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DYNAMICS AND VIEWING DISTANCE DEPENDENCE OF EYE MOVEMENTS DURING TRANSIENT LATERAL MOTION

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INTRODUCTION

As foveal vision emerged, accompanied by vergence eye movements and stereopsis, novel visual mechanisms evolved in order to stabilize binocular gaze on the depth plane of interest (9, 10). In primates, these visual mechanisms are complemented by a special vestibulo-ocular reflex known as the translational vestibulo-ocular reflex (TVOR) that is capable of eliciting short-latency (< 12 ms) compensatory eye movements in response to high frequency translational stimuli (> 0.5-1 Hz) (1-3, 5, 11-13, 15).

Testing of the TVOR has mainly been done with high frequency oscillations, where responses exhibit strongly high-pass filtered characteristics that can only be described by higher-order functions (1, 3, 15). In this respect, the dynamics of the TVOR are different from those of the rotational VOR (RVOR) which exhibit more band-pass frequency response characteristics and can be approximated by a first-order system with a dominant time constant of > 10-20 s (17). During a transient rotational movement, for example, eye velocity decays slowly to zero. On the other hand, responses to transient linear motion stimuli have typically only been characterized during the first few tens of milliseconds of motion, without either a characterization of the steady-state performance or the response dynamics (2, 4, 5, 13). Here, we summarize the basic characteristics and quantitative description of transient TVOR responses in non-human primates that have been trained to maintain vergence angle in darkness.

METHODS

A total of six animals (juvenile rhesus monkeys 3-5 kg) implanted with a head-restraint ring and dual eye coils were used in the present study. All surgical procedures were performed in accordance to institutional guidelines. All animals participating in these experiments were pre-trained using juice rewards to fixate targets paired with an auditory cue for variable time periods, then to maintain fixation after the target was turned off, for as long as the auditory tone was present (at least 1 s). As explained in more detail elsewhere (1-3), special care was taken to tightly and securely fasten the animal's head and magnetic coils to the stiff inner gimbal of the 3-D turntable. No

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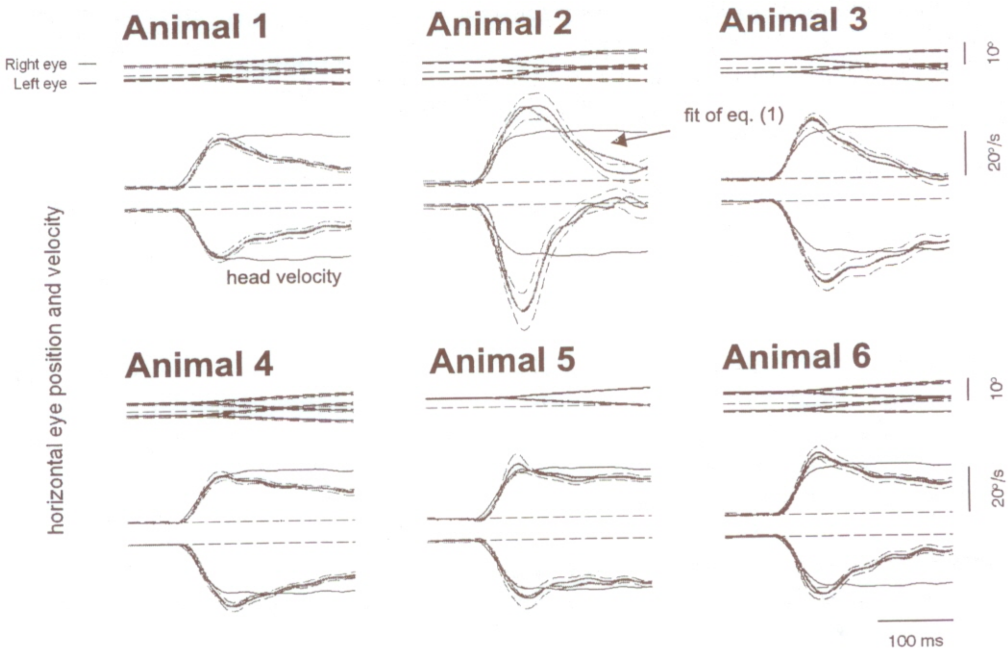

Fig. 1. *The mean (± SD) horizontal position of the right and left eyes, as well as the velocity of the right eye (bottom traces) are plotted for each of six animals.*
Prior to the movement that took place in complete darkness, animals fixated a target located approximately in between the two eyes at a distance of 20 cm. Dotted lines illustrate zero position (straight ahead gaze) and zero eye velocity. The translational velocity of the head (computed as the integral of the output of a linear accelerometer mounted on the animal's head) has been superimposed with thin black solid lines in the plots from each animal (peak linear head velocity: 22 cm/s; peak linear acceleration: 0.5 G). Positive sled velocity is to the right and elicits leftward (positive) eye velocity. Both directions of motion are plotted. Only monocular (right) eye movements were recorded in animal 5. The gray lines that have been superimposed on the right eye velocity traces represent fits of equation (1) (parameters in Table 1).

detectable head movement was present during transient motion (the signals from a 'head coil' were often monitored as a control; see 1-3). Because the animals were trained to maintain fixation on the target in darkness under the auditory tone guidance, loss of vergence was an uncommon problem in these experiments. As shown in Figure 1, trained animals maintained vergence for the whole duration of motion.

