

Transforming retinal velocity into 3D motor coordinates for pursuit eye movements

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Abstract— Saccade planning requires a geometric transformation between the retinal stimulus position and the desired motor plan to acquire the target. This reference frame transformation problem has, however, never been considered for velocity signals. Therefore we asked whether a separate 3D visuomotor transformation of velocity signals was theoretically required by modeling the underlying geometry. We used quaternions to model the 3D eye-in-head geometry. Our model predicted that a visuomotor velocity transformation would require extra-retinal 3D eye-in-head position to convert the retinal velocity input into spatially accurate behavior and includes three different components; (1) the same retinal velocity results in different eye rotation axes depending on eye-in-head position, (2) false torsion due to off-axes eye positions must be compensated for and (3) ocular torsion (e.g. due to the VOR) must be accounted for. To test these predictions, subjects were required either to pursue a moving target viewed under different vertical (prediction 1) or oblique (prediction 2) eye positions, or viewed under different head roll angles generating VOR-induced eye torsion (prediction 3). We measured 3D eye and head orientation and analyzed the open-loop gaze pursuit response, i.e. the first 100ms after pursuit onset. We then compared the observed pursuit response to the predictions of the model: if no transformation was performed, pursuit direction should best correlate with the retinal target movement direction; a complete 3D velocity transformation would be reflected in spatially accurate pursuit. We found that for all 3 predictions, the direction of pursuit initiation was spatially accurate and did not follow the retinal (no transformation) hypothesis. This suggests that the brain performs a complete 3D visuomotor velocity transformation for smooth pursuit eye movements that is different from the previously described visuomotor transformation of position signals for saccades.

Keywords— visuomotor transformation, reference frames, geometry, smooth pursuit, retinal slip.

I. INTRODUCTION

To produce a geometrically accurate motor command from visual input, the brain has to interpret the sensory information from the retina depending on the current body geometry. This process is known as the visuomotor transformation, a process at the heart of motor planning for saccades and arm movements [2,6-7]. For example, in case of ocular torsion and/or head roll, the brain has to generate a

reaching movement from rotated visual information about the hand and target location [2]. One shortcoming of the current description of this sensorimotor conversion is that it is purely static, i.e. only position signals of non-moving targets have been considered while subjects remain immobile in a certain configuration. However, our visual environment is constantly changing, either because objects of interest move in the world or because we are moving. Therefore, the visuomotor transformation must also account for dynamic as well as static situations.

In the brain, static (position) and dynamic (velocity) visual signals are processed by largely segregated anatomical structures [9,11,14]. Importantly, the pathways for both signals separate very early on in the dorsal stream, much earlier than areas believed to be involved in the visuomotor transformation of static position signals, i.e. the posterior parietal cortex [3,7,15]. Indeed, the position and velocity pathways can be dissociated as early as V1 [12-13]. This has a very important implication for how the brain performs visuomotor transformations for velocity signals. If the brain interprets velocity signals in a geometrically congruent fashion so as to generate accurate movement commands from visual input, a separate visuomotor transformation of those velocity signals is necessary. Without such a velocity transformation, large errors in motor commands towards moving targets should be expected. This is not only true when tracking objects in motion or during self-motion, but also when extrapolating trajectories based on their velocity, e.g. to catch a moving ball.

In the present study, we aim to reach the first milestone in the description of visuomotor velocity transformations for eye movements. We describe the theoretical framework of the visuomotor velocity transformation geometry for eye movements and demonstrate the need of the latter, without which we predict specific error patterns for smooth pursuit and catch-up saccades to moving targets. In a second step, we test those predictions experimentally and report that the brain fully compensates for geometrical differences between the retinal input and the required motor output to produce spatially accurate behavior. We discuss the implication of this study for other visuomotor or vision experiments using moving stimuli and make predictions about the hypothesized neurophysiology underlying the visuomotor velocity transformation.

II. METHODS

A. Model

The question we wanted to address was if and how retinal velocity signals need to be transformed in order to produce a geometrically accurate eye movement. Underlying this question is the fact that retinal input and extra-ocular muscle commands are encoded in different frames of reference. It has been shown for saccades that position signals must undergo a transformation between the retinal (visual input) and head-centered (motor output) reference frames. Here we investigate this reference frame transformation for velocity signals.

We used a model of 3D eye position and simulated different hypotheses for the visuomotor velocity transformation. 3D eye position follows Listing's law, which we implemented in our model. We also incorporated the static and dynamic VOR in order to account for ocular counter-roll with different gains. Retinal geometry was modeled using spherical projections (see also [2]). Using quaternion algebra, eye-in-head rotation can be described as the following quaternion q [16]:

$$q = q_L q_{PP} \quad (1)$$

$$\text{with } q_L = \sqrt{-\begin{bmatrix} 0 \\ \vec{e} \end{bmatrix}} q_{LP} \quad (2)$$

$$\text{and } q_{PP} = \sqrt{q_{LP}^{-1} [0 \ 0 \ 1 \ 0]^T} \quad (3)$$

q_L is the Listing's law quaternion and q_{PP} is the quaternion describing the primary position of the eyes in the orbit. \vec{e} is the normalized vector of the direction of the eyes with respect to the head and q_{LP} describes the gravity tilt of Listing's plane (static vestibulo-ocular reflex, VOR).

$$q_{LP} = \begin{bmatrix} 0 \\ 0 \\ \cos \alpha \\ -\sin \alpha \end{bmatrix}, \text{ with } \alpha = \alpha_0 + g_P \cdot \alpha_P \quad (4)$$

