Fixational eye movements across vertebrates: Comparative dynamics, physiology, and perception

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During visual fixation, human eyes are never still. Instead, they constantly produce involuntary "fixational eye movements." Fixational eye movements overcome neural adaptation and prevent visual fading: thus they are an important tool to understand how the brain makes the environment visible. The last decade has seen a growing interest in the analysis of fixational eye movements in humans and primates, as well as in their perceptual and physiological consequences. However, no comprehensive comparison of fixational eye movements across species has been offered. Here we review five decades of fixational eye movement studies in non-human vertebrates, and we discuss the existing evidence concerning their physiological and perceptual effects. We also provide a table that summarizes the physical parameters of the different types of fixational eye movements described in non-human vertebrates.

Keywords: fixation, comparative physiology, non-human, primates, mammals, monkey, cat, rabbit, birds, reptiles, turtle, amphibians, salamander, fish, evolution, oculomotor, microsaccades, drifts, tremor

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Introduction

When we fixate our gaze on an object of interest, our eyes are never still. Instead we constantly produce small involuntary eye movements, generally called "fixational eye movements." If these eye movements are eliminated, our perception of stationary objects fades, due to neural adaptation (Ditchburn & Ginsborg, 1952; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; Riggs & Ratliff, 1952; Troncoso, Macknik, & Martinez-Conde, 2008). When our eyes are free to move across the image once again, visual perception reappears (Yarbus, 1967). Due to their role in counteracting visual adaptation, fixational eye movements are an important tool to understand how the brain makes the environment visible, both in normal and pathological vision (Martinez-Conde, 2006). Further, because we fixate our gaze most of the time during visual exploration (Martinez-Conde, 2006; Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008), fixational eye movements are often responsible for driving our visual experience.

Fixational eye movements can help us understand the underpinnings of visual awareness (Martinez-Conde & Macknik, 2007b) in a number of ways:

1. Fixational eye movements drive the visibility (and counteract the fading of) stationary objects during fixation. Thus fixational eye movements can help constrain the spatiotemporal characteristics of visible stimuli. Moreover, the neural responses triggered by fixational eye movements along the visual pathway must encompass the neural code for visibility (Martinez-Conde, 2006; Martinez-Conde, Macknik, & Hubel, 2000, 2002).
2. Fixational microsaccades in human subjects may drive perceptual alternations for a variety of multistable stimuli (Martinez-Conde, 2006; Martinez-Conde & Macknik, 2007b; Martinez-Conde et al., 2006; Troncoso, Macknik, & Martinez-Conde, 2008; Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008; van Dam & van Ee, 2006).
3. Fixational microsaccades may indicate attentional or cognitive engagement (Engbert & Kliegl, 2003b; Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; Martinez-Conde & Macknik, 2007b; Otero-Millan et al., 2008).
4. Human subjects are unaware of their fixational eye movements (Martinez-Conde, Macknik, & Hubel, 2004). That is, despite the continuous motion caused by fixational eye movements, the world remains perceptually stable when we fixate. This perceptual stability can be foiled: the "visual jitter" illusion shows that in the absence of fixational eye movement compensation the world is seen as unstable and jittery (Murakami & Cavanagh, 1998). Thus the neuronal circuits, populations, etc., that constitute the neural correlates of visual awareness must sustain perceptual stability during fixation.

Research in fixational eye movements is one of the fastest moving fields of vision research today. The last decade has seen a proliferation of fixational eye movement studies, including a few reviews of the published literature