Translational stimuli consisted of a step-like linear acceleration profile, followed by a short period of constant velocity (peak linear acceleration: 0.5 G; peak linear velocity: 22 cm/s). Target distance was varied between 10 and 314 cm. Each trial was initiated under computer control when the animal had satisfactorily fixated the target for a random period of ~ 300-1000 ms. Separate gaze angles and behavioural windows were computed for each eye, taking into account target distance and eccentricity, as well as interocular distance (e.g., 2, 3, 15). The target light was extinguished immediately before the onset of acceleration and remained off for the entire motion. Throughout the first ~ 250 ms of movement, the auditory tone remained on, in order to provide guidance for the trained animals regarding the duration of the required fixation of the memorized target. Intermingled runs where animals were required to fixate but no sled movement occurred were also routinely used. In all experimental protocols, the direction of sled motion (positive, negative and no motion were presented in a pseudo-random fashion.

For each recording session, signals were low-pass filtered (200 Hz, 6-pole Bessel) and digitized at a rate of 833.33 Hz (Cambridge Electronics Design, model 1401, initially 12 and later 16-bit resolution). An automated analysis routine displayed each experimental run sequentially and allowed the experimenter to select only saccade-free runs to be included for grand-averages and further analysis. In addition, this step allowed direct inspection of vergence throughout the motion profile. If there was an obvious loss of vergence (usually associated with a saccade), the run was discarded and excluded from further analysis.

Quantification of the dynamic properties of the transient responses was obtained by simulating the time domain response of a simple model, consisting of the eye plant, the neural integrator, as well as central processing (1). Specifically, the transfer function, $H_o(s)$, related the linear acceleration stimulus to the neural integrator, i.e.,

$$H(s) = \frac{\text{eye velocity}}{\text{linear velocity}} = s^2 H_o(s) H_{int}(s) H_e(s) \qquad (1)$$

where $H_{int}(s)$ is the velocity-to-position neural integrator and $H_e(s)$ is the oculomotor plant (see also 1). The simplest function that could satisfactorily describe the data was:

$$H_o(s) = \frac{K(s+2\pi f_o)}{s+2\pi f_p} e^{-\tau_d s} \qquad (2)$$

where τ_d is the reflex delay. Fitted parameters have been included in Table 1.

Table 1. - *Parameters of tranfer function fits.*

		f_o (Hz)	f_p (Hz)	K	time delay, τ_d (ms)
animal 1	(p)	0.8	0.30	0.12	9
	(n)	0.7	0.14	0.12	7
animal 2	(p)	> 20	7.53	0.10	8
	(n)	1.5	3.34	0.37	17
animal 3	(p)	12	> 20	0.27	7
	(n)	3.1	0.94	0.16	7
animal 4	(p)	1.4	0.20	0.11	7
	(n)	2.5	0.70	0.13	8
animal 5	(p)	1.4	< 0.01	0.11	7
	(n)	1.5	< 0.01	0.12	7
animal 6	(p)	0.8	< 0.01	0.14	8
	(n)	0.3	< 0.01	0.15	8

Parameters of the transfer function H (s) = $\frac{Ks^2(s+2\pi f_o)}{s+2\pi f_p} e^{-\tau_d s} H_{int}(s) H_e(s)$ that was fitted to the data from each animal.

RESULTS

Average response profiles from each of six animals at a viewing distance of 20 cm have been plotted in Figure 1. Responses to both motion directions have been superimposed (each response is illustrated as mean ± SD from ~ 40-50 runs). The top traces in each subplot illustrate binocular eye position, whereas the bottom traces plot right eye velocity. A typical eye velocity profile consisted of a relatively fast rise to peak that was reached approximately at the time that head velocity reached steady-state (Fig. 1). For the particular stimulus profile (22 cm/s, 0.5 G), horizontal eye velocity peaked within ~70 ms after stimulus onset (~ 40 ms after peak linear acceleration), with a time constant of 36.2 ± 6.2 ms. Despite maintained translation at constant velocity, eye velocity decreased thereafter, following a rather exponential decay to a steady-state level with a short time constant.

