stimuli presented to the eye in such a way as to nullify all concurrent eye movements—providing a tantalizing glimpse of vision in the absence of change. No research to date has achieved perfect retinal stabilization, however, and so other work has devised substitute ways to counteract eye motion, such as by studying the perception of afterimages or of the entoptic images formed by retinal vessels, which are completely stable with respect to the eye. Yet other research has taken the alternative tack to control eye motion by behavioural instruction to fix one's gaze or to keep one's gaze still, during concurrent physiological and/or psychophysical measurements. Here, we review the existing data—from historical and contemporary studies that have aimed to nullify or minimize eye motion—on the perceptual and physiological consequences of perfect versus imperfect fixation. We also discuss the accuracy, quality and stability of ocular fixation, and the bottom-up and top-down influences that affect fixation behaviour.

This article is part of the themed issue 'Movement suppression: brain mechanisms for stopping and stillness'.

## 1. The quality of ocular fixation: how well do we keep our eyes still?

Human eyes never stop moving, despite our subjective experience to the contrary. Indeed, neuroscience students are often surprised when they learn about their constant eye motion, presumably because they had not previously noted it. Yet, the study of ocular instability has a long history—starting with Jurin's 1738 observation [1] that the 'trembling of the eye' is unremitting—but it has proceeded in spurts and starts, and it is only in recent years that it has become a mainstay of oculomotor and visual neuroscience. It is perhaps owing to uneven research progress in this field that such terms as visual 'fixation' or 'fixational eye movements', have come to exist, given that there is no such thing as gaze fixation. Even when we attempt to anchor our eyes to an object or feature of interest, we still produce so-called fixational eye movements—namely microsaccades, drift and tremor (figure 1).



**Figure 1.** Fixational eye movements and microsaccades. (a) Fixational eye movements recorded during a 2 s fixation. Drift (blue) is erratic, whereas microsaccades (red) are ballistic and their trajectories are more linear. Adapted from [2]. (b) Microsaccadic peak velocity–magnitude relationship. Main panel: each black dot represents a microsaccade with peak velocity indicated on the *y*-axis and magnitude on the *x*-axis. Panels (i) and (ii): microsaccade magnitude and peak–velocity distributions. Adapted from [3].

### (a) Microsaccades

A diminutive version of classical saccades—the rapid eye movements that change the line of sight from one fixation target to the next—microsaccades or fixational saccades are small-magnitude saccades produced during the attempt to fixate one's gaze on a target [4–6]. The largest and fastest of the three fixational eye movement types, microsaccades carry the retinal image across several dozen to several hundred photoreceptors [7,8]. They occur at a rate of one to two per second during sustained fixation attempts [9], and at a rate of approximately 0.5 per second during the brief fixations that occur while freely viewing a visual scene [10]. Fourteen per cent of fixations during free visual exploration of natural scenes contain microsaccades (although certain characteristics of the image can elevate both the percentage of fixations containing microsaccades, and the microsaccade rates per fixation) [10,11]. Recent research has established that classical saccades and fixational microsaccades have a common oculomotor origin [5,10,12,13]. Accordingly, there is a growing list of shared properties of microsaccades and saccades. For instance, both microsaccades are typically binocular and conjugate eye movements [14–16]; microsaccade and saccade peak velocities are parametrically related to microsaccade and saccade amplitudes [10,17] and durations [18,19], a relationship known as the (micro)saccadic main sequence (figure 1b); visual perception thresholds are raised during both microsaccades and saccades, a phenomenon known as (micro)saccadic suppression [20]; and both microsaccades and saccades are linked to attentional shifts [21–23]. Microsaccades activate neurons in multiple areas of the visual pathway [8,24,25] (see [5] for a review). Microsaccade occurrence is moreover associated with increased target visibility and various other perceptual effects [19,26–33]. In addition, microsaccades appear to contribute critically to information extraction during visual scanning [11] and the performance of high-acuity tasks [34].

### (b) Drift

Drift is the slow (usually less than  $2 \text{ deg s}^{-1}$ ), curvy motion that occurs during the periods of relative fixation between microsaccades and/or saccades. Referred to as 'slow control' in some

early studies, drift is typically not conjugate and it resembles a random walk [35] (figure 1a). The physiological and perceptual consequences of drift are less well known than those of microsaccades. Some reports have linked drift production to the sustained activation of area V1 neurons [36] (as opposed to the transient activation triggered by microsaccade production [8,24]). Recent research indicates that whereas only microsaccades effectively restore visibility after perceptual fading during fixation [26], both microsaccades and drift serve to prevent fading from occurring in the first place [33].

### (c) Tremor

Also known as ocular microtremor, tremor occurs simultaneously with drift. It is the smallest of the three fixational eye movements, with an amplitude roughly equal to one photoreceptor width, and dominant frequencies averaging approximately 84 Hz and ranging from 70 to 103 Hz [4,37]. Tremor's minute nature has posed a significant challenge to its non-invasive measurement. Thus, little is known about the physiological or perceptual consequences of tremor on primate vision [4]. No studies to date, to the best of our knowledge, have found a direct link between tremor production and human visual perception [38].

### (d) The changing sizes of microsaccades: early versus contemporary studies

To measure the quality of ocular fixation, one must be able to establish how often, and to what extent, eye motion intrudes upon perfect fixation. Because fixational eye movements are the main disruptors of gaze stillness during fixation, one must objectively ascertain their basic dynamic properties, such as frequency, speed and amplitude, to determine the extent and limitations of gaze (in)stability. As mentioned earlier, many more studies have been conducted on microsaccades than on drift and especially tremor, because the properties of the latter (e.g. the minute magnitude of tremor) challenge the capabilities of most eye-tracking systems. Yet, it is the magnitude of microsaccades that has been an object of controversy for the better part of the past decade and a half.

Briefly, many early studies considered microsaccadic eye movements to be smaller than 12 arc min [39]. This original

cut-off arose from observations that the distribution of microsaccadic sizes fell off drastically after 12 arc min, but later research was unable to replicate the finding. Instead, studies conducted in the new millennium typically found microsaccadic magnitudes to reach up to (and sometimes go beyond) 1° of visual angle [5,9] (see also figure 1b(i)). Various possible explanations for this discrepancy have been proposed, including

