Similar Kinematic Properties for Ocular Following and Smooth Pursuit
Eye Movements

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Adeyemo, Babatunde and Dora E. Angelaki. Similar kinematic properties for ocular following and smooth pursuit eye movements. J Neurophysiol 93: 1710–1717, 2005. First published October 20, 2004; doi:10.1152/jn.01020.2004. Ocular following (OFR) is a short-latency visual stabilization response to the optic flow experienced during self-motion. It has been proposed that it represents the early component of optokinetic nystagmus (OKN) and that it is functionally linked to the vestibularly driven stabilization reflex during translation (translational vestibuloocular reflex, TVOR). Because no single eye movement can eliminate slip from the whole retina during translation, the OFR and the TVOR appear to be functionally related to maintaining visual acuity on the fovea. Other foveal-specific eye movements, like smooth pursuit and saccades, exhibit an eye-position-dependent torsional component, as dictated by what is known as the “half-angle” rule of Listing’s law. In contrast, eye movements that stabilize images on the whole retina, such as the rotational vestibuloocular reflex (RVOR) and steady-state OKN do not. Consistent with the foveal stabilization hypothesis, it was recently shown that the TVOR is indeed characterized by an eye-position-dependent torsion, similar to pursuit eye movements. Here we have investigated whether the OFR exhibits three-dimensional kinematic properties consistent with a foveal response (i.e., similar to the TVOR and smooth pursuit eye movements) or with a whole-field stabilization function (similar to steady-state OKN). The OFR was elicited using 100-ms ramp motion of a full-field random dot pattern that moved horizontally at 20, 62, or 83°/s. To study if an eye-position-dependent torsion is generated during the OFR, we varied the initial fixation position vertically within a range of ±20°. As a control, horizontal smooth pursuit eye movements were also elicited using step-ramp target motion (10, 20, or 30°/s) at similar eccentric positions. We found that the OFR followed kinematic properties similar to those seen in pursuit and the TVOR with the eye-position-dependent torsional tilt of eye velocity having slopes that averaged 0.73 ± 0.16 for OFR and 0.57 ± 0.12 (means ± SD) for pursuit. These findings support the notion that the OFR, like the TVOR and pursuit, are foveal image stabilization systems.

INTRODUCTION

Ocular following responses (OFR) are slow tracking eye movements with short latency (≈50–80 ms), evoked by sudden drifting movements of a large-field visual stimulus. Signals generating OFR arise from relatively low-level preattentive cortical processing that infer the observer’s motion by detecting the pattern of optic flow (Busettini et al. 1997; Miles 1993, 1998; Miles and Busettini 1992; Miles et al. 1991; Schwarz et al. 1989; Yang et al. 1999), and/or binocular disparity cues (Busettini et al. 1994, 1996a,b). OFR has been postulated to represent the early component of primate optokinetic nystagmus (OKN) but to be different from smooth pursuit, which is strongly influenced by attention and cognitive cues (Chen et al. 2002; Krauzlis 2004; Van Donkelaar and Drew 2002).

Although postulated to represent the fast, early component of OKN, OFR differs from steady-state OKN in several aspects. For example, in contrast to steady-state OKN that is sensitive to peripheral field stimulation, the optimal stimulus for OFR is visual motion in the central 20–40° of the retina (Miles et al. 1986). In several review articles, Miles (1993, 1995, 1998) has proposed that OFR and steady-state OKN have different functional and phylogenetic origins. Specifically, steady-state OKN has long been thought to be the visual contribution to gaze stabilization during rotational motions, operating in synergy with the rotational vestibuloocular reflex (RVOR). In contrast, OFR could represent the visual complement of the translational vestibuloocular reflex (TVOR), the function of which would be to provide a fast mechanism for gaze stabilization during translational movements (Busettini et al. 1991; Schwarz and Miles 1991; Schwarz et al. 1989).