In contrast to robust initial responses, the steady-state eye velocity was highly variable among animals (Fig. 1). For example, in three of the animals (animals 1, 4 and 5), the elicited eye velocity was symmetric for rightward and leftward motion directions. In the remaining animals, steady-state responses were either slightly or strongly asymmetric (animals 2, 3 and 6). When steady state eye velocity was less than 37% of peak value and a decay time constant could be measured (this was usually possible for the nearest targets), it averaged 68.1 ± 22.3 ms.

Eye velocity responses were fitted by the transfer function described by equation (1). Fits have been superimposed in the eye velocity responses of Figure 1, whereas parameters have been included in Table 1. In general, responses were well described by a simple first-order function, $H_o(s)$, cascaded by the neural integrator and the eye plant (1, 8). Fitted parameter values spanned a large range, reflecting the great response variability among animals. The fitted numerator (zero) frequency was usually within the range of 0.3-3 Hz. The fitted denominator (pole) frequency was typically less than 1 Hz. As a general observation, the pole frequency tended to be lower than the zero frequency for most animals.

In general, responses were consistently undercompensatory for near target view-

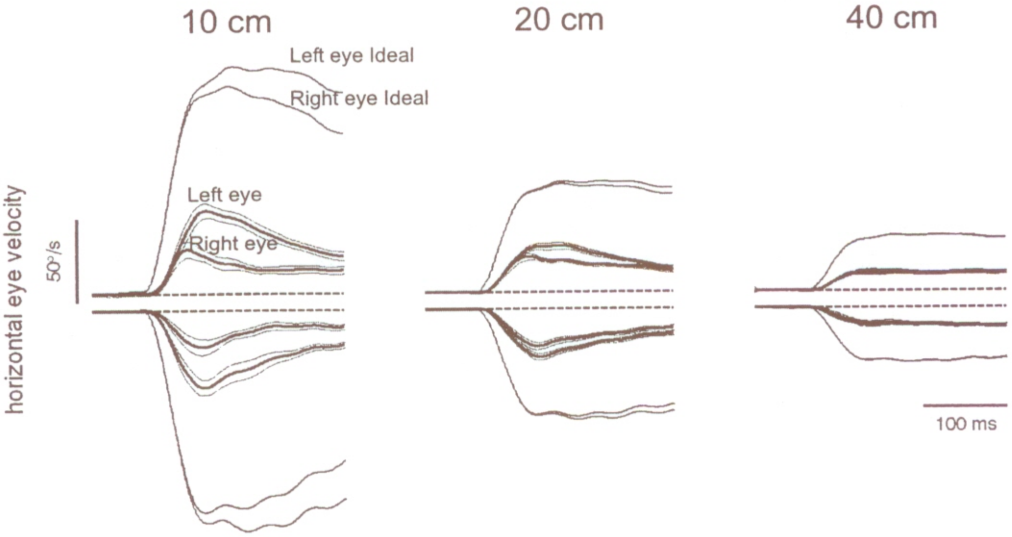

Fig. 2. - *Mean (± SD) right and left eye velocity at different viewing distances (10, 20 and 40 cm) during both rightward (eliciting positive, i.e., leftward, horizontal velocity) and leftward (eliciting negative, i.e., rightward, horizontal velocity) motion.*
Ideal right and left eye velocities have been superimposed with thin lines. Data from animal 4.

ing (10-40 cm; Fig. 2), as illustrated by comparing actual with ideal responses (i.e., the eye velocity that would have been elicited to continuously foveate the target during motion). In addition, both ideal and actual eye velocities differed for the two eyes. As expected based on the kinematic requirements of the reflex [1], left eye velocity was greater than right eye velocity during rightward motion (Fig. 2, top traces). The opposite was true during leftward motion (Fig. 2, bottom traces). However, the actual difference between left and right eye responses was generally larger than that expected based on theoretical considerations. Responses became closer to compensatory as viewing distance increased. Even though robust and nearly compensatory responses were observed in darkness immediately following fixation on far targets, eye movements were highly variable and small in amplitude when sudden transients were applied in darkness (without controlling viewing distance). This was so despite the fact that the average 'default' vergence angle in maintained darkness was ~1 MA (i.e., the two gaze directions intersect on average at ~1 m; see 1).

Translational VOR responses exhibited a strong dependence on viewing distance. The viewing distance-dependence was not similar throughout the response profile, being stronger earlier than later into the motion (Fig. 2). In fact, response dynamics depended on prior viewing distance. The closer the target, the more phasic the response profile, particularly for the abducting eye (e.g., left eye during translation to the right). Similarly, the further away the target the more tonic the eye velocity response profile (i.e., the more it resembled linear head velocity). Only the early components of the response scaled linearly with viewing distance. For example, twenty-five ms after motion onset (and while the movement of the two eyes was conjugate), linear regression coefficients varied between 0.75 and 0.97 (Table 2). However, the dependence became strongly non-linear as soon as the two eyes diverged from each other for the near target viewing conditions (> 25 ms; Table 2).