- (a) Use of naive versus trained subjects. Rolfs has proposed that, whereas contemporary studies typically rely on naive subjects with minimal fixation experience, older studies used to rely on highly trained observers—often the scientists conducting the research—who were able to maintain unusually stable gaze fixation [40]. However, various contemporary studies have found that trained and naive subjects exhibit equivalent microsaccade magnitudes [19,27]. Winterson & Collewijn [41] found that naive subjects could be taught to transiently suppress their microsaccade production, but it is unclear if this reduction in rate was accompanied by a size decrease [42].
- (b) Higher signal-to-noise ratio in contemporary eye-trackers. Collewijn & Kowler [39] have argued that current video-oculography methods produce noisier data than the optical levers from the 1960s and 1970s. One limitation of this hypothesis is that, whereas noise in the signal might lead to unreliable detection of the smallest microsaccades (i.e. 5 arc min), it does not explain the shift to the larger maximum sizes [42]. Conducting simultaneous recordings of human microsaccades with video-oculography (EyeLink 1000, SR research) and a contact lens-mounted search coil, McCamy *et al.* [43] found good correspondence of microsaccade detection from video-tracking and search coil data, except that 5% of the microsaccades classified in one system were not classified in the other. This minor discrepancy was largely constrained to microsaccades smaller than 0.5°. At the opposite end, 100% of microsaccades larger than 0.5° detected with the search coil were also detected with the video-tracker, and 99.8% of microsaccades larger than 0.5° detected with video-tracking were also detected with the search coil method.
- (c) The optical lever method used in the early studies may have reduced the sizes of microsaccades by hindering eye motion [5]. Indirect support for this possibility comes from the observation of reduced magnitudes in microsaccades recorded with a piezoelectric sensor requiring contact with the surface of the eye [38].
- (d) Contemporary video-based eye-trackers measure different ocular structures from the older techniques, and the movements of these structures may differ during a microsaccade. Most current eye trackers measure pupil movements, whereas older techniques such as the optical lever tracked other structures more aligned with the movement of the eyeball as a whole (as do search coils). Nystrom *et al.* [42] analysed eye images to compare the motion between the first and the fourth Purkinje reflections as well as the pupil during underlying microsaccades, and found pupil-based eye-trackers to overestimate the peak velocity and overshoot amplitude of microsaccades. However, McCamy *et al.*'s [38] simultaneous recordings of human microsaccades via search coil and video-tracking techniques produced no significant differences in the

magnitudes of microsaccades recorded with one method versus the other. Yet, it is possible that search coils could distort the eye movement dynamics during coil- and video-systems co-recordings [42].

- (e) Contemporary automated microsaccade-detecting algorithms can produce larger estimates of microsaccade magnitudes than the manual detection methods used in early studies. Nystrom *et al.* [42] found larger microsaccade magnitudes, on average, with the popular microsaccade-detecting algorithm developed by Engbert & Kliegl [23] than with manual tagging.
- (f) Early microsaccade analyses might have omitted square wave-jerks (SWJs), whereas contemporary studies are likely to include them. SWJs are comprised of an initial microsaccade that takes the eye away from the fixation target, shortly followed by a corrective microsaccade back towards the target: both microsaccades tend to be larger than 0.5° [44–48].
- (g) An additional obstacle to comparing microsaccade data from early and contemporary studies is that the early studies did not usually disclose 'the exact computation of onset, offset, or amplitude, even though results including amplitudes were reported' [42, p. 18].
- (h) Other possible discrepancies between older and contemporary studies include differences in the amount of head motion allowed by bitebars versus chinrests, as well as 'changes in behavioral strategies due to contact lens wear, and differences in visual recording environments' [42, p. 18].

The reasons behind the considerable increase in microsaccadic size in the new millennium remain largely undetermined at the time of this writing. Nystrom *et al.* [42] conducted the most comprehensive attempt to date to explain the difference (in terms of the ocular structures tracked by early and current studies, and the use of automated algorithms to detect microsaccades in recent work). Their data, they concluded, may account for 'a twofold difference in amplitude', but 'it cannot explain the fivefold increase in maximal amplitude from 12 min arc to about one degree' [42, p. 23]. A definite reason (or combination of reasons) for the historical difference may no longer be within our reach, but despite this lack of closure, current consensus seems to have largely consolidated around a definition of microsaccades that includes magnitudes up to 1° [5,9].

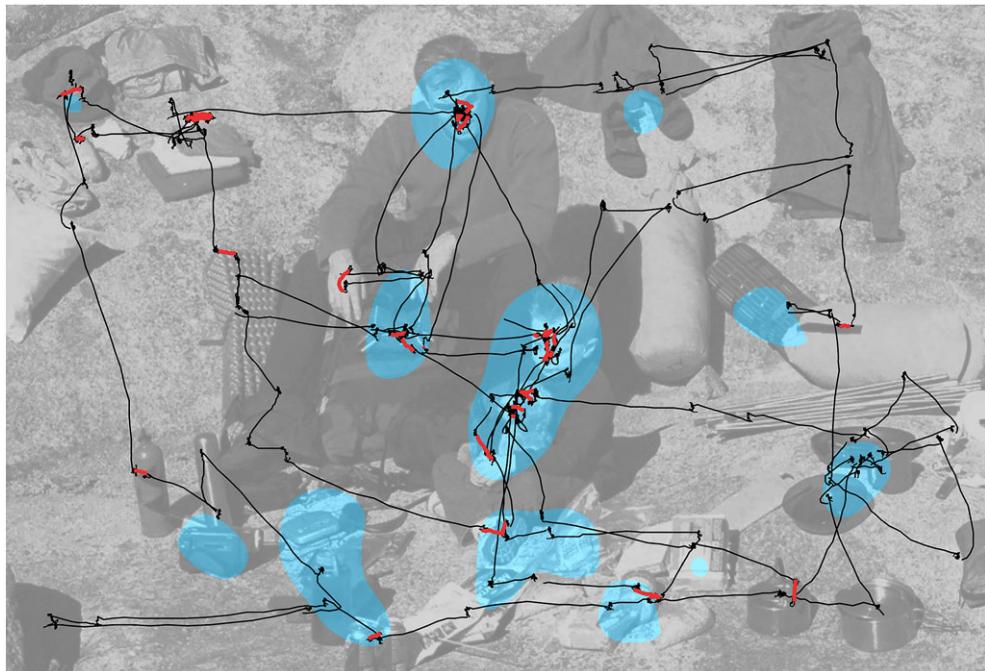
## (e) Visual and cognitive determinants of fixation accuracy

Bottom-up, as well as top-down factors, have been shown to affect fixational dynamics in humans and primates. Here we review some of the visual and cognitive influences on gaze stability.

### (i) Visual factors

During prolonged fixation, the physical parameters of the fixation target—such as its size [46,49], shape [50,51], colour [52] or eccentricity [53]—can affect fixational eye movements. For instance, microsaccade rates decrease linearly and microsaccade magnitudes increase linearly with target size [46]. Fixation target luminance has little effect on microsaccade rates and magnitudes, however [46,49].

During exploration and search, the characteristics of the visual scenes presented also affect fixational eye movements. For instance, blank visual scenes result in decreased saccade



**Figure 2.** Microsaccades concentrate on scene locations that are consistently fixated across observers. Consistently fixated regions are denoted in blue; inconsistently fixated regions are denoted in grey. Black traces indicate the eye positions of one subject over 45 s of free exploration; red lines denote microsaccades. From [11].

and microsaccade production, compared with natural scenes [10,54]. Microsaccades are also less frequent, albeit larger, in the dark, whereas drifts are both larger and more frequent. Dark backgrounds, moreover, produce a fixational upshift, driven mainly by microsaccades, in which fixation is directed above the fixation target. The upshift is caused by the background's low luminance, rather than by low contrast between the background and the fixation target [14,55–57].

The content of natural scenes also affects microsaccade production, with higher rates of microsaccades concentrating on salient parts of the scene (i.e. on faces versus non-faces, and on objects versus backgrounds) [10,11]. McCamy *et al.* [11] found that observers generate more microsaccades on more informative than less informative natural scene regions (figure 2) and proposed that the visual system uses microsaccades to increase information acquisition from informative locations. This same study also found that microsaccade rates were higher in scene regions that had low redundancy in terms of their classical statistics (i.e. high contrast, high entropy and low correlation). The size of the visual scene explored also affects (micro)saccadic rates and magnitudes. A recent study measured eye movements during fixation and exploration of natural and blank scenes of diminishing sizes. As the scene sizes decreased, subjects scanned them with smaller and less frequent (micro)saccades [58] (figure 3).