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	Type of eye movement	Amplitude	Frequency/ intersaccadic interval	Duration	Max speed	Mean speed	Conjugate	Study
				Mammals				
Primate	**Microsaccade**	8.4–16.2 min (means for 2 monkeys)	2.3–2.5 Hz (mean frequencies for 2 monkeys)	at least 8 msec	–	–	–	Horwitz and Albright (2003)
	Microsaccade	~40 min (mean)	–	–	–	~30 deg/sec	–	Snodderly et al. (2001)
	Microsaccade	~20 min (mean)	~3–5 Hz	29 msec (mean)	–	~30 deg/sec	–	Martinez-Conde et al. (2000)
	Microsaccade	48 min (mean)	0.3–1.4 Hz (means for 2 monkeys)	25 ms (mean)	9–110 deg/sec (median: 40 deg/sec)	~30 deg/sec	–	Bair and O’Keefe (1998)
	Microsaccade	10.1 min (median)	0.597 sec (median)	20 msec (mean)	–	–	–	Leopold and Logothetis (1998)
	Microsaccade	9.9–40.3 min (medians for 4 monkeys)	0.8–7.4 sec (medians for 4 monkeys)	–	–	–	–	Skavenski et al. (1975)
	Microsaccade	40 min (mean; minimum amplitude: 23 min)	–	–	–	–	–	Steinman et al. (1973)
	Drift	–	–	–	–	6 min/sec (mean for 1 monkey)	–	Bair and O’Keefe (1998)
	Drift	–	–	–	–	0.42–11.91 min/sec (means for 4 monkeys)[a]	–	Skavenski et al. (1975)
Cat	**Microsaccade**	“somewhat smaller” than in humans	“far fewer” than in humans	–	–	–	No (mostly monocular, and some binocular)	Hebbard and Marg (1960)
	Microsaccade	35 min[b]	–	–	–	–	–	Pritchard and Heron (1960)
	Drift	–	–	–	–	14.7 min/sec (mean for 3 cats)	–	Winterson and Robinson (1975)
	Drift	–	–	–	–	–	–	Hebbard and Marg (1960)
	Drift	“Usually ~25 min, but can exceed 2 deg”[b]	–	–	–	30 min/sec	–	Pritchard and Heron (1960)

	Type of eye movement	Amplitude	Frequency/ intersaccadic interval	Duration	Max speed	Mean speed	Conjugate	Study
	Tremor	5.6–73.3 s (average 31 s)^b	35–65 Hz (average 50 Hz)	–	–	–	No	Hebbard and Marg (1960)
	Tremor	0.4 min^b	2–40 Hz (unable to record faster rates)	–	–	–	–	Pritchard and Heron (1960)
Rabbit	**Drift**	–	–	–	–	25–50 min/sec	–	Van der Steen and Collewijn (1984)
	Drift	≤4 deg^b	–	–	≥1 deg/sec (unable to record faster rates)	1.5 min/sec	–	Collewijn and van der Mark (1972)
	Tremor	“small amplitude”	–	–	–	–	–	Collewijn and van der Mark (1972)
				Birds				
Pigeon	**Microsaccade**	–	“very low”	<20 msec	–	–	–	Nye (1969)
	Impulse	Up to 2 deg	–	–	–	–	–	Nye (1969)
	Drift	3–5 deg (occasionally exceeding the limit of the recording system: 7.5 deg)	–	–	–	1–5 deg/sec	–	Nye (1969)
	Oscillation	Up to several deg (peak-to-peak)	Short bursts with a frequency of 28–35 Hz, usually separated by intervals of 1–2 sec	Up to 0.8 sec	–	–	–	Nye (1969)
Owl	**Microsaccade**	≤1 deg	–	–	10 deg/sec	–	–	Steinbach and Money (1973)
	Drift	≤1 deg	–	–	–	–	–	Steinbach and Money (1973)
	Tremor	1 min	20 Hz	–	–	–	–	Steinbach and Money (1973)
	Oscillation	1.5 deg	Short bursts with a frequency of 20 Hz, about 4 times a minute	0.25 sec	–	–	–	Steinbach and Money (1973)
				Reptiles				
Turtle	**Drift-like**	–	–	–	–	4.8 ± 2 min/sec	–	Greschner et al. (2002)
	Periodic	Up to 5 min	5 Hz	–	Up to 21.4 deg/sec	–	–	Greschner et al. (2002)

