Motor Scaling By Viewing Distance of Early Visual Motion Signals During Smooth Pursuit

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Zhou, Hui-Hui, Min Wei, and Dora E. Angelaki. Motor scaling by viewing distance of early visual motion signals during smooth pursuit J Neurophysiol 88: 2880–2885, 2002; 10.1152/jn.00476.2002. The geometry of gaze stabilization during head translation requires eye movements to scale proportionally to the inverse of target distance. Such a scaling has indeed been demonstrated to exist for the translational vestibulococular reflex (TVOR), as well as optic flow–selective translational visuomotor reflexes (e.g., ocular following, OFR). The similarities in this scaling by a neural estimate of target distance for both the TVOR and the OFR have been interpreted to suggest that the two reflexes share common premotor processing. Because the neural substrates of OFR are partly shared by those for the generation of pursuit eye movements, we wanted to know if the site of gain modulation for TVOR and OFR is also part of a major pathway for pursuit. Thus, in the present studies, we investigated in rhesus monkeys whether initial eye velocity and acceleration during the open-loop portion of step ramp pursuit scales with target distance. Specifically, with visual motion identical on the retina during tracking at different distances (12, 24, and 60 cm), we compared the first 80 ms of horizontal pursuit. We report that initial eye velocity and acceleration exhibits neither or a very small dependence on vergence angle that is at least an order of magnitude less than the corresponding dependence of the TVOR and OFR. The results suggest that the neural substrates for motor scaling by target distance remain largely distinct from the main pathway for pursuit.

INTRODUCTION

A phylogenetically novel gaze stabilization mechanism that has evolved in parallel with foveal vision and stereopsis is the translational vestibulococular reflex (TVOR). The TVOR comprises vestibular-driven compensatory eye movements that seem to be optimized to keep images stationary on both foveae and to minimize binocular disparity during natural activities (Angelaki and Hess 2001; Crane and Demer 1997; Miles 1993, 1998). Motion parallax and simple geometrical considerations dictate that the amplitude of these translation-specific eye movements should be inversely proportional to viewing distance. Indeed, numerous studies over the past years have demonstrated a strong, although typically not optimal, dependence of TVOR on the inverse of viewing distance (Angelaki and McHenry 1999; McHenry and Angelaki 2000; Paige and Tomko 1991a,b; Schwarz et al. 1989; Schwarz and Miles 1991; Telford et al. 1997). Because the sensory output of these signals that generate these eye movements are independent of target location, it is commonly assumed that this scaling occurs in central premotor pathways (Angelaki et al. 2001; Chen-Huang and McCrea 1999; McConville et al. 1996; Snyder and King 1996).

These vestibular-driven eye movements have been proposed to complement and work closely in synergy with phylogenetically novel translational visuomotor reflexes (e.g., ocular following, OFR) that result from relatively low-level preattentive cortical processing and that sense the observer’s motion by decoding either the pattern of optic flow (Busettini et al. 1997; Miles 1993, 1995, 1998; Miles et al. 1986, 1991; Miles and Busettini 1992; Schwarz et al. 1989; Yang et al. 1999) or depth and binocular disparity cues (Busettini et al. 1994, 1996a,b). In contrast to the TVOR, the sensory signals to generate these translation-selective visuomotor reflexes are inherently scaled for viewing distance. Thus it was surprising when Busettini et al. (1991) (see also Yang et al. 1999) demonstrated that the open-loop OFR did scale inversely proportional to viewing distance, similarly to the TVOR, even when the size and speed of the visual stimulus was adjusted to preserve a constant retinal image. These puzzling results were interpreted to suggest that TVOR and OFR share common premotor neural processing.

The neural substrates of OFR include the middle temporal (MT, MST), the dorsolateral pontine nuclei, and the ventral paraflocculus (Gomi et al. 1998; Kawano and Shidara 1993; Kawano et al. 1990; Kobayashi et al. 1998; Shidara and Kawano 1993; Takehara-Nishikawa et al. 2001). Considering that the neural substrates for the TVOR involve mainly brain stem/cerebellar structures, one could then postulate that the motor scaling by a neural correlate of viewing distance occurs either in cerebellar and/or premotor vestibular nuclei neurons (Chen-Huang and McCrea 1999; Snyder and King 1996). These same areas have also been implicated, however, in the sensorimotor transformations for smooth pursuit eye movements. Specifically, Purkinje cells in the flocculus/ventral paraflocculus and eye movement-sensitive cells in the vestibular nuclei have been considered to represent important premotor substrates for the generation of smooth pursuit (Krauzlis and Lisberger 1994b; Stone and Lisberger 1990; Zee et al. 1981). Thus, if processing in all three systems (TVOR, OFR, and pursuit) involves common cerebello-pontine neurons, one would expect that open-loop pursuit responses would also scale inversely proportional to target
distance. This study was undertaken to address this issue. We report that, contrary to OFR, the initial eye acceleration and velocity during open-loop pursuit only exhibits a small or negligible scaling with target distance when retinal image motion and size remain constant.