### (ii) Cognitive factors

In 1952, Barlow [59] proposed that microsaccades represented shifts in visual attention. Numerous studies conducted subsequently have established a powerful link between attention targeting and microsaccade production (see [5] for a review of the cognitive influences on microsaccade rates and directions). Thus, it makes sense that attentional cues should affect microsaccade rates. Notably, attentional shifts can cause the eyes to stop briefly. The microsaccadic rate transiently drops approximately 100–200 ms after the onset of an attentional cue, followed by a transient rate enhancement. This phenomenon,

known as microsaccadic inhibition, or the 'microsaccadic signature', was first reported by Engbert & Kliegl [23] and follows a comparable time course to that described previously for large saccades [21].

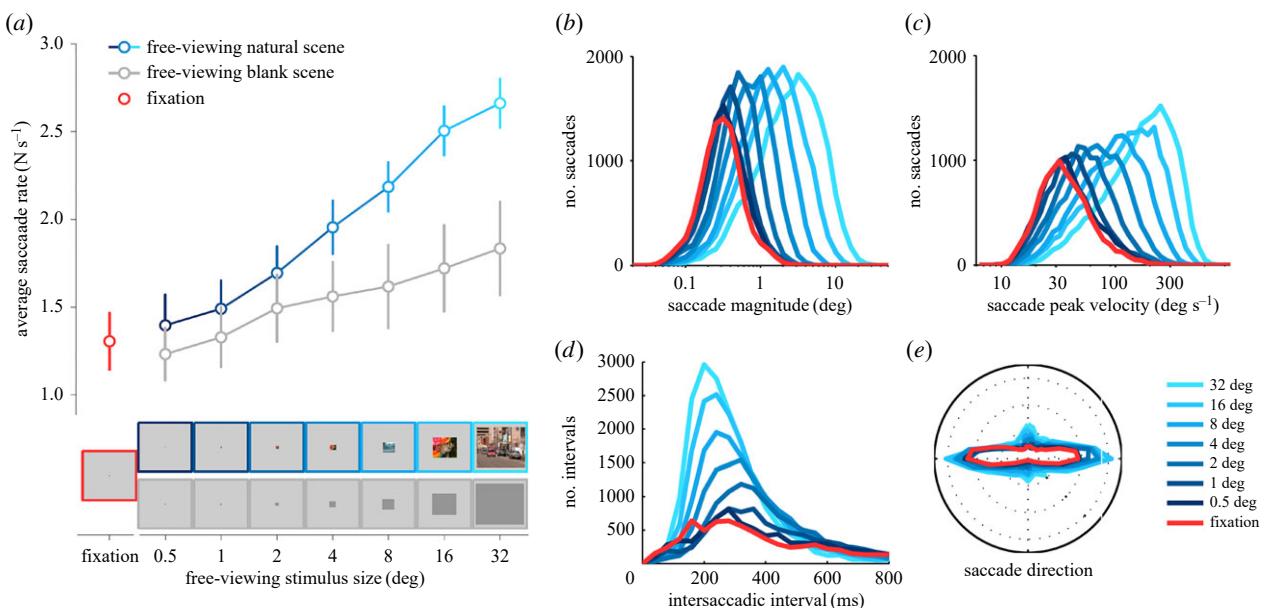
Cognitive factors also affect fixation and microsaccade production during the performance of non-visual tasks. A recent study found that increased difficulty in a mental arithmetic task resulted in decreased microsaccade rates and increased microsaccade magnitudes [3] (figure 4). More generally, mental fatigue owing to increased time-on-task has the effect of destabilizing fixation by decreasing saccadic and microsaccadic velocities and increasing drift velocity [60,61]. These findings have potentially critical implications for the replication of experimental data collected from tired subjects. Certain alterations to the physiological environment, such as hypobaric hypoxia, also produce unstable fixations and increased drift velocities [62].

### Gaze fixation versus 'gaze holding'

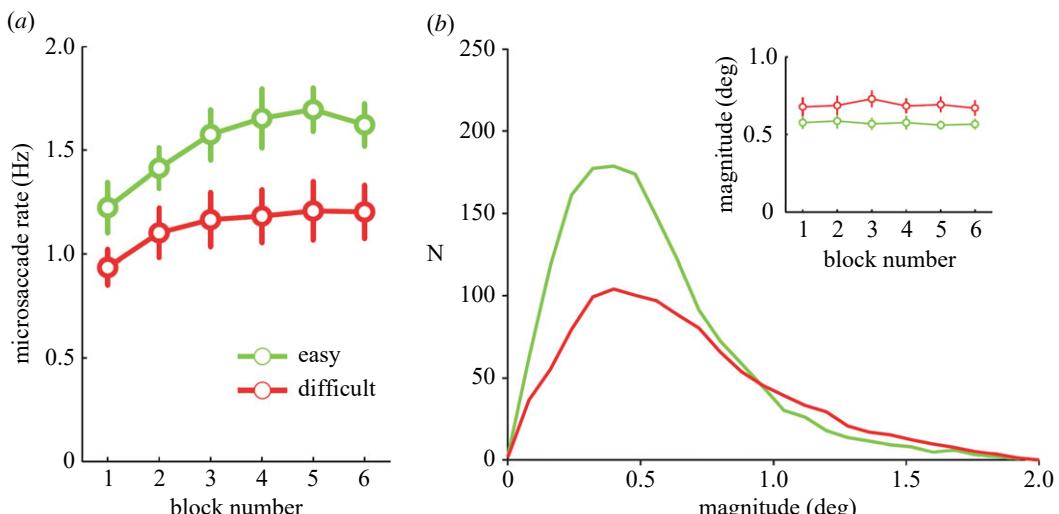
Classic studies found that experimental subjects could be trained to suppress microsaccade production for several seconds at a time [63–65]. The directions given to subjects, in particular, affected their microsaccade production: participants produced fewer microsaccades when instructed to 'hold' their eyes in place than when instructed to merely 'fixate' [63]. Winterson & Collewijn [41] also found that naive subjects could reduce their microsaccade rates from 2 to 0.5 Hz 'with minimal instruction'. More recently, Tse *et al.* reported that, in task conditions where the goal is to maintain very accurate fixation, the sudden onset of a stimulus—which typically captures attention—has no influence on microsaccade or drift dynamics [66,67].

### Microsaccade production during the performance of high-acuity tasks

In the late 1970s, Winterson & Collewijn [41] and Bridgeman & Palca [68] set out to study microsaccade dynamics during the performance of fine visuomotor tasks. Winterson and Collewijn found microsaccadic rates to be diminished while subjects



**Figure 3.** (Micro)saccade rates and magnitudes decrease with image size. (a) Rates decrease parametrically as the size of the scene decreases. (b–e) The saccadic continuum found for (micro)saccadic rates extends to (micro)saccade magnitude, peak velocity, intersaccadic interval and direction. Data from the natural scene condition (plots) and blank scene condition (not shown) were equivalent. From [58].