(Engbert, 2006; Martinez-Conde, 2006; Martinez-Conde et al., 2004). However, the differences and similarities in fixational eye movements across species, as well as their potential significance, have been neglected so far. Despite wide-reaching interest in this topic (Martinez-Conde & Macknik, 2007a), a comprehensive comparative review has not been published. Here we review the comparative dynamics, the physiology, and the perceptual consequences of fixational eye movements across all species studied to date. To the best of our knowledge, our review includes all Medline-indexed studies (as well as several book chapters and other non-indexed publications) of fixational eye movements in non-human vertebrates. These span 48 years of research: from the first studies in the cat, published in 1960 (Hebbard & Marg, 1960; Pritchard & Heron, 1960), to the most recent studies in the salamander and archer fish, published in 2007 and 2008 (Baccus, Olveczky, Manu, & Meister, 2008; Olveczky, Baccus, & Meister, 2007; Segev, Schneidman, Goodhouse, & Berry, 2007). As a result of our analysis we have generated a table (Table 1) that summarizes the physical parameters of the different types of fixational eye movement across non-human vertebrates. We will relate, whenever possible, fixational eye movements in non-human vertebrates to human fixational eye movements.

	Type of eye movement	Amplitude	Frequency/ intersaccadic interval	Duration	Max speed	Mean speed	Conjugate	Study
				Amphibians				
Salamander	**Tremor-like**	About 12.5 min	–	–	–	–	–	Manteuffel et al. (1977)
	Respiratory	Up to 30 min	–	–	–	–	–	Manteuffel et al. (1977)
				Fish				
Goldfish	**Drift**	–	–	0.1–5.5 sec	≤1 deg/sec	0.36 deg/sec	No. Simultaneous in both eyes but convergent in the light	Mensh et al. (2004)
	Drift	Typically <5 deg	–	–	–	–	No. Simultaneous in both eyes but convergent	Easter (1971)
Archer Fish	**Microsaccade**	–	“rarely” found	–	–	–	–	Segev et al. (2007)
	Drift	–	0.2–1 Hz	1.33 sec	≤0.4 deg/sec	–	–	Segev et al. (2007)
	Tremor	0.1–0.2 deg	5 Hz	–	4 deg/sec	~1 deg/sec	–	Segev et al. (2007)

Table 1. Characteristics of fixational eye movements in non-human vertebrates, according to different studies. *Note*: [a]Calculated from horizontal and vertical components. [b]Vector values from H-components: a conversion factor of √2 has been assumed.

Fixational eye movements in mammals

Fixational eye movements in the primate

Fixational eye movements were originally discovered and characterized in human subjects (Ditchburn & Ginsborg, 1952, 1953; Ratliff & Riggs, 1950). Human fixational eye movements comprise three main types: microsaccades (called “*flicks*” in early studies), drift, and tremor (Figure 1). Microsaccades are the fastest and largest of the three types of fixational eye movements (Supplementary Video 1). They travel in a straight trajectory, carrying the retinal image across a range of several dozen to several hundred photoreceptor widths. Drifts are slow curvy motions that occur between microsaccades, and tremor is a very fast (~90 Hz) and extremely small oscillation (about the diameter of a foveal cone) superimposed on drifts (see Tables 1–3 of Martinez-Conde et al., 2004 for a review of fixational eye movement parameters in humans).

Fixational eye movements in old-world monkeys are very similar to human fixational eye movements (Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002; Skavenski, Robinson, Steinman, & Timberlake, 1975; Snodderly, 1987; Snodderly & Kurtz, 1985). Several macaque species have been studied to date: *Macaca*