**METHODS**

Three *Rhesus* monkeys were chronically prepared with skull bolts to restrain the head and implanted with a search coil on each eye for binocular eye-movement recordings using the magnetic search coil technique. 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). Both stimulus presentation and data acquisition were controlled with custom-written scripts within the Spike2 software environment using CED (Cambridge Electronics Device, Model 1041 plus) data acquisition system. Binocular eye and target position signals were filtered (6-pole Bessel, DC-200 Hz), digitized at 833 Hz, and stored on the hard disk of a PC for analysis.

Visual stimuli were created by a dedicated computer and back projected using a DLP projector (DLV1280-DX, Christie Digital System, 100 Hz vertical refresh rate and 1280 × 1024 resolution) onto a tangent screen placed 12, 24, or 60 cm in front of the monkey. Animals were trained to pursue targets moving in different directions and speeds using step-ramp stimuli (Rashbass 1961). Each trial began when the monkey fixated a straight-ahead target aligned with his left eye. 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 a constant velocity (11.8 or 22.6 °/s) in a direction toward and then beyond the initial straight-ahead position (Fig. 1A, top). The movement lasted for 700–1,000 ms. Both targets were at the same vertical level and the horizontal position difference between them formed the “step.” 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. Eye movement recordings and behavioral control was binocular (thus reinforcing appropriate vergence angle for each distance), although quantitative data analyses focused on the movement of the left eye (see following text).

Since the goal of the present study was to vary viewing distance while keeping retinal image motion constant, special care was taken to preserve retinal image size and motion as the distance between the target and the animal changed. Therefore, for each distance, the size of the target on the screen was adjusted to always be a white square of a constant retinal size of 0.5 × 0.5°. In addition, target motion on the screen was adjusted such that it always moved identically on the retina. That is, the distance that the target traveled on the screen was inversely proportional to screen distance from the animal, such that for all distances the same eye movement would be required to keep the target stable on the retina. In initial experiments, target velocities (corresponding to 11.8 or 22.6 °/s of eye velocity) were chosen such that at all distances target motion was an integer multiple of a pixel for each refresh of the projector (10 ms). In later experiments (comprising all data presented here), however, visual motion was generated in OpenGL (and Oxygen GVX1 Pro, 3Dlabs video card), taking advantage of the special features and lack of pixelization and aliasing problems.

Since the parameters of open-loop pursuit depend on target position on the retina (Lisberger and Westbrook 1985), the initial fixation target was always aligned with the left eye, whose motion was subsequently analyzed. Because of this dependence on retinal posi-

**FIG. 1.** A: example of a step-ramp pursuit. The trial began with a target centered on the left eye. After satisfactory fixation, a second target appeared on the left and started moving rightward (22.6 °/s) as soon as the central fixation target was turned off. Top: target position (T) and eye position (E) traces. Middle: target (T) and eye (E) velocity. Bottom: mean eye velocity (blue line) has been superimposed on 37 individual trials (green). B: mean left eye velocity during pursuit of a 0.5° target aligned with the left eye that moved rightward (positive traces) or leftward (negative traces) on screens placed at different distances from the animal (12 cm: red traces; 24 cm: blue traces; 60 cm: green traces). Data were recorded on the same experimental day in animal P.
Our analyses focused on the open-loop interval during the first 80 ms of pursuit that describes the system’s output in response to a visual input (Krauzlis and Lisberger 1994a; 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 Dubovsky and Cullen (2002). Specifically, the onset position was defined as the point of intersection between a baseline regression and an initial response 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. Linear regressions were also applied to the eye velocity traces over the intervals of $0–20$, $20–40$, $40–80$, and $0–80$ ms from eye movement onset. The slope of the best-fit line was used as the estimate of mean eye acceleration in that interval. In addition to eye acceleration, the eye velocity at 80 ms, as well as mean eye velocity in the interval 300–400 ms after eye motion onset, was also computed. The latter values were used to verify that steady-state eye velocity was the same for all viewing distances. Statistical comparisons have been based on ANOVA.