**Figure 4.** Task difficulty during mental arithmetic decreases microsaccade rates and increases microsaccade magnitudes. (a) Average microsaccade rate during easy (count forward by twos) and difficult (count backwards by thirteen) mental arithmetic tasks. (b) Microsaccade magnitude distributions across conditions. Error bars represent the s.e.m. across participants. Modified from [3].

either shot a rifle or threaded a sewing needle, and concluded that microsaccades were 'neither important nor essential for the successful completion' of such tasks. Bridgeman & Palca [68] reported similar results with a high-acuity task that was purely visual in nature. Thirty years later, Ko *et al.* [34] re-examined the question by asking subjects to thread a needle in a virtual environment. Unlike the previous studies, they found that microsaccades produced during their high-acuity task were critical to its performance, in that they sequentially relocated the centre of gaze between the tip of the thread and the eye of the needle, to help maintain their relative alignment.

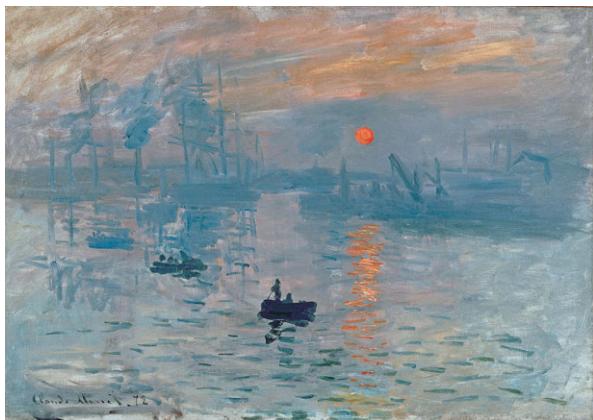
## (f) Neurological conditions resulting in increased fixation instability

Various neurological disorders present with increased instability during gaze fixation, which can result in blurred

and shaky vision. Recent research efforts have focused on characterizing fixational eye movements, especially microsaccades, in neurological disease, seeking a better understanding of its pathogenesis, and aiming to improve early and differential diagnosis (see [5,69] for reviews).

## 2. Retinal stabilization then and now: classic studies and contemporary research

Scientists have pondered the perceptual effects of ocular motion, and those of its counterpart, ocular stillness, for over 200 years. In the late 1700s, more than 50 years after Jurin's report of relentless eye trembling, Erasmus Darwin (a grandfather of Charles Darwin) documented that fixing one's gaze (which minimizes eye motion without stopping it completely) can dramatically affect perception. Darwin



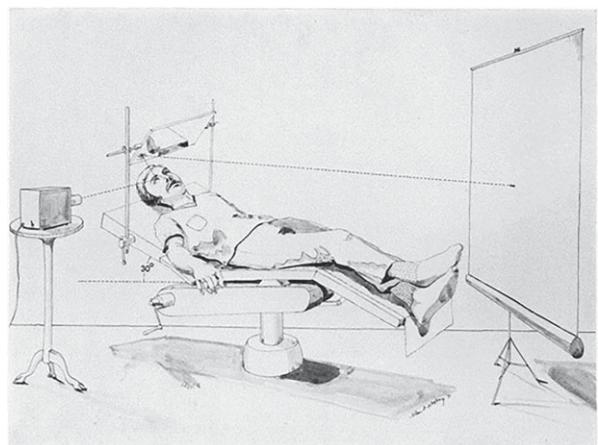
**Figure 5.** Troxler fading. In *Impression, Sunrise*, by Claude Monet, the rising sun appears brighter than the rest of the scene, but has the same physical luminance as the background clouds [72]. Equiluminant objects are very susceptible to Troxler fading: fixating one's gaze on the sailor for a few seconds makes the solar disc fade from perception [73].

wrote that staring at a small sample of scarlet silk on white paper for a long time caused the fabric to grow ever dimmer in colour until it appeared to vanish [70]. In 1804, the Swiss philosopher Ignaz Paul Vital Troxler rediscovered the phenomenon [71], and noted that deliberately focusing one's gaze on a target can make unmoving images in the surrounding region gradually fade away—this type of vanishing illusion is known today as Troxler fading (figure 5).

The mechanisms producing and thwarting Troxler fading are not well understood, although they presumably result from the interaction between eye movement production (or lack thereof) and neural adaptation (i.e. decreased or absent neural responses to unchanging stimulation). Helmholtz [74] originally suggested that the incessant 'wandering of the gaze' prevented retinal 'fatigue'. It is likely, however, that neural adaptation ensuing from lack of eye motion affects neurons throughout the visual pathway. In the late 1950s, Clarke made a connection between Troxler's fading and the fading of stabilized images in the laboratory (see paragraphs below), and attributed both phenomena to neural adaptation [75–78]. McCamy *et al.* [33] have proposed that the prevention and reversal of visual fading, although they appear phenomenologically complementary, may involve different neural mechanisms as well as adaptation timescales.

The effects of ocular stillness on perception became a focused area of research in the 1950s, when technological developments allowed for the first time the study of vision in conditions of 'retinal stabilization' [79–82]. Retinal stabilization techniques entail shifting any and all visual stimuli presented to the eye in such a way as to nullify all concurrent eye motion. Many of the initial investigations relied on Yarbus's novel implementation of the suction cup technique, where a suction device served to attach a tightly fitting contact lens assembly to the eyeball. The contact lens assembly displayed an image (which the subject viewed through a powerful lens), so that every gaze displacement resulted in the image moving with the eye and negating the effects of eye motion. The motion cancellation (even if less than perfect, owing to contact lens slippage and other difficulties [83]) led to rapid visual fading, usually after a few seconds (but sometimes taking longer).

In 1956, Cornsweet [55] found that perceptual fading under gaze stabilization conditions did not increase the frequency of microsaccades or the size of drift, and concluded



**Figure 6.** Stevens's full-body paralysis experiment. The subject laid down on an operating table. A projector illuminated a small mirror mounted on a stalk attached to a tight fitting contact lens. This produced a dot on the screen that followed the subject's eye movements. From [84].

that target disappearance is not the stimulus for saccades (later studies replicated his conclusion [54]). We note, however, that even if reduced visibility fails to raise microsaccade rates, microsaccade occurrence does have the effect of enhancing visibility (see 'Tightly timed correlations' section for details). This kind of one-directional relationship is quite common in physiology (increased exercise has the habitual effect of raising one's heart rate, even if decreased heart rates do not trigger bouts of physical activity). As to what, then, serves to jumpstart microsaccade production: the evidence supports a combined role of both fixation error and neural noise in triggering microsaccades, with the contribution of each signal depending on the magnitude of the fixation error (see [48] for a review).

More heroic attempts to completely eliminate eye motion were to follow. In 1976, John K. Stevens underwent the intravenous injection of a paralytic drug with the intent to obliterate eye movements (he received artificial ventilation during the experiment; figure 6). An arterial tourniquet prevented local blood flow to one of Stevens' arms, allowing him to use his unparalysed fingers to provide simultaneous reports of his perception. Stevens's perceptual experience was greatly hampered by image fading, which 'became a real problem' during his full-body paralysis [84].

Later approaches to gaze stabilization moved away from the suction cup technique, measuring instead the movements of the eye in a non-invasive fashion, and then transmitting the eye-position data to a projection system that moves the image with the eye [85,86]. This transmission is not instantaneous, however, but it includes a significant delay (7.5–10 ms in some recent studies; see for instance [54]), which may produce the unintended refresh of the retinal image and thus the disruption of fading. Such unaccounted for, or residual, eye motion, can greatly complicate data interpretation and replication of retinal stabilization studies.