As summarized here, several studies have indeed provided experimental support for this hypothesis. First and foremost, the patterns of eye movements generated by the sudden motion of a large-field visual stimulus are identical to the TVOR. That is, a horizontally drifting visual stimulus elicits conjugate horizontal eye movements, whereas a vertically drifting stimulus elicits vertical eye movements. Both components of OFR scale with the inverse of viewing distance, a property that is shared with the TVOR (Busettini et al. 1991; Paige and Tomko 1991; Schwarz and Miles 1991; Schwarz et al. 1989) but not smooth pursuit eye movements (Zhou et al. 2002). Radial optic flow, on the other hand, elicits purely vergence eye movements (Yang et al. 1999) as is also the case for the TVOR during forward/backward motions (Hess and Angelaki 2003; McHenry and Angelaki 2000; McHenry and Angelaki 2000; McHenry and Angelaki 2000; McHenry and Angelaki 2000; McHenry and Angelaki 2000). These vergence eye movements are also scaled by viewing distance in a manner identical to the TVOR (McHenry and Angelaki 2000; Yang et al. 1999).

Recently a functional distinction has been made between the visual stabilization strategies for the RVOR and the TVOR: the RVOR’s goal is to stabilize images on the whole retina, and it achieves this by rotating the eye about an axis specified by the axis of head rotation. In contrast, the amount of slip of objects on the retina during translation depends on their spatial location, thus precluding the possibility that a single eye movement can stabilize the whole visual field. A reasonable solution to

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this dilemma (and the one that seems to be followed by the TVOR) is to preferentially stabilize images on the fovea. Indeed, the amplitude and direction of the horizontal and vertical eye movements for the TVOR exhibit a dependence on gaze and heading directions, as expected from the geometry for foveal image stabilization (Angelaki and Hess 2001; Hess and Angelaki 2003; McHenry and Angelaki 2000).

If the horizontal and vertical components of the eye movement during translation are specified by the underlying geometry for foveal image stability, what about the third degree of freedom of the eye, ocular torsion? For the RVOR and steady-state OKN, the answer is simple: the amount of eye torsion is determined by the roll component of the stimulus. As long as the rotation of the head does not include a roll component, a purely horizontal/vertical compensatory eye velocity is called for. What about foveal stabilization reflexes, such as the TVOR? In this case, the visual goal only defines the horizontal and vertical components of the eye movement, whereas ocular torsion remains unspecified. In recent years, several studies have demonstrated that foveal-guided eye movements and foveal-image stabilization systems, like saccades, smooth pursuit, and the TVOR, are subject to robust kinematic constraints whereby the rotation vectors describing eye position lie on a plane (i.e., remain 2-dimensional) by minimizing ocular rotations about a unique gaze direction known as primary position (a property known as Listing’s Law, LL) (see Hepp 1990; Tweed et al. 1992; Tweed and Vilis 1987, 1990).

For eye position to remain in Listing’s plane, the often unintuitive mathematics of three-dimensional (3D) rotations require that the axis of rotation of the eye tilts out of this plane by an amount equal to half the gaze angle, a property known as the “half-angle rule” (Misslisch et al. 1994; Tweed and Vilis 1987, 1990; Tweed et al. 1992). This tilt occurs because a torsional eye velocity is generated simultaneously with horizontal eye velocity whenever gaze is directed upward or downward during both pursuit and the TVOR (Angelaki et al. 2003; Tweed et al. 1992; Walker et al. 2004). This kinematic strategy provides a solution to the third-degree of freedom uncertainty for foveal eye movements. In contrast, the primate RVOR does not follow LL, such that eye velocity remains aligned with the stimulus axis and does not exhibit any significant gaze dependence during yaw and pitch rotations (Angelaki et al. 2003; Misslisch and Hess 2000) [although humans follow a compromised strategy, where the RVOR vector tilts only half as far, i.e., it follows a “quarter angle rule” (Misslisch et al. 1994; Walker et al. 2004)].

Similar to the RVOR, steady-state OKN also does not follow LL and the associated eye position dependence (Fetter et al. 1995; Tweed et al. 1992). According to the functional link hypothesis between the OFR and the TVOR, one might then expect that, contrary to steady-state OKN, OFR exhibits an eye-position-dependent torsional velocity similar to the TVOR. Here we have investigated this hypothesis by comparing the 3D ocular kinematics of OFR with those during pursuit of a small moving target. A clear demonstration that the OFR (unlike the RVOR and steady-state OKN) exhibits the same 3D organization as the TVOR and pursuit eye movements is important for understanding the functional roles of these recent evolutionary acquired reflexes and will provide further support of the proposed hypothesis regarding their functional synergy (Miles 1993, 1998). Our results support the notion that, contrary to the RVOR and steady-state OKN, the function of OFR, like the TVOR, is to stabilize images on the fovea (rather than the whole retina). Preliminary results have been presented in abstract form (Adyemo and Angelaki 2004).