For comparison with the pursuit dependence on target distance, the TVOR was also studied during 5 Hz ($\pm 0.25$ g) sinusoidal left–right motion while the animals fixated a central target using the same screen-projector arrangement or back projected onto the screen using a laser/mirror galvanometer assembly. Similar to pursuit testing, targets were presented in a lightly illuminated room.

**RESULTS**

A typical example of a step-ramp pursuit response in one of the animals (P) during a rightward target motion at $22.6^\circ$ is shown in Fig. 1A. The top traces in Fig. 1A show the position profile of the eye and the target. The middle traces show the corresponding eye and target velocity. Superimposed eye velocity traces from several repetitions of the stimulus are shown in Fig. 1A, bottom. The eye velocity in this animal (P) accelerated slowly to a steady-state level, which remained constant for all viewing distances, as shown in Fig. 1B, which plots mean leftward and rightward eye velocity for three different target distances recorded sequentially in one experimental day. As illustrated by comparing the average traces, initial eye velocity and the rate of change in eye velocity tended to be slightly larger the closer the target to the animal. The difference in eye velocity for the different target distances diminished over time after the end of the open-loop period, as expected for proper pursuit since target motion remained constant on the retina.

As will be further elaborated below, whereas differences in open-loop pursuit were often visible and sometimes statistically significant, they were always much smaller than those of the TVOR and OFR. In fact, the small distance dependence of open-loop pursuit velocity for animal P (Fig. 1B) was the largest seen in these experiments. The absence of a large dependence of open-loop velocity and acceleration on target distance is further illustrated in Fig. 2, where average data from all three animals are displayed. Mean eye acceleration in the 0–80-ms interval and eye velocity at 80 ms after pursuit onset for the 12-cm target was on average $4–12\%$ larger than that for 60-cm pursuit in monkeys P and K (Table 1). Eye velocity during the open loop interval for 12- and 60-cm target distances were not significantly different for the responses of animal R (Fig. 2, right traces) (Table 1).

**DISCUSSION**

We found that initial eye velocity and acceleration during the open-loop portion of step-ramp pursuit exhibit either small
TABLE 1. Initial velocity and acceleration

<table>
<thead>
<tr>
<th>D = 12 cm</th>
<th>n</th>
<th>D = 60 cm</th>
<th>n</th>
<th>Percent change, %</th>
<th>Increase per m⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>80-ms velocity (°/s)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Animal P</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rightward pursuit</td>
<td>10.6 ± 3.4</td>
<td>295</td>
<td>9.5 ± 2.7</td>
<td>281</td>
<td>11.2*</td>
</tr>
<tr>
<td>Leftward pursuit</td>
<td>12.7 ± 3.6</td>
<td>301</td>
<td>11.5 ± 2.6</td>
<td>263</td>
<td>10.4*</td>
</tr>
<tr>
<td>Animal K</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rightward pursuit</td>
<td>23 ± 2.9</td>
<td>91</td>
<td>22 ± 3.2</td>
<td>82</td>
<td>4.4*</td>
</tr>
<tr>
<td>Leftward pursuit</td>
<td>21.9 ± 3.5</td>
<td>104</td>
<td>20.8 ± 2.6</td>
<td>161</td>
<td>5.4*</td>
</tr>
<tr>
<td>Animal R</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rightward pursuit</td>
<td>19.8 ± 4.1</td>
<td>125</td>
<td>20.2 ± 3.9</td>
<td>151</td>
<td>−1.8</td>
</tr>
<tr>
<td>Leftward pursuit</td>
<td>21.7 ± 4.4</td>
<td>163</td>
<td>21.2 ± 4.2</td>
<td>157</td>
<td>1.9</td>
</tr>
<tr>
<td>0–80-ms mean acceleration (°/s²)</td>
<td></td>
<td></td>
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<tr>
<td>Animal P</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Rightward pursuit</td>
<td>133.2 ± 41</td>
<td></td>
<td>120.7 ± 34</td>
<td></td>
<td>10.4*</td>
</tr>
<tr>
<td>Leftward pursuit</td>
<td>160.8 ± 45</td>
<td></td>
<td>144.4 ± 35</td>
<td></td>
<td>11.4*</td>
</tr>
<tr>
<td>Animal K</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rightward pursuit</td>
<td>310.9 ± 41</td>
<td></td>
<td>289.7 ± 46</td>
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<td>7.3*</td>
</tr>
<tr>
<td>Leftward pursuit</td>
<td>298.3 ± 47</td>
<td></td>
<td>278.9 ± 36</td>
<td></td>
<td>7.0*</td>
</tr>
<tr>
<td>Animal R</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Rightward pursuit</td>
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<td>261.4 ± 53</td>
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<tr>
<td>Leftward pursuit</td>
<td>291.2 ± 59</td>
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<td>277.8 ± 57</td>
<td></td>
<td>4.8*</td>
</tr>
</tbody>
</table>