### (a) Caveats of retinal stabilization studies

Starting in the 1950s, and throughout subsequent decades, there was a proliferation of attempts to study vision during retinal stabilization conditions, with and without superimposing simulated eye motion on the purportedly stabilized image. Unfortunately, no historical or currently available method

ensures perfect retinal stabilization, particularly in the presence of microsaccades and saccades, owing to their high velocity—except perhaps in the case of entoptic images, which are limited in their experimental scope. Such obstacles to complete stabilization pose an important caveat to data interpretation. Indeed, studies from different groups have often arrived at contradictory results, perhaps owing to different amounts of undetermined residual motion in different experiments. Another problem with visual stimulation during retinal stabilization conditions is that even perfectly stabilized eye movements may result in associated corollary discharges from oculomotor areas—thus introducing another confounding factor in the interpretation of findings.

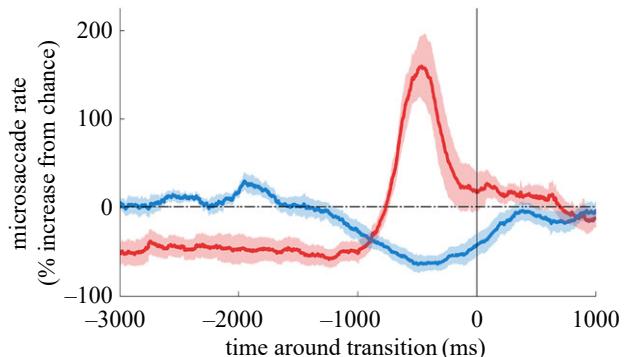
One might wonder whether pharmacological paralysis of the extraocular muscles could be a better way to stop eye motion (as opposed to traditional retinal stabilization). Yet, eye paralysis also has a number of caveats (in addition to its invasiveness), including the fact that any attempted eye movements during eye paralysis may still produce corollary discharges. Thus, attempted saccades during eye paralysis might result in the perceived displacement of the visual field. Eye paralysis moreover precludes simultaneous or interleaved recordings of behavioural or neural responses to eye motion and to stimulus motion, as well as—for all practical purposes—recording from the same neurons before and after eye paralysis. More critically, no currently available technique ensures perfect eye paralysis in an awake animal or subject [25].

### (b) Eye paralysis in the clinic

Some clinical conditions resulting in eye paralysis provide a rare, albeit intriguing, glimpse into the characteristics of everyday vision in the absence of eye movements. Gilchrist and co-workers conducted a series of studies in a patient (A.I.) who was unable to make saccades [87,88]. One might have expected A.I. to struggle with frequent instances of visual fading (owing to neural adaptation resulting from her lack of eye motion). Instead, the young woman was able to conduct normal visual and visuomotor activities with little difficulty, including reading at normal speed or making herself a cup of tea [88]. The reason for A.I.’s visual proficiency is that she had learned to produce ‘head saccades’. That is, she constantly moved her head in such a way as to mimic regular eye saccades (indeed, A.I.’s head saccades were comparable to standard saccades in their amplitude, duration of intersaccadic intervals, length of intervening fixations and range of visual scanning during the exploration of an image, even though they had lower speeds). It is interesting to note that A.I.’s pathology did not preclude her from producing small-amplitude drifts. Yet, she supplemented her (presumably insufficient) drift motion with saccadic motion via her head movements. The authors concluded that the brain preferentially samples visual information in a discrete fashion (via ‘saccadic movements, of the head or the eye’), rather than via the smooth, continuous scanning of a scene [87].

### (c) Alternatives to retinal stabilization: entoptic images, afterimages and tightly timed correlations

Aiming to study how lack of eye motion affects perception, some classic and recent research has moved away from



**Figure 7.** Microsaccade rates increase shortly before transitions ( $t = 0$ ) to perceptual intensification (red) and decrease before transitions to fading. From [26].

stabilization attempts, relying instead on alternative approaches to achieving ocular stillness.

#### (i) Entoptic images

One clever way to get around the various technical issues that stand in the way of *perfect* retinal stabilization is the study of entoptic images, which—together with afterimages—provide a tantalizing glimpse of everyday vision in the absence of eye motion. In 1996, Coppola & Purves [89] set out to study the perception of the entoptic images (formed by retinal vessels and other structures within the eye that become briefly visible when illuminated), which are completely stable with respect to the eye because the vessels are attached to the retina. They found that visual fading could happen in less than 80 ms.

#### (ii) Afterimages

Unlike our perception of regular images, our perception of afterimages is eminently unstable, in that afterimages appear to wobble during fixation, presumably owing to the concurrent production of fixational eye movements [90]. Because of their perfect correspondence with eye motion, afterimages may be a useful tool to study the interaction between gaze (in)stability, perception and the time course of adaptation.

#### (iii) Tightly timed correlations

Unlike the strategies discussed thus far, this approach does not attempt to eliminate or minimize ocular motion. Instead, it depends on identifying precisely when eye movements occur, to then relate them to ongoing changes in perceptual or neurophysiological responses, via tightly timed correlations and analyses. Martinez-Conde *et al.* [27] developed such a method to study how microsaccade production affects visibility during a Troxler fading task. Reasoning that the perceptual fluctuations one experiences during Troxler fading (figure 5) might be due to changes in microsaccade occurrence, the authors asked human subjects to continuously report on the visibility of a visual target (which was designed to fade from view about 50% of the time during fixation), while measuring their concurrent fixational eye movements. The results showed increased microsaccade rates before transitions to increased visibility, and decreased microsaccade rates before transitions to fading or decreased visibility (figure 7), both for targets presented peripherally and parafoveally [27]. Later studies extended the results to foveal presentations of fading stimuli ([26], including minute

visual targets entirely circumscribed to the area of the fovea [31]) and to targets of varied contrasts [31] and spatial frequencies [91].

However, the correlations observed between increased microsaccade rates and higher visibility did not necessarily prove that microsaccades enhanced perception. Instead, it could be that a third, unknown process, produced both changes in perception and changes in microsaccade rates. To rule out this possibility, McCamy *et al.* [26] conducted a new experiment in which subjects had to report on the visibility of a target that varied physically in contrast. The authors then used the reaction times to such physical changes to estimate the times at which perceptual fluctuations occurred for targets that did not change physically. The results showed changes in microsaccade rates to precede the perceptual changes, and thus indicated a causal relationship between microsaccade occurrence and target visibility.

This same study also developed quantitative analyses of the contribution and efficacy of microsaccades (and other eye movements) on perception, defining the microsaccadic *contribution* as the percentage of perceptual changes caused by microsaccades, and the microsaccadic *efficacy* as the percentage of microsaccades that caused perceptual changes. The results showed microsaccades to be the most important contributor to restoring the visibility of faded targets during fixation [26]. An ensuing study asked about the role of the different fixational eye movements not on the reversal of fading, but on its prevention [33]. The findings indicated that the *reversal* of fading (i.e. the restoration of visibility) and the prevention of fading are mediated by different fixational eye movements, and likely have different neural bases. Whereas microsaccades are most important to the restoration of visibility *after* fading, both microsaccades and drift may prevent fading from occurring in the first place. Put another way, the combined action of microsaccades and drifts prevents the regular occurrence of fading in natural vision, but not perfectly. When fading does occur (despite the combined actions of microsaccades and drift), microsaccades are most effective to reverse it and restore visibility during fixation. Indeed, the available evidence suggests that microsaccades are capable of restoring the visibility of any and all targets that do fade during fixation.