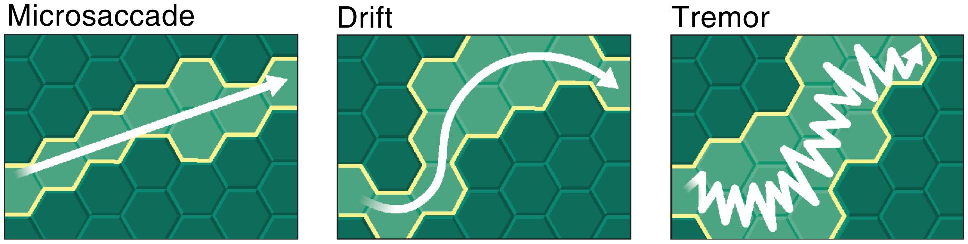

Figure 1. Cartoon representation of fixational eye movements in humans and primates. Microsaccades (straight and fast movements), drifts (curvy slow movements), and tremor (oscillations superimposed on drifts) transport the visual image across the retinal photoreceptor mosaic. From Martinez-Conde and Macknik (2007b).

mulatta (Goffart, Quinet, Chavane, & Masson, 2006; Horwitz & Albright, 2003; Leopold & Logothetis, 1998; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002; Motter & Poggio, 1984; Skavenski et al., 1975; Snodderly, Kagan, & Gur, 2001; Steinman, Haddad, Skavenski, & Wyman, 1973), *Macaca fascicularis* (Snodderly, 1987; Snodderly et al., 2001; Snodderly & Kurtz, 1985), and *Macaca nemestrina* (Bair & O'Keefe, 1998), with no substantial differences in the spatiotemporal characteristics of fixational eye movements (rate, velocity and magnitude profiles, etc.) between them. Microsaccade velocities are parametrically related to microsaccade amplitudes, following the "main sequence" in both macaques (Martinez-Conde et al., 2000) and humans (Engbert, 2006; Martinez-Conde, 2006; Martinez-Conde et al., 2006; Zuber & Stark, 1965). Fixational microsaccades have also been observed in the baboon (*Papio papio*), with amplitudes up to 2.5 degrees (Marchetti, Gauthier, & Pellet, 1983).

It is important to note that microsaccades cannot be defined according to their amplitude alone, because small exploratory or voluntary saccades can be the same size as microsaccades. Microsaccades can be defined only *operationally,* as *the involuntary saccades that are produced while the subject attempts to fixate* (Martinez-Conde, 2006). This "attempt to fixate" includes both holding the eyes still and static while foveating the visual target and also orienting the fovea toward a target. It is worth noting that microsaccade production may require the presence of a visual and/or attentional target (Otero-Millan et al., 2008).

Thus, there is no known physical parameter (or combination of parameters) that separates saccades from microsaccades. Mounting evidence points toward a common neural generator of saccades and microsaccades (Engbert, 2006; Martinez-Conde et al., 2004; Otero-Millan et al., 2008; Rolfs, Kliegl, & Engbert, 2008; Rolfs, Laubrock, & Kliegl, 2006; Zuber & Stark, 1965). However, one should note that most of the available data in support of a shared microsaccade–saccade generator are indirect. To date, only two physiological studies have directly addressed the question of the oculomotor mechanisms leading to the generation of microsaccades. In those studies, Van Gisbergen and colleagues found that putative motoneurons in the primate abducens nucleus and burst neurons in the nearby pontomedullary reticular formation were similarly active during saccades and microsaccades (Van Gisbergen, Robinson, & Gielen, 1981; Van Gisbergen & Robinson, 1977). Future research should further explore the neural bases underlying the generation of microsaccades and other fixational eye movements.

Simultaneous recordings of microsaccades and neural responses have been conducted at multiple levels of the primate visual pathway, including the lateral geniculate nucleus (LGN), area V1, and the extrastriate visual cortex (Bair & O'Keefe, 1998; Leopold & Logothetis, 1998; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002; Reppas, Usrey, & Reid, 2002; Snodderly et al., 2001). Microsaccades are predominantly excitatory at all these levels, leading to firing rate increases in both early and higher visual areas. The firing rate increases following microsaccades in the LGN and V1 are of visual origin (Figure 2) and result from the microsaccade-induced displacement of visual receptive fields over stationary stimuli. Microsaccade-driven increases in firing rate tend to be clustered in tight bursts of spikes (Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002). A recent study has suggested that primate microsaccades may improve the efficient sampling of fine spatial detail (Donner & Hemilä, 2007).