Values are means ± SD with percentages in parentheses. Percent changes were computed as increases (for positive changes) of the D = 12 cm target pursuit parameters relative to the values for D = 60 cm targets. For the statistically significant differences, increases in initial eye velocity and acceleration have also been computed per m⁻¹ (last column). Corresponding TVOR percent increases were measured to be 40, 40, and 33% per m⁻¹ for animals P, K, and R, respectively. * Statistically significant changes (ANOVA, P < 0.05); TVOR, translational vestibulo-ocular reflex.

FIG. 3. A: percentage increases in mean eye acceleration for different time intervals after pursuit onset. B: dependence of eye velocity 80 ms after pursuit onset on the inverse of viewing distance. Error bars (shown only for rightward pursuit) represent SDs. Filled symbols are used for statistically significant changes (open symbols are used otherwise). Data from different animals during both rightward and leftward pursuit (gray circles: animal P; black squares: animal K; open triangles: animal R).

or negligible scaling with target distance when stimulus size and velocity remained constant on the retina. Even if these differences were significant in two of the three animals, such a dependence of open-loop pursuit velocity and acceleration on target distance was at least an order of magnitude smaller than corresponding changes in the TVOR and the OFR (present data; see also Busettini et al. 1991). Thus, in contrast to the short-latency translational visuomotor reflexes that share common substrates with the TVOR (Miles 1993, 1998; see also Schwarz et al. 1989), the premotor processing of smooth pursuit seems to utilize largely distinct premotor pathways that bypass the viewing distance–dependent element that has been postulated to exist for TVOR and OFR. Alternatively, the present results suggest that the viewing distance–dependent gain element could be shared by all three systems only if an inverse gain element existed that was specific for pursuit eye movements. We consider that such an inverse and redundant engineering solution is less likely, particularly since there might have been little harm to the overall performance of the pursuit system if the open-loop responses were allowed to scale similarly as the OFR.

Motor scaling by a neural estimate of target distance is a necessary and important component in the computations that convert primary otolith afferent signals into motor commands for the generation of short-latency, compensatory eye movements during head translation. Indirect evidence suggests that the neural substrates for this on-line modulation of reflex gain might involve the cerebellar flocculus/ventral paraflocculus and its projections to premotor neurons in the vestibular nuclei (Chen-Huang and McCrea 1999; Snyder and King 1996). These same cerebellar/brain stem pathways have also been implicated in the generation of translational optic flow-selective visuomotor responses (Gomi et al. 1998; Kawano and...
Shidara 1993; Kobayashi et al. 1998; Shidara and Kawano 1993) as well as smooth pursuit eye movements (Krauzlis and Lisberger 1994b; May et al. 1988; Mustari et al. 1988; Shidara et al. 1993; Stone and Lisberger 1990). Indeed, the early components of both ocular following and radial flow vergence responses exhibit such viewing distance–dependent modulation (Busettini et al. 1991; Yang et al. 1999).

Since motor scaling by viewing distance was never before tested for smooth pursuit eye movements, the present study was considered an important step for understanding viewing distance–dependent premotor processing. The present results demonstrating small, if any, dependence of open-loop pursuit parameters on viewing distance suggest that OFR/TVOR and pursuit signals probably remain largely segregated within separate neuronal populations of the cerebellar pontine structures that mediate this viewing distance–dependent scaling.

In parallel to the MT-pontine nuclei-FL network for pursuit, an additional pathway involving the frontal pursuit areas (Lynch 1987; MacAvoj et al. 1991) also exists that appears to be specific for pursuit and not for full-field visuomotor responses (Keating et al. 1996). Frontal pursuit neurons project through the pontine nuclei and the nucleus reticularis tegmental pontis to the vermal lobules VI/VI and the fastigial nuclei, areas that also participate in the generation of visually guided pursuit (Krauzlis and Miles 1998; Robinson et al. 1997; Takagi et al. 2000). At present, little is known about the functional significance of the different flocculus versus vermal/fastigial pursuit pathways for pursuit. The more than 10-fold difference between the premotor scaling by viewing distance for pursuit versus OFR/TVOR might also be due to a larger contribution of the vermal cerebellar pathways to the initiation of pursuit.

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