**Methods**

Binocular eye movements were recorded in three rhesus monkeys during OFR and another three animals during step ramp pursuit. All animals were implanted with dual coils for binocular 3D eye-movement recordings (Hess 1990) and were trained to fixate or follow targets. All surgeries, animal treatment, and handling were in accordance with National Institutes of Health and institutional guidelines. During each experiment, the monkey was comfortably seated in a stationary primate chair that was placed in the center of a three-field magnetic coil system (CNC Engineering). Eye movements were calibrated by requiring the animals to monocularly fixate far targets at different horizontal and vertical eccentricities (Angelaki and Hess 2001; Angelaki et al. 2000). To generate single target stimuli for fixation and saccades, a laser beam was back-projected onto a flat screen at a distance of 20 cm from the animal using a laser/mirror galvanometer system (General Scanning). To elicit OFR, a second mirror galvanometer system was used to project a full-field random-dot pattern onto the same screen. The visual stimulus for OFR (84° × 97°) was a ramp movement of a random-dot pattern, lasting 100 ms, after which the screen went blank for 0.5–2 s with the animal in complete darkness. Each ramp started ~20–50 ms after the end of a saccade directed toward a centrally located target. This target for the centrifugal saccade was always in the midsagittal plane, at one of several vertical eccentricities (0, ±10°, and ±20°). Three different pattern speeds (20, 62, and 83°/s) were randomly interleaved with the direction of motion of the visual stimulus (i.e., rightward or leftward) and initial eye position also varying in a pseudorandom fashion. The monkeys were given a drop of juice after the ramp ended while in darkness to keep them alert and facilitate fast saccades at the beginning of each trial.

Animals were also trained to pursue targets moving in different directions and speeds using step-ramp stimuli (Rashbass 1961). Each trial began when the monkey fixated a target (either at 0 or ±20° vertical eccentricities). After a random fixation period (750–2,500 ms), the target was extinguished. At exactly the same time, a second target appeared at a different location and immediately began to move at constant velocity (20 and 10 or 30°/s) in a direction toward and then beyond the initial fixation position. Both targets were at the same vertical level and the horizontal position difference between them formed the “step.” The movement lasted for 700–1,000 ms. The monkey was rewarded with juice at the end of each trial if he maintained eye position within 2° of the stationary target and within 3–4° of the ramp target throughout the trial. The direction and speed of target motion were presented in a pseudorandom fashion.

Both stimulus presentation and data acquisition were controlled with custom-written scripts within the Spike2 software environment using a Cambridge Electronics Device (CED, model 1401) data-acquisition system. Data were anti-alias filtered (200 Hz, 6-pole Bessel), and digitized by the CED at a rate of 833.33 Hz (16-bit resolution). Off-line, raw data from each animal’s left eye were first converted into rotation vectors, using straight-ahead as the reference position. Positive directions were leftward, downward, and clockwise (from the animal’s viewpoint) for the horizontal, vertical, and torsional components, respectively. These positions were subsequently transformed into eye velocity by taking the derivative of eye position (dE/dt = where E is 3D eye position). Finally, angular eye velocity (Ω) was computed from the previous two values by the equation Ω = 2 (dE/dt + E x dE/dt)/(1 + [E]²) (where x designs the cross vector product) (Angelaki et al. 2000; Hepp 1990). Similar to all 3D kinematic studies for pursuit, saccades, and the VOR, analyses here

For OFR responses, data from different repetitions were aligned at the initiation of the ramp stimulus, and averages were computed for each of the horizontal and torsional velocity components. Pursuit analyses focused on the open-loop interval during the first 100 ms of pursuit that describes the system's output in response to a visual input (Krauzlis and Lisberger 1994; Lisberger and Westbrook 1985). The time of initiation of smooth pursuit was computed on a trial-by-trial basis, using criteria similar to those described by Dubrovsky and Cullen (2002) and Zhou et al. (2002). Specifically, the onset position was defined as the point of intersection between a baseline and an initial response linear regression. The baseline regression was calculated over the interval of −25 to +75 ms with respect to the onset of target motion. The initial response regression was computed between the point where the eye deviated from the baseline by 2.5 SD and 45 ms later. Each trial was visually assessed to ensure the accuracy of the procedure. Data were averaged for each eye position, velocity, and direction aligned at the initiation of pursuit.