Microsaccades counteract visual fading and increase visibility during fixation in human subjects (Martinez-Conde et al., 2006; Troncoso, Macknik, & Martinez-Conde, 2008). Numerous studies have also reported that human microsaccade rates and/or directions are modulated by cognitive processes, such as the allocation of spatial attention (Betta & Turatto, 2006; Engbert & Kliegl, 2003a, 2003b, 2004; Galfano et al., 2004; Hafed & Clark, 2002; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Otero-Millan et al., 2008; Turatto, Valsecchi, Tamè, Betta, 2007; Valsecchi, Betta, & Turatto, 2007; but see also Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007 and Tse, Sheinberg, & Logothetis, 2004).

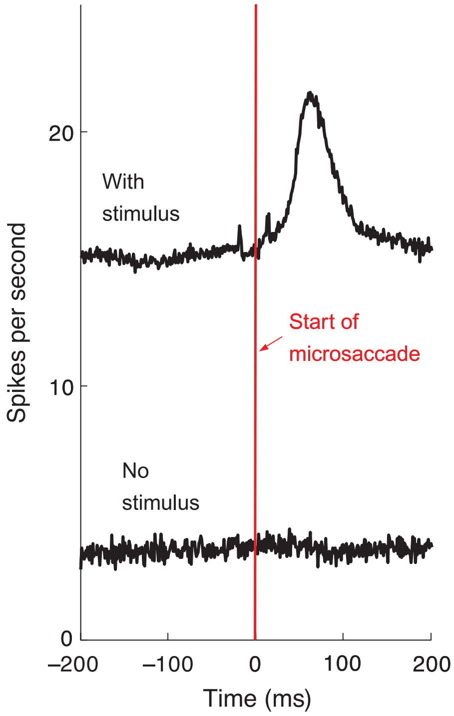

Figure 2. Microsaccades drive neural activity in primate area V1. Microsaccades lead to firing rate increases in V1 neurons (n = 308) of the awake primate. In the absence of visual stimulation, microsaccades do not increase neural activity in area V1 (n = 37 neurons). The results—shown here for the average of all neurons—were consistent with responses from individual neurons (data not shown). Modified from Martinez-Conde et al. (2000, 2002).

Neural responses to drifts have received considerably less attention than neural responses to microsaccades. This may be due to the fact that drifts are more difficult to characterize objectively than microsaccades (which are more easily detected by automatic algorithms that combine amplitude and velocity thresholds). Thus drifts are usually identified indirectly as the eye position changes that occur between microsaccades (Snodderly et al., 2001). However, this method has the potential flaw that one may unintentionally attribute non-drift-related activity (for instance, undetected tremor) to drifts. Drifts may increase firing in a subset of primate V1 neurons (Snodderly et al., 2001). However, they generate less variability in neuronal responses than a combination of drifts and microsaccades (Gur, Beylin, & Snodderly, 1997). No studies to date have recorded primate neuronal responses in correlation to tremor (but see Hennig & Wörgötter, 2007 for the responses of a model macaque retina to simulated drift and tremor).