### 3. Conclusion

The concept of ocular fixation must be understood in relative, rather than absolute terms. This is both because there is no such thing as perfect fixation—owing to the constant occurrence of microsaccades, drift and tremor while one tries to fixate—and because no current technologies enable the complete removal, or perfect compensation, of eye motion. Yet, there is a long history of investigations concerning the perceptual effects of eliminating—or at least, minimizing—eye motion. These studies have encompassed approaches including various kinds of retinal stabilization techniques, work on entoptic images and afterimages, tightly timed analyses of perceptual and ocular events, and occasional clinical case studies of patients suffering from reduced ocular motion. This combined body of research highlights the instability of human gaze, even in conditions of sustained fixation in which our subjective experience wrongly informs us that our eyes are steady. Such relentless eye motion serves many critical functions, such as the efficient sampling of our visual environment, as well as the prevention of the neural adaptation and perceptual fading that would ensue whenever we faced unchanging visual stimulation. More generally, the findings reviewed here underline the conclusion that natural vision, although often characterized in terms of its spatial properties, is also a temporal process, in which many of its time-based characteristics are derived from the dynamics of eye movements—even during the attempt to fix one's gaze.

**Authors' contributions.** S.M.-C. and S.L.M. contributed to drafting and revising the article, and both approved the final version to be published.

**Competing interests.** We declare we have no competing interests.

**Funding.** This work was supported by a challenge grant from Research to Prevent Blindness Inc. to the Department of Ophthalmology at SUNY Downstate, by the Empire Innovation Programme (Awards to S.M.-C. and S.L.M.), and by the National Science Foundation (Award 1523614 to S.L.M.).

**Acknowledgements.** We thank Rosario Malpica and Daniel Cortes-Rastrollo for administrative and technical assistance.

## References

1. Jurin. 1738 An essay on distinct and indistinct vision. In *A compleat system of opticks in four books, viz. a popular, a mathematical, a mechanical, and a philosophical treatise. To which are added remarks upon the whole* (ed. R Smith), pp. 115–171. Cambridge, UK: Published by the author.
2. Engbert R, Mergenthaler K, Sinn P, Pikovsky A. 2011 An integrated model of fixational eye movements and microsaccades. *Proc. Natl. Acad. Sci. USA* **108**, E765–E770. (doi:10.1073/pnas.1102730108)
3. Siegenthaler E, Costela FM, McCamy MB, Di Stasi LL, Otero-Millan J, Sonderegger A, Groner R, Macknik S, Martinez-Conde S. 2014 Task difficulty in mental arithmetic affects microsaccadic rates and magnitudes. *Eur. J. Neurosci.* **39**, 287–294. (doi:10.1111/ejn.12395)
4. Martinez-Conde S, Macknik SL, Hubel DH. 2004 The role of fixational eye movements in visual perception. *Nat. Rev. Neurosci.* **5**, 229–240. (doi:10.1038/nrn1348)
5. Martinez-Conde S, Otero-Millan J, Macknik SL. 2013 The impact of microsaccades on vision: towards a unified theory of saccadic function. *Nat. Rev. Neurosci.* **14**, 83–96. (doi:10.1038/nrn3405)
6. McCamy MB, Macknik SL, Martinez-Conde S. 2014 Natural eye movements and vision. In *The new visual neurosciences* (eds JS Werner, LM Chalupa), pp. 849–864. Cambridge, MA: The MIT Press.
7. Ratliff F, Riggs LA. 1950 Involuntary motions of the eye during monocular fixation. *J. Exp. Psychol.* **40**, 687–701. (doi:10.1037/h0057754)
8. Martinez-Conde S, Macknik SL, Hubel DH. 2000 Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys [published erratum appears in *Nat. Neurosci.* 2000 Apr 3, 409]. *Nat. Neurosci.* **3**, 251–258. (doi:10.1038/72961)
9. Martinez-Conde S, Macknik SL, Troncoso XG, Hubel DH. 2009 Microsaccades: a neurophysiological analysis. *Trends Neurosci.* **32**, 463–475. (doi:10.1016/j.tins.2009.05.006)
10. Otero-Millan J, Troncoso XG, Macknik SL, Serrano-Pedraza I, Martinez-Conde S. 2008 Saccades and microsaccades during visual fixation, exploration, and search: foundations for a common saccadic generator. *J. Vis.* **8**, 21.1–21.18.
11. McCamy MB, Otero-Millan J, Di Stasi LL, Macknik SL, Martinez-Conde S. 2014 Highly informative

natural scene regions increase microsaccade production during visual scanning. *J. Neurosci.* **34**, 2956–2966. (doi:10.1523/JNEUROSCI.4448-13.2014)

12. Rolfs M, Kliegl R, Engbert R. 2008 Toward a model of microsaccade generation: the case of microsaccadic inhibition. *J. Vision* **8**, 1–23. (doi:10.1167/8.11.5)

13. Hafed ZM, Goffart L, Krauzlis R. 2009 A neural mechanism for microsaccade generation in the primate superior colliculus. *Science* **323**, 940–943. (doi:10.1126/science.1166112)

14. Ditchburn RW, Ginsborg BL. 1953 Involuntary eye movements during fixation. *J. Physiol.* **119**, 1–17. (doi:10.1113/jphysiol.1953.sp004824)

15. Krauskopf J, Cornsweet TN, Riggs LA. 1960 Analysis of eye movements during monocular and binocular fixation. *J. Opt. Soc. Am.* **50**, 572–578. (doi:10.1364/JOSA.50.000572)

16. Lord MP. 1951 Measurement of binocular eye movements of subjects in the sitting position. *Brit. J. Ophthalm.* **35**, 21–30. (doi:10.1136/bjo.35.1.21)

17. Zuber BL, Stark L, Cook G. 1965 Microsaccades and the velocity–amplitude relationship for saccadic eye movements. *Science* **150**, 1459–1460. (doi:10.1126/science.150.3702.1459)

18. Bahill AT, Clark MR, Stark L. 1975 The main sequence, a tool for studying human eye movements. *Math. Biosci.* **24**, 191–204. (doi:10.1016/0025-5564(75)90075-9)

19. Troncoso XG, Macknik SL, Martinez-Conde S. 2008 Microsaccades counteract perceptual filling-in. *J. Vision* **8**, 214. (doi:10.1167/8.14.15)

20. Zuber BL, Crider A, Stark L. 1964 Saccadic suppression associated with microsaccades. *QPR* **74**, 244–249.

21. Reingold EM, Stampe D. 2000 *Saccadic inhibition and gaze contingent research paradigm. Reading as perceptual process*. Amsterdam, The Netherlands: Elsevier.