The amount of axis tilt in the animal's sagittal plane was then evaluated by plotting horizontal versus torsional eye velocity and fitting a line through the spatial trajectory. For ocular following, the fit was made to the 50- to 100-ms eye-velocity segment after full-field motion onset. For pursuit, the line was fitted to the first 100 ms of pursuit. A “torsional tilt angle” was then computed as the angle between the line and the horizontal axis. Positive angles corresponded to clockwise rotation, as viewed from the right ear (e.g., Figs. 2 and 4). For both pursuit and OFR, this analysis was performed on both the mean eye velocity responses and on data from each individual run. Subsequently, torsional tilt angles were plotted versus vertical eye position and regression lines were used to quantitatively describe this dependence. The slopes of these lines were computed for the torsional tilt angles obtained from either the mean eye velocity data or those for each individual run. Results obtained by fitting mean eye velocity or data from individual runs were identical.

RESULTS

Figure 1 plots the horizontal and torsional eye velocity elicited in response to the sudden horizontal motion (62°/s) of a large random-dot pattern. The stimulus was delivered 20–50 ms after a centrifugal horizontal saccade to one of several targets, all lying in the midsagittal plane at different vertical eccentricities, 20° and 10° down, 0°, as well as 10° and 20° up. Figure 1A shows individual runs, whereas mean ± SD (dotted lines) eye velocity traces from several repetitions of the full-field visual motion stimulus have been illustrated in Fig. 1B. Responses were evoked with latencies of ~60 ms (vertical dashed lines illustrate the start of the visual motion stimulus). Horizontal eye velocity accelerated slowly to a peak response, which was similar for all vertical eye position eccentricities. During ocular following with gaze straight-ahead (0° eccentricity), responses were mainly horizontal, with only small torsional eye velocity being generated (Fig. 1A, green traces). When OFR was elicited from vertically eccentric positions, torsional eye velocity systematically changed as a function of vertical eye position, shifting from positive to negative responses as gaze changed from 20° up to 20° down (Fig. 1A, blue, cyan, green, magenta and red traces on the right).

These observations from the individual examples of Fig. 1A are further illustrated in the mean eye velocity responses shown in Fig. 1B. Although the horizontal component exhibited little

![FIG. 1. Dependence of horizontal ocular following (OFR) on vertical gaze. A: horizontal and torsional eye velocity (Ω hor, Ω tor) for 20° down (blue), 10° down (cyan), center (green), 10° up (magenta), and 20° up (red) gaze during leftward OFR (62°/s). B: mean ± SD horizontal and torsional eye velocity (Ω hor, Ω tor) for the same gaze angles during rightward and leftward OFR (62°/s). The vertical dashed lines illustrate the start of the full-field visual motion.](http://jn.physiology.org/)
change, torsional eye velocity was larger when the visual motion stimulus was delivered with the eye at vertically eccentric positions. For leftward OFR (Fig. 1B, top), clockwise (positive) torsion was observed during down gaze (blue and cyan lines) and counterclockwise (negative) torsion was evoked with up gaze (red and magenta lines). The opposite was true for rightward OFR (Fig. 1B, bottom). Note that because eye movements were expressed relative to straight-ahead, which does not necessarily coincide with primary eye position, the center target was not necessarily associated with zero torsional eye velocity (Angelaki and Hess 2004; Angelaki et al. 2003; Tweed and Vilis 1987, 1990; Tweed et al. 1992). Thus what is important in this analysis is the systematic change in torsional eye velocity during horizontal OFR at different vertical eccentricities and not its exact magnitude at any given gaze direction.