Fixational eye movements in the cat

The cat's fixational eye movements have been investigated in a handful of studies, and their conclusions remain somewhat controversial. In 1960, Hebbard and Marg (1960) found fixational eye movements in the cat to be quite comparable to those in humans, although cat microsaccades were scarcer and smaller than in humans. Pritchard and Heron (1960) also found that the cat's fixational eye movements included microsaccades, drifts, and tremor. Microsaccades were much rarer in the cat than in humans, however, possibly related to the fact that the cat lacks a well-developed fovea. Delgado-Garcia, del Pozo, and Baker (1986) also observed some putative microsaccades in the alert behaving cat. Other studies found no microsaccades in the cat (Conway, Timberlake, & Skavenski, 1981; Winterson & Robinson, 1975). However, in these last studies microsaccades were defined as "saccades smaller than 10 minutes of arc", which is well below the average microsaccade amplitude found in recent human and primate studies (see Martinez-Conde et al., 2004 for a review of microsaccade parameters in humans and primates). More recently, several studies have addressed the contribution of fixational eye movements to neural responses in the cat's visual system. Hennig, Kerscher, Funke, and Wörgötter (2002) found increased responses from neurons in cat areas 17 and 18 during stimulus motions that mimicked fixational eye movements. Using a model retina, they also found that:

1. simulated fixational eye movements increased neural responses, and
2. simulated tremor improved spatial acuity.

Hennig and Wörgötter (2004) later reported that a combination of tremor and microsaccades improved the performance of simulated ganglion cells in a hyperacuity task in the retinal periphery (but not in the central retina). Miller, Denning, George, Marshak, and Kenyon (2006) also investigated the effects of simulated tremor on a model of the cat's retina and suggested that tremor may selectively enhance the processing of large stimuli.

Fixational eye movements in the rabbit

In contrast to foveate species, such as primates (including humans) and cats (which have an area centralis, if not a proper fovea), the rabbit (*Oryctolagus cuniculus*) displays few spontaneous eye movements, especially in the absence of head motion (Collewijn, 1977; Collewijn & van der Mark, 1972; Fuller, 1980, 1981; Van der Steen & Collewijn, 1984). In normal visual conditions, the rabbit's eyes are very stable but not perfectly immobile. Small amplitude *tremor* can be observed, as well as very slow *drift*. Microsaccades have not been observed. However, drift is occasionally corrected by fast saccadic movements (Collewijn, 1977; Collewijn & van der Mark, 1972; Van der Steen & Collewijn, 1984). These differences may be related to the fact that the rabbit does not have a fovea but an elongated horizontal streak with elevated ganglion cell counts. Olveczky, Baccus, and Meister (2003) recorded from ganglion cells in the rabbit and salamander retinas while presenting visual stimuli that were jittered to simulate fixational eye movements (based on parameters from previously published studies by Manteuffel, Plasa, Sommer, & Wess, 1977 and Van der Steen & Collewijn, 1984). In both species, fixational eye movements helped segregate a moving foreground from a complex background in a population of ganglion cells.

Fixational eye movements in birds

Fixational eye movements in the pigeon

There are some remarkable differences between fixational eye movements in birds and mammals. Nye (1969) identified four types of fixational eye movements in the pigeon (*Columba livia*): flicks (i.e., *microsaccades*), *impulse* movements, *drift,* and *oscillations*. No tremor was detected. Microsaccade frequency was very low relative to humans. Impulse movements occurred more frequently, usually between bursts of oscillations, with amplitudes ranging up to 2 degrees. Drift velocities ranged from 1 to 5 degrees per second. Both microsaccades and drifts occurred in response to moving stimuli. Oscillations occurred in short bursts at rates of about 30 Hz and could be quite large (up to several degrees of amplitude). Bloch, Rivaud, and Martinoya (1984) reported microsaccades, drifts, and oscillations "similar to those described by Nye," but none of these were analyzed in detail.

Cyclotorsional oscillations are an integral part of avian saccades (Wallman, Pettigrew, & Letelier, 1994). Thus one might speculate that oscillations are associated with avian microsaccades as well, especially if saccades and microsaccades share a common generator (Engbert, 2006; Otero-Millan et al., 2008; Rolfs et al., 2008, 2006; Zuber & Stark, 1965). However, this possibility has not yet been addressed in the literature. The function of oscillations is unknown (Carpenter, 1988), but one hypothesis is that they serve to facilitate the delivery of arterial blood to the ocular capillary bed (Pettigrew, Wallman, & Wildsoet, 1990; Wallman et al., 1994).