22. Hafed ZM, Clark JJ. 2002 Microsaccades as an overt measure of covert attention shifts. *Vision Res.* **42**, 2533–2545. (doi:10.1016/S0042-6989(02)00263-8)

23. Engbert R, Kliegl R. 2003 Microsaccades uncover the orientation of covert attention. *Vision Res.* **43**, 1035–1045. (doi:10.1016/S0042-6989(03)00084-1)

24. Martinez-Conde S, Macknik SL, Hubel DH. 2002 The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *Proc. Natl Acad. Sci. USA* **99**, 13 920–13 925. (doi:10.1073/pnas.212500599)

25. Troncoso XG, McCamy MB, Jazi AN, Cui J, Otero-Millan J, Macknik SL, Costela FM, Martinez-Conde S. 2015 V1 neurons respond differently to object motion versus motion from eye movements. *Nat. Commun.* **6**, 8114. (doi:10.1038/ncomms9114)

26. McCamy MB, Otero-Millan J, Macknik SL, Yang Y, Troncoso XG, Baer SM, Crook SM, Martinez-Conde S. 2012 Microsaccadic efficacy and contribution to foveal and peripheral vision. *J. Neurosci.* **32**, 9194–9204. (doi:10.1523/JNEUROSCI.0515-12.2012)

27. Martinez-Conde S, Macknik SL, Troncoso XG, Dyar TA. 2006 Microsaccades counteract visual fading during fixation. *Neuron* **49**, 297–305. (doi:10.1016/j.neuron.2005.11.033)

28. van Dam LC, van Ee R. 2006 Retinal image shifts, but not eye movements per se, cause alternations in awareness during binocular rivalry. *J. Vis.* **6**, 1172–1179. (doi:10.1167/6.11.3)

29. Troncoso XG, Macknik SL, Otero-Millan J, Martinez-Conde S. 2008 Microsaccades drive illusory motion in the enigma illusion. *Proc. Natl Acad. Sci. USA* **105**, 16 033–16 038. (doi:10.1073/pnas.0709389105)

30. Laubrock J, Engbert R, Kliegl R. 2008 Fixational eye movements predict the perceived direction of ambiguous apparent motion. *J. Vision* **8**, 13.1–13.17. (doi:10.1167/8.14.13)

31. Costela FM, McCamy MB, Macknik SL, Otero-Millan J, Martinez-Conde S. 2013 Microsaccades restore the visibility of minute foveal targets. *PeerJ* **1**, e119. (doi:10.7717/peerj.119)

32. Otero-Millan J, Macknik SL, Martinez-Conde S. 2012 Microsaccades and blinks trigger illusory rotation in the ‘rotating snakes’ illusion. *J. Neurosci.* **32**, 6043–6051. (doi:10.1523/JNEUROSCI.5823-11.2012)

33. McCamy MB, Macknik SL, Martinez-Conde S. 2014 Different fixational eye movements mediate the prevention and the reversal of visual fading. *J. Physiol.* **592**, 4381–4394. (doi:10.1113/jphysiol.2014.279059)

34. Ko HK, Poletti M, Rucci M. 2010 Microsaccades precisely relocate gaze in a high visual acuity task. *Nat. Neurosci.* **13**, 1549–1553. (doi:10.1038/nn.2663)

35. Engbert R, Kliegl R. 2004 Microsaccades keep the eyes’ balance during fixation. *Psychol. Sci.* **15**, 431–436. (doi:10.1111/j.0956-7976.2004.00697.x)

36. Snodderly DM, Kagan I, Gur M. 2001 Selective activation of visual cortex neurons by fixational eye movements: implications for neural coding. *Vis. Neurosci.* **18**, 259–277. (doi:10.1017/S0952523801182118)

37. Bolger C, Bojanic S, Sheahan NF, Coakley D, Malone JF. 1999 Dominant frequency content of ocular microtremor from normal subjects. *Vision Res.* **39**, 1911–1915. (doi:10.1016/S0042-6989(98)00322-8)

38. McCamy MB *et al.* 2013 Simultaneous recordings of ocular microtremor and microsaccades with a piezoelectric sensor and a commercial video tracking system. *PeerJ* **1**, e14. (doi:10.7717/peerj.14)

39. Collewijn H, Kowler E. 2008 The significance of microsaccades for vision and oculomotor control. *J. Vis.* **8**, 20.1–20.21.

40. Rolfs M. 2009 Microsaccades: small steps on a long way. *Vision Res.* **49**, 2415–2441. (doi:10.1016/j.visres.2009.08.010)

41. Winterson BJ, Collewijn H. 1976 Microsaccades during finely guided visuomotor tasks. *Vision Res.* **16**, 1387–1390. (doi:10.1016/0042-6989(76)90156-5)

42. Nystrom M, Hansen DW, Andersson R, Hooge I. 2016 Why have microsaccades become larger? Investigating eye deformations and detection algorithms. *Vision Res.* **118**, 17–24. (doi:10.1016/j.visres.2014.11.007)

43. McCamy MB, Otero-Millan J, Leigh RJ, King SA, Schneider RM, Macknik SL, Martin-Conde S. 2015 Simultaneous recordings of human microsaccades and drifts with a contemporary video eye tracker and the search coil technique. *PLoS ONE* **10**, e0128428. (doi:10.1371/journal.pone.0128428)

44. Costela FM *et al.* 2015 Characteristics of spontaneous square-wave jerks in the healthy macaque monkey during visual fixation. *PLoS ONE* **10**, e0126485. (doi:10.1371/journal.pone.0126485)

45. Otero-Millan J, Serra A, Leigh RJ, Troncoso XG, Macknik SL, Martinez-Conde S. 2011 Distinctive features of saccadic intrusions and microsaccades in progressive supranuclear palsy. *J. Neurosci.* **31**, 4379–4387. (doi:10.1523/JNEUROSCI.2600-10.2011)

46. McCamy MB, Najafian Jazi A, Otero-Millan J, Macknik SL, Martinez-Conde S. 2013 The effects of fixation target size and luminance on microsaccades and square-wave jerks. *PeerJ* **1**, e9. (doi:10.7717/peerj.9)

47. Otero-Millan J, Schneider R, Leigh RJ, Macknik SL, Martinez-Conde S. 2013 Saccades during attempted fixation in Parkinsonian disorders and recessive ataxia: from microsaccades to square-wave jerks. *PLoS ONE* **8**, e58535. (doi:10.1371/journal.pone.0058535)

48. Otero-Millan J, Macknik SL, Serra A, Leigh RJ, Martinez-Conde S. 2011 Triggering mechanisms in microsaccade and saccade generation: a novel proposal. *Ann. NY Acad. Sci.* **1233**, 107–116. (doi:10.1111/j.1749-6632.2011.06177.x)

49. Steinman RM. 1965 Effect of target size, luminance, and color on monocular fixation. *JOSA* **55**, 1158–1165. (doi:10.1364/JOSA.55.001158)

50. St Cyr GJ, Fender DH. 1969 The interplay of drifts and flicks in binocular fixation. *Vision Res.* **9**, 245–265. (doi:10.1016/0042-6989(69)90004-2)

51. Thaler L, Schutz AC, Goodale MA, Gegenfurtner KR. 2013 What is the best fixation target? The effect of target shape on stability of fixational eye movements. *Vision Res.* **76**, 31–42. (doi:10.1016/j.visres.2012.10.012)

52. Fender DH. 1955 Variation of fixation direction with colour of fixation target. *Br. J. Ophthalmol.* **39**, 294–297. (doi:10.1136/bjo.39.5.294)

53. Sansbury RV, Skavenski AA, Haddad GM, Steinman RM. 1973 Normal fixation of eccentric targets. *J. Opt. Soc. Am.* **63**, 612–614. (doi:10.1364/JOSA.63.000612)

54. Poletti M, Rucci M. 2010 Eye movements under various conditions of image fading. *J. Vis.* **10**, 1–18. (doi:10.1167/10.3.6)

55. Cornsweet TN. 1956 Determination of the stimuli for involuntary drifts and saccadic eye movements. *J. Opt. Soc. Am.* **46**, 987–993. (doi:10.1364/JOSA.46.000987)

56. Snodderly DM, Kurtz D. 1985 Eye position during fixation tasks: comparison of macaque and human. *Vision Res.* **25**, 83–98. (doi:10.1016/0042-6989(85)90083-5)

57. Barash S, Melikyan A, Sivakov A, Tauber M. 1998 Shift of visual fixation dependent on background illumination. *J. Neurophysiol.* **79**, 2766–2781.