This systematic change in torsional velocity as a function of eye position was always such that it caused a rotation of the eye velocity vector in the same direction as the gaze angle. This is shown in Fig. 2, where horizontal and torsional eye velocities are plotted relative to each other. The thin solid lines in Fig. 2 illustrate the spatial trajectories that OFR eye velocity followed in the sagittal plane (for clarity, only data from 3 vertical gaze eccentricities are plotted). Results were the same for all visual motion velocities (Fig. 2, A–C). During leftward (positive) horizontal OFR with gaze up, for example, torsional velocity was negative (counterclockwise relative to the animal, as viewed from the right ear; Figs. 1B, top, and 2, red traces). The opposite was true for down gaze (Figs. 1B, top, and 2, blue traces). The reverse pattern was seen for rightward OFR (i.e., negative horizontal eye velocity; Fig. 1B, bottom; see also Fig. 2). Thus for both leftward and rightward OFR, the instantaneous axis of rotation of the eye tilted away from a purely head-horizontal axis in the same direction as gaze and through approximately half the gaze angle.

To evaluate the magnitude of these effects, lines were fitted to the 50- to 100-ms segment of OFR. The torsional tilt angle was then computed as the angle between the fitted line and the horizontal axis. Torsional tilt angles were plotted versus vertical gaze and regression lines were used to quantitatively describe this relationship, as illustrated in Fig. 3 (same data as in Fig. 2). Significant correlations were observed for all animals and velocities. For OFR, straight-ahead gaze did not always correspond to zero torsional eye velocity (Fig. 1, see also Fig. 2). However, in all cases, gaze up and gaze down rotated eye velocity in opposite directions around the 0°-gaze angle data.

To directly compare these observations with the 3D kinematics of pursuit, we also recorded 3D eye movements during step-ramp horizontal pursuit at different vertical elevations. Pursuit results were similar to those for OFR (Fig. 4). Figure 4A shows typical examples of step-ramp horizontal pursuit responses to leftward target motion at 20°/s, starting from three different vertical eccentricities, 20° down, 0°, and 20° up. The top traces in Fig. 4A show horizontal and torsional eye position, superimposed on the target ramp (T). The bottom traces show the corresponding eye velocities. During horizontal smooth pursuit with gaze straight-ahead (0° eccentricity), responses were mainly horizontal, with small torsional eye velocity being generated (Fig. 4A, green traces). When gaze was
directed upward or downward, the direction and amplitude of torsional eye velocity changed (Fig. 4A, blue and red traces). Notice again that because primary position was generally different from straight-ahead, pursuit at center gaze was characterized by nonzero torsional velocity. Similar to OFR, what is important to characterize the 3D kinematics of these responses is the change in torsional velocity as a function of vertical gaze angle.

Mean (± SD) eye velocity traces from several repetitions of the pursuit stimulus are shown in Fig. 4B. Compared with pursuit responses for straight-ahead gaze (Fig. 4B, green traces), torsional eye velocity was systematically altered when the eyes were at vertically eccentric positions. For leftward pursuit (Fig. 4B, top), clockwise (positive) torsion was observed during down gaze (blue lines) and counterclockwise (negative) torsion was evoked with up gaze (red lines). The opposite was true for rightward pursuit (Fig. 4B, bottom). When a similar analysis to OFR was done for the first 100 ms of pursuit, results were the same for the two visuomotor responses: the amplitude of torsional eye velocity, and the corresponding tilt of the eye velocity, were proportional to
vertical eye position, the effect being largest for the most eccentric gaze angles.

Figure 5 summarizes the mean slope values of these regression lines for all three animals. The slopes of the eye-position dependence of eye velocity averaged 0.73 ± 0.16 for OFR (n = 18, 3 animals × 3 ramp amplitudes × 2 directions) and 0.57 ± 0.12 for pursuit (n = 12, 3 animals × 2 ramp amplitudes × 2 directions). These values were identical whether obtained from fits to average eye velocity data (as in Fig. 3) or from fits to the eye velocity from individual trials. Although OFR slope values tended to be larger than those of Fig. 3) or from fits to the eye velocity from individual trials. Although OFR slope values tended to be larger than those of Fig. 3) or from fits to the eye velocity from individual trials. Although OFR slope values tended to be larger than those of pursuit, the difference was not statistically significant (t-test, P > 0.05). Larger than pursuit values were also seen for the TVOR slope, which averaged 0.7 ± 0.07 [Fig. 5, open bars; from Angelaki et al. (2003)]. The OFR slope values from the present experiments were not different from those for the TVOR (t-test, P > 0.05).