Fixational eye movements in the owl

Steinbach and Money (1973) recorded fixational eye movements in the great horned owl (*Bubo virginianus*), a species previously thought incapable of moving its eyes. The owl's fixational eye movements include: flicks or *microsaccades, drift, tremor,* and *oscillations*. Microsaccades seemed correlated to visual events of interest to the owl, they were 1 deg or less in amplitude and had peak velocities of about 10 deg/sec. Drifts were slow motions of the eye in between fixations, with amplitudes of 1 degree or less. Tremor amplitude was about 1 arcmin, with frequencies around 20 Hz. High-frequency oscillations (25 Hz) of short duration (0.25 sec) were very similar to those previously found in the pigeon (Nye, 1969). No studies to date have examined the perceptual or physiological effects of fixational eye movements in any bird species.

Fixational eye movements in reptiles

Fixational eye movements in the turtle

Greschner, Bongard, Rujan, and Ammermüller (2002) identified two types of fixational eye movements in the turtle (*Pseudemys scripta elegans*), which they called "*drift-like*" and "*periodic*." Drift-like motions were small and slow (with velocities comparable to human drift) and were superimposed by larger and faster periodic components. Periodic motion had retinal amplitudes on the order of the diameter of a photoreceptor, which are comparable to those of human tremor. On the other hand, periodic motion's frequency (5 Hz), velocity, and orderly relationship between velocity and amplitude are closer to those of human microsaccades (see Martinez-Conde et al., 2004 for a review of tremor and microsaccade parameters in humans).

Simulated periodic motion generated strong synchronous firing in the turtle's retina, whereas simulated drift-like motion had little effect (Figure 3). These results agree with previous physiological and modeling studies in the primate visual system, in which strong neural transients were observed in response to microsaccades (Donner & Hemilä, 2007; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002). Such neural transients may underlie the behavior of cortical neurons as coincidence detectors (Shelley, McLaughlin, Shapley, & Wielaard, 2002; Williams & Shapley, 2007). Moreover, neural transients to stimuli onsets and terminations (similar to those produced by microsaccades in the primate visual system; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002) have been related to target visibility in visual masking paradigms (Macknik & Livingstone, 1998; Macknik & Martinez-Conde, 2004; Macknik, Martinez-Conde, & Haglund, 2000).

In the turtle retina, periodic motion-driven neurons with receptive fields located along contrast borders were moreover synchronized and reliably indicated the preceding motions. The authors proposed that this synchronization of retinal activity could be used by the brain to