58. Otero-Millan J, Macknik SL, Langston RE, Martinez-Conde S. 2013 An oculomotor continuum from

exploration to fixation. *Proc. Natl Acad. Sci. USA* **110**, 6175–6180. (doi:10.1073/pnas.1222715110)

59. Barlow HB. 1952 Eye movements during fixation. *J. Physiol.* **116**, 290–306. (doi:10.1113/jphysiol.1952.sp004706)

60. Di Stasi LL, McCamy MB, Catena A, Macknik SL, Canas JJ, Martinez-Conde S. 2013 Microsaccade and drift dynamics reflect mental fatigue. *Eur. J. Neurosci.* **38**, 2389–2398. (doi:10.1111/ejn.12248)

61. Di Stasi LL, McCamy MB, Pannasch S, Renner R, Catena A, Cañas JJ, Velichkovsky BM, Martinez-Conde S. 2015 Effects of driving time on microsaccadic dynamics. *Exp. Brain Res.* **233**, 599–605. (doi:10.1007/s00221-014-4139-y)

62. Di Stasi LL *et al.* 2014 Intersaccadic drift velocity is sensitive to short-term hypobaric hypoxia. *Eur. J. Neurosci.* **39**, 1384–1390. (doi:10.1111/ejn.12482)

63. Steinman RM, Cunitz RJ, Timberlake GT, Herman M. 1967 Voluntary control of microsaccades during maintained monocular fixation. *Science* **155**, 1577–1579. (doi:10.1126/science.155.3769.1577)

64. Fiorentini A, Ercole AM. 1966 Involuntary eye movements during attempted monocular fixation. *Atti Fond Giorgio Ronchi* **21**, 199–217.

65. Steinman RM, Haddad GM, Skavenski AA, Wyman D. 1973 Miniature eye movement. *Science* **181**, 810–819. (doi:10.1126/science.181.4102.810)

66. Tse PU, Sheinberg DL, Logothetis NK. 2002 Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Res.* **42**, 1663–1669. (doi:10.1016/S0042-6989(02)00076-7)

67. Tse PU, Sheinberg DS, Logothetis NK. 2004 The distribution of microsaccade directions need not reveal the location of attention. *Psychol. Sci.* **15**, 708–710. (doi:10.1111/j.0956-7976.2004.00745.x)

68. Bridgeman B, Palca J. 1980 The role of microsaccades in high acuity observational tasks. *Vision Res.* **20**, 813–817. (doi:10.1016/0042-6989(80)90013-9)

69. Martinez-Conde S. 2006 Fixational eye movements in normal and pathological vision. *Prog. Brain Res.* **154**, 151–176. (doi:10.1016/S0079-6123(06)54008-7)

70. Darwin E. 1795 *Zoonomia; or the laws of organic life, in three parts*, 4th American edn. Philadelphia, PA: Edward Earle.

71. Troxler D (IPV). 1804 Ueber das Verschwinden gegebener Gegenstände innerhalb unseres Gesichtskreises. In *Ophthalmologische Bibliothek. II.2* (ed. JA HKuS), pp. 1–53. Jena, Germany: Springer.

72. Livingstone MS. 2002 *Vision and Art: The Biology of Seeing*. New York, NY: Abrams.

73. Safran AB, Landis T. 1998 The vanishing of the sun: a manifestation of cortical plasticity. *Surv. Ophthalmol.* **42**, 449–452. (doi:10.1016/S0039-6257(97)00134-3)

74. Helmholtz H. 1985 *Helmholtz's treatise on physiological optics*. Translated from 3rd German edition ed. Southall JPC, ed. Birmingham, AL: Gryphon Editions, Ltd.

75. Clarke FJJ. 1957 Rapid light adaptation of localised areas of the extra-foveal retina. *Opt. Acta* **4**, 69–77. (doi:10.1080/713826067)

76. Clarke FJJ. 1960 A study of Troxler's effect. *Opt. Acta* **7**, 219–236. (doi:10.1080/713826335)

77. Clarke FJJ. 1961 Visual recovery following local adaptation of the peripheral retina (Troxler's effect). *Opt. Acta* **8**, 121–135. (doi:10.1080/713826370)

78. Clarke FJJ, Belcher SJ. 1962 On the localization of Troxler's effect in the visual pathway. *Vision Res.* **2**, 53–68. (doi:10.1016/0042-6989(62)90063-9)

79. Yarbus AL. 1957 The perception of an image fixed with respect to the retina. *Biophysics* **2**, 683–690.

80. Yarbus AL. 1967 *Eye movements and vision*. New York, NY: Plenum Press.

81. Riggs LA, Ratliff F. 1952 The effects of counteracting the normal movements of the eye. *J. Opt. Soc. Am.* **42**, 872–873.

82. Ditchburn RW, Ginsborg BL. 1952 Vision with a stabilized retinal image. *Nature* **170**, 36–37. (doi:10.1038/170036a0)

83. Barlow HB. 1963 Slippage of contact lenses and other artifacts in relation to fading and regeneration of supposedly stable retinal images. *Q. J. Exp. Psychol.* **15**, 36–51. (doi:10.1080/17470216308416550)

84. Stevens JK, Emerson RC, Gerstein GL, Kallos T, Neufeld GR, Nichols CW, Rosenquist AC. 1976 Paralysis of the awake human: visual perceptions. *Vision Res.* **16**, 93–98. (doi:10.1016/0042-6989(76)90082-1)

85. Kelly DH. 1975 New method of stabilizing retinal images. *JOSA* **65**, 1184. (doi:10.1364/JOSA.65.001512)

86. Rucci M, Desbordes G. 2003 Contributions of fixational eye movements to the discrimination of briefly presented stimuli. *J. Vision* **3**, 852–864. (doi:10.1167/3.11.18)

87. Gilchrist ID, Brown V, Findlay JM. 1997 Saccades without eye movements. *Nature* **390**, 130–131. (doi:10.1038/36478)

88. Gilchrist ID, Brown V, Findlay JM, Clarke MP. 1998 Using the eye-movement system to control the head. *Proc. R. Soc. Lond. B* **265**, 1831–1836. (doi:10.1098/rspb.1998.0509)

89. Coppola D, Purves D. 1996 The extraordinarily rapid disappearance of entoptic images. *Proc. Natl Acad. Sci. USA* **93**, 8001–8004. (doi:10.1073/pnas.93.15.8001)

90. Verheijen F. 1961 A simple after image method demonstrating the involuntary multidirectional eye movements during fixation. *J. Mod. Opt.* **8**, 309–312. (doi:10.1080/713826390)

91. Costela FM, McCamy MB, Coffelt M, Otero-Millan J, Macknik S, Martinez-Conde S. 2016 Changes in visibility as a function of spatial frequency and microsaccade occurrence. *Eur. J. Neurosci.* [Epub ahead of print]. (doi:10.1111/ejn.13487)