**Discussion**

We have shown here that the 3D kinematic properties of ocular following are similar to those characterizing smooth pursuit eye movements and the TVOR. Unlike the RVOR and steady-state OKN, where the eye-position dependence of the eye-velocity vector is small or negligible, consistent with a role in full-field image stabilization, the large gaze dependence of the OFR and TVOR supports their functional role in foveal image stabilization. The present 3D analyses of OFR, along with similar studies for the TVOR (Angelaki et al. 2000, 2003; Walker et al. 2004), extend results based solely on horizontal and vertical eye movements regarding a foveal goal for both reflexes (Angelaki and Hess 2001; McHenry and Angelaki 2000; Miles et al. 1986; Paige and Tomko 1991). In addition, the present results provide further support for the functional synergy hypothesis proposed by Miles (1993, 1998); in which OFR represents the visual complement of the TVOR for spatial constancy during translation, in a way similar to the function steady-state OKN serves for the RVOR.

**Functional synergy of OFR and TVOR**

There are now several pieces of experimental evidence supporting the idea that OFR and TVOR share similar functional goals to provide visual stability during translation. First, both reflexes generate similar patterns of ocular responses: conjugate horizontal and vertical eye movements during sensory stimulation associated with lateral or vertical plane motions as well as disjunctive horizontal eye movements during sensory stimulation resulting from forward or backward displacements (Busettini et al. 1994, 1996a,b, 1997; Hess and Angelaki 2003; McHenry and Angelaki 2000; Miles 1993, 1998; Paige and Tomko 1991; Schwarz and Miles 1991; Schwarz et al. 1989; Yang et al. 1999). Second, both the OFR and the TVOR scale inversely with viewing distance (Angelaki and McHenry 1999; Busettini et al. 1991; McHenry and Angelaki 2000; Paige and Tomko 1991; Schwarz and Miles 1991; Schwarz et al. 1989; Yang et al. 1999). Such a scaling is expected for the TVOR, as the sensory vestibular signal is independent of viewing conditions, while geometry dictates that the magnitude of compensatory eye movements must scale inversely with the distance of objects to be stabilized. However, the reported distance scaling of the OFR represents a puzzling observation because the sensory signals driving a visual tracking system, like the OFR, already have taken this property into account (motion parallax). In fact, the observation that OFR scales inversely with distance has been taken as evidence that TVOR and OFR share central pathways (Miles 1993, 1998). A small sensitivity to vergence angle has been found in MST neurons that might mediate the OFR, although such a dependence was only ~30% of that shown by the OFR (Inoue et al. 1998).

The third similarity between the two visual stabilization systems arises from another aspect of geometry during translation. Specifically, displacements along paths that are nearly parallel to gaze direction result in differential spatial representation of motion across the retina. Thus no single eye movement could generally result in stabilization of the whole visual field. One solution to this dilemma would be to have the OFR and the TVOR organized such that they stabilize images on the fovea. Such a requirement dictates that eye movements during translation be scaled, not only by a signal related to the inverse of target distance but also by a signal proportional to a sinusoidal function of eye position. Several TVOR studies have indeed shown that vestibularly evoked eye movements are appropriately organized to reflect these geometrical requirements, not only during lateral and fore-aft motion but also along any heading direction (Angelaki and Hess 2001; Hess and Angelaki 2003; McHenry and Angelaki 2000; Paige and Tomko 1991). Although comparable studies for the OFR are missing, the optimal stimulus for OFR arises from visual motion in the central 20–40° of the retina (Miles et al. 1986). In contrast, for steady-state OKN, peripheral field stimulation is important.