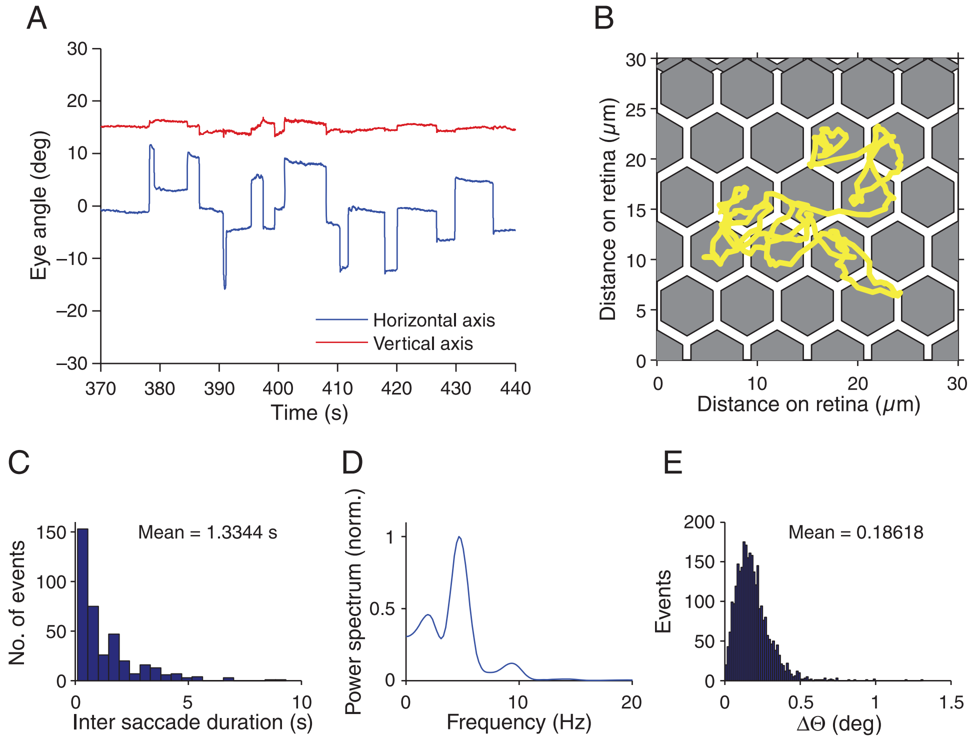

Figure 4. Archer fish eye movements. (A) Example trace of eye position as a function of time, as measured by search coil. (B) Example of a single 1.5-s fixation superimposed on a grid representing the photoreceptor mosaic. The back and forth movement is caused by tremor. (C) Distribution of fixation durations (taken as time interval between saccades). (D) Power spectrum of horizontal fixational eye movements. (E) Distribution of tremor amplitude (data taken from 1 animal in a 15-min session). Modified from Segev et al. (2007).

et al. (2007) identified three types of fixational eye movements in the archer fish: microsaccades, drift, and tremor. Microsaccades were rare and were not analyzed in detail. Drift velocities were ≤0.40 deg/sec. Tremor was a high-frequency oscillatory movement (the primary component was 5 Hz) with peak-to-peak amplitude of 0.1–0.2 deg (corresponding to an image displacement of 1–2 photoreceptors) and velocity of about 1 deg/sec (Figure 4). Whereas the amplitude and velocity of tremor in the archer fish is comparable to those in humans, its frequency is much lower (5 Hz vs. >40 Hz). Interestingly, archer fish tremor is very similar, both in amplitude (photoreceptor widths covered) as well as in frequency (5 Hz), to the tremor-like *periodic* motion in the turtle (discussed earlier; Greschner et al., 2002).

Segev et al. (2007) trained archer fish to perform a size discrimination task: the fish had to distinguish a medium-sized target from larger and smaller distracters (they indicated their choice by shooting a jet of water). To relate this behavior to responses from retinal neurons, the authors recorded from populations of retinal ganglion cells while presenting objects of different sizes, moved to simulate saccades, drifts, and tremor. Drifts and tremor elicited weak neuronal responses that were not very informative about the spatial structure of the stimulus (although they did provide some information about target size, in agreement with the results of Greschner et al., 2002 in the turtle). Moreover, performance was similar for tremor alone and for tremor plus drift, indicating that drift plays a negligible role in revealing spatial structure (also in agreement with Greschner et al., 2002).

When present, the firing rate was phase-locked to tremor. Saccades were more effective than drifts or tremor in driving informative responses from the ganglion cells (consistent with theoretical and physiological studies of microsaccade-driven neuronal activity in the primate retina and LGN; Donner & Hemilä, 2007; Martinez-Conde et al., 2002). Segev et al. (2007) proposed that in primates, both saccades and microsaccades (which are rare in the archer fish) may contribute to size discrimination tasks as well as enhance spatial detail, whereas drifts and tremor by themselves may not be sufficient to improve visual perception. However, it is important to remember that *central* vision in humans can be maintained by tremor and/or drift, even when microsaccades are suppressed during strict fixation (Martinez-Conde, 2006; Martinez-Conde et al., 2004, 2006). On the other hand, one cannot rule out the possibility that, if one could completely eliminate drifts and tremor, microsaccades might then suffice to sustain both *central and peripheral* vision in primates and humans. Future experiments are needed to further explore these ideas.

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