DISCUSSION

Robust, short-latency eye movements were generated in darkness during transient lateral displacements. The horizontal response sensitivity was characterized by small latencies (~ 8-12 ms) and was scaled by prior viewing distance, as early as within the first few milliseconds from response onset (2). However, only the first ~ 100 ms of the response scaled clearly with prior viewing distance. Steady-state eye velocity was relatively independent of viewing distance and highly variable among

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[1] The sensitivity of the horizontal TVOR component can be approximated by (Angelaki et al., 2000; Telford et al., 1997):

$$\frac{d\theta_{R,L}/dt}{d\Delta y/dt} = (1/D)\cos^2\theta_{R,L}$$

As target eccentricity increases during the movement, the $\cos^2\theta$ term differs for the two eyes. Thus, the two eyes are predicted to move disjunctively.

Table 2. - *Dependence of eye velocity on the inverse of prior viewing distance: First and second order regression coefficients.*

	Rightward motion		Leftward motion	
	first order	second order	first order	second order
R eye velocity (25 ms)	0.96 (74.3)	0.99	0.93 (-82.6)	0.99
L eye velocity (25 ms)	0.97 (86.9)	0.99	0.75 (-43.3)	0.97
R eye velocity (50 ms)	0.87 (164)	0.99	0.88 (-285)	0.98
L eye velocity (50 ms)	0.88 (271)	0.99	0.58 (-97.8)	0.97
R eye velocity (100 ms)	0.07 (32.9)	0.95	0.88 (-257)	0.95
L eye velocity (100 ms)	0.91 (309)	0.99	0.08 (26.1)	0.88
R eye velocity (239 ms)	0.06 (10.7)	0.22	0.88 (-147)	0.89
L eye velocity (239 ms)	0.85 (130)	0.96	0.21 (43.9)	0.21

Average data (5 animals) at different times after stimulus onset (25, 50, 100 and 239 ms). The numbers in parentheses represent the slope of the first order linear regression lines (in units of °/s/cm^{-1}). R: right eye; L: left eye.

animals. A similar frequency (or time)-varying viewing distance dependence has also been previously reported during steady-state motion (15).

The shape of the transient response profile also reflected this viewing distance-dependent dynamics. For far targets, horizontal eye velocity seemed to follow a delayed, scaled replica of linear head velocity. For near target viewing, however, horizontal responses were more phasic and seemed to also resemble the profile of linear acceleration. Eye velocity was large during the acceleration phase of the stimulus but decayed fast, as soon as steady-state velocity was reached, with a time constant of ~ 50-100 ms.

The observed differences in response profile and dynamics as a function of target distance can be attributed to two separate components in the TVOR: A component that is independent of viewing distance and a component that is scaled by the inverse of viewing distance. The latter component seems to have more high-pass filtered characteristics, whereas the viewing distance-independent component seems to more precisely encode linear head velocity. A similar functional division of viewing distance-dependent and independent components have been reported during high frequency, steady-state sinusoidal responses (3, 15).

A consistent result of this and previous TVOR studies is the strongly undercompensatory nature of the response during near target viewing. Satisfactory ocular compensation has been previously also observed only for far targets (> 1-2 m; 7, 13, 15). Therefore, even though eye velocity increases with the inverse of viewing distance, this increase is insufficient to compensate for the relative target movement. In contrast to the undercompensatory responses measured during purely lateral head displacements, a nearly perfect ocular compensation has been reported during eccentric rotations (6, 14, 16). Differences in animal training could present one explanation. Whereas 'naïve' responses were the goal of the present studies (similarly as in 13), behavioural windows imposed during and after the motion might have trained primates to perform a nearly ideal VOR during eccentric rotation (14). Another, and perhaps more likely explanation for the large VOR gains reported during eccentric rotation might be the simultaneous activation of semicircular canals. The nature of these interactions awaits further investigation.

CONCLUSION

As foveal vision and stereopsis evolved, novel visual and vestibular mechanisms also developed in order to stabilize binocular gaze on the depth plane of interest during translatory movements. The role of vestibular signals in this task is described here during transient lateral displacements. In agreement with previous reports, initial eye velocity responses were robust and exhibited a strong dependence on viewing distance. In contrast, > 100 ms into the motion, after head acceleration decayed to zero, responses were small, variable, often asymmetric and exhibited little dependence on viewing distance. These dynamics are described by a function with a first-order approximation for the central processing of otolith-ocular signals.

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