**LL or minimum rotation strategy?**

In addition to the two-dimensional analysis summarized in the preceding text, the foveal stabilization hypothesis would also have implications regarding the torsional component of the eye movement. In general, the eyes could assume an infinite number of torsional eye orientations and still foveate the target. Among the different possible orientations that the eyes could assume, two have been described as providing unique, although distinct, advantages during foveal-specific eye movements the goal of which is to control the direction of gaze with little regard for the peripheral retina. One is the “minimum rotation” strategy, where the eye follows the shortest
possible path to acquire the target. The second is referred to as the “Listing’s” strategy, where the amount of ocular torsion is minimized. A kinematic requirement for both the minimum rotation strategy and LL is a specific eye-position dependence of the axis of rotation of the eye. For the minimum rotation strategy, the eye-velocity axis would tilt through the same angle as gaze (full-angle rule), while for the Listing’s strategy, the eye-velocity axis tilts by half the angle of gaze (half-angle rule) (Misslisch et al. 1994; Tweed and Vilis 1987, 1990; Tweed et al. 1992).

It is now well-established that smooth pursuit, and in general all conjugate, visually-guided, foveal-specific, eye movements, obey LL (Haslwanter et al. 1991; Tweed and Vilis 1987, 1990; Tweed et al. 1992). In contrast, both of these strategies would be detrimental for a system like the RVOR the goal of which is to stabilize images on the whole retina and whose sensory input can uniquely specify all three-degrees-of-freedom of the eye. Indeed, RVOR does not follow LL (Misslisch and Hess 2000; Misslisch et al. 1994). Recently, it was shown that, unlike the RVOR, the horizontal TVOR exhibits a large and systematic dependence on vertical gaze (Angelaki et al. 2000, 2003; Walker et al. 2004). The slopes for this eye-position dependence in monkeys averaged 0.7 ± 0.07 for the TVOR as compared with 0.6 ± 0.07 for visually guided pursuit eye movements and 0.18 ± 0.09 for the RVOR (Angelaki et al. 2003). As the torsional tilt versus vertical gaze slopes during translation were slightly higher than those during pursuit, 3D eye movements during translation could partly reflect a compromise between the two different solutions for foveal gaze control, that of LL and minimum velocity strategies. It is interesting that, although not statistically different from pursuit, the slope of the eye-position dependence for OFR averaged 0.73 ± 0.16, values that are similar to those of the TVOR.

Neural processing for OFR

Accumulating evidence exists that the early OFR responses are mediated at least in part by the medial superior temporal area of the cortex (MST), the dorsolateral pontine nuclei (DLPN), and the parafloccular lobes of the cerebellum (VPFL) (Gomi et al. 1998; Shidara et al. 1993; Takemura et al. 2001). Lesions in any of these regions impair OFR (Dursteler and Wurtz 1988; Inoue et al. 2000; May et al. 1988; Miles et al. 1986; Zee et al. 1981; see Takemura and Kawano 2002 for a review). In addition, single-unit recordings in these regions have revealed many directionally selective cells that respond early enough during OFR to be involved in its generation (Kawano et al. 1992, 1994a,b; Shidara and Kawano 1993).

The areas involved in generating OFR are also known to be part of the neural substrate for smooth pursuit eye movements. Indeed, when MST, DLPN, or VPFL are lesioned, both smooth pursuit and OFR are impaired (Dursteler and Wurtz 1988; May et al. 1988; Zee et al. 1981). Some MST/DLPN/VPFL neurons modulate during both pursuit and full-field visual stimulation (Buttner and Waespe 1984; Kawano et al. 1992, 1994a,b; Shidara and Kawano 1993). Thus it is possible that at least some neurons in the MST-DLPN-VPFL pathway might carry visual signals for guiding both pursuit and OFR (Kawano et al. 1994a,b). The present results, showing similar 3D kinematic properties for OFR and pursuit are consistent with such a view. Yet, there is some behavioral evidence that pursuit and OFR signals might be carried at least partly by different neurons because only the OFR and the TVOR, but not pursuit eye movements, scale their amplitude with vergence angle (Zhou et al. 2002).

In conclusion, the present results support the hypothesis that OFR and TVOR are functionally related and differ from steady-state OKN and the RVOR (Miles 1993, 1998). Ocular movements during rotation represent a phylogenetically old process, with a functional demand for full-field image stabilization, optimally suited for a global, viewing-distance independent visual stability. In contrast, the eye movements during translation are not only optimized for anticipating motion parallax and minimizing binocular disparities (Angelaki and Hess 2001; Busettini et al. 1991, 1994; Schwarz and Miles 1991), but also, as shown here, exhibit 3D kinematic properties that are consistent with a foveal-image stabilization strategy and a true gaze stabilization function.

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