For the simulations performed here, we used a default tilt angle for Listing's plane in the head upright position that was $\alpha_0 = 5$ deg. When the head moves around the nasal-temporal axis (head pitch movement) about an angle α_P , the Listing's plane pitches with an average gain of $g_P = 0.05$ [4,8]. In addition to the pitch component of the rotational static VOR, we also implemented the ocular counter-roll for both the static and dynamic conditions.

$$q_{OCR} = \begin{bmatrix} \cos \beta \\ 0 \\ \sin \beta \\ 0 \end{bmatrix},$$

$$\text{with } \beta = g_{R,S} \cdot \beta_R + g_{R,D}(f) \cdot \beta_R \quad (5)$$

The counter-roll angle β depended on the head roll angle β_R and was composed of a static VOR component (gain $g_{R,S}$) and a frequency (f) dependent dynamic VOR component (gain $g_{R,D}$). The total quaternion description of eye-in-head position was then $Q = qq_{OCR}$ and a position p in retinal coordinates was transformed into head-centered coordinates p' using quaternion rotation, i.e. $p' = \overline{Q}pQ$, where \overline{Q} is the quaternion conjugate. Please see [2] for a summary of quaternion algebra.

We used numerical differentiation to obtain velocity signals from successive static positions in the retinal and head-centered reference frames, i.e.

$$v(t) = \frac{p(t + \Delta t) - p(t)}{\Delta t}, \text{ with } \Delta t = 1 \text{ ms. Transforming}$$

two static positions is mathematically equivalent to transforming a velocity vector and its attachment point together. This is because the interpretation of the retinal velocity information is retinal position-dependent.

We had two working hypotheses. (1) retinal velocity input is used as is to generate the motor command in an invariable way, i.e. there is no reference frame transformation involved, or (2) retinal velocities are interpreted differently for different eye positions so as to produce a reference frame transformation, as this has been shown for position signals (e.g. [2,6]). In the first section of the Results, we will first investigate if hypothesis 1 would lead to any errors in the motor command and how large they would be under different circumstances, i.e. due to the retinal projection geometry, due to "false torsion" and due to VOR-induced ocular torsion. (Note: "false torsion" is the fact that for oblique eye positions, the screen vertical does not align with the retinal vertical, generating a false impression of torsion despite a zero torsional component in the rotation axis.). The below-described experiments target each of these components separately.

B. Experiment

Subjects sat in complete darkness in front of a 90cm distant screen. In experiments 1-2, their head was restrained

by a chin rest, whereas in experiment 3, their head was free to move. Green and red 0.2deg laser spots were projected onto the screen by means of mirror galvanometers. Movements of both eyes were recorded at 400Hz using a Chronos head-mounted 3D video eye tracker. Head movements (in experiment 3) were recorded at 200Hz using a Codamotion system and three infrared diodes on the Chronos helmet. Target presentation and synchronization signals for eye and head movement recordings were generated at 1kHz using a dedicated real-time computer and LabView. Subjects were presented with a series of blocks of trials. There were three different experiments in a session.

Experiment 1 (eye rotation geometry): A red fixation spot was presented for a random duration between 750ms and 1,250ms at one of three vertical eccentricities, i.e. 0deg or ± 20 deg. After this initial fixation, the target jumped either left or right (± 25 deg horizontal) and immediately started moving to the left or to the right at 20deg/s for 500ms.

Experiment 2 (retinal projection geometry – “false torsion”): Subjects fixated one of three oblique, red fixation spots for a random time between 750ms and 1,250ms. The oblique fixation positions were (H,V): (0,0)deg; ($\pm 25, 25$) deg. Then the target started moving at 20deg/s for 500ms randomly in one of the cardinal directions.

Experiment 3 (head roll – torsional counter-roll): Subjects had to fixate a straight-ahead red fixation spot for 1,000ms. Then, the fixation spot turned green for 750ms, which indicated to the subjects that they had to move their head either to the left or right shoulder (fixed within a block of trial). After that, the fixation spot turned red again for 250ms and then started moving at 20 deg/s for 500ms in one of the cardinal directions (randomly selected in each trial).

Measured eye orientation was low-pass filtered (50Hz) and differentiated twice. Saccades were detected using a 500deg/s^2 acceleration threshold. Smooth pursuit onset was detected using a velocity backward interpolation technique [1,5,10]. We then computed the initial pursuit eye movement direction and related eye rotation axes based on the 100ms open-loop period after movement onset.

For experiment 3, the position of the three head-mounted infrared markers was low-pass filtered (autoregressive forward-backward filter, cutoff frequency = 50Hz) and the used to calculate the head orientation quaternion. Head orientation was then computed as the difference (calculated in terms of quaternion rotation) between a reference position and measured head position during the test trials.

III. RESULTS

The first prediction of our model concerns the rotational geometry of the eyes. Two different example configurations

are shown in Fig 1, where a horizontal pursuit eye movement has to be generated as a response to a horizontally moving target viewed under two different vertical eye positions, i.e. central eye position (dotted, green) and 20 deg upward eye position (solid, red). Both situations result in exactly the same retinal input (retinal projection patterns on the right in Fig 1), i.e. the moving target falls onto the retinal horizon and the retinal velocity input is thus purely horizontal. However, the motor output for spatially accurate pursuit depends on the vertical eye position; the required rotation axis for pursuit initiation under straight-ahead viewing is purely vertical (dotted, green), whereas pursuit initiation during vertical fixation requires a rotation axis that is tilted by the same amount as vertical eye position (solid, red). This means that the brain must take vertical eye position into account when interpreting identical visual input to generate spatially accurate pursuit initiation. Although we restricted ourselves to vertical eye position, the same principles apply when generating vertical pursuit from different horizontal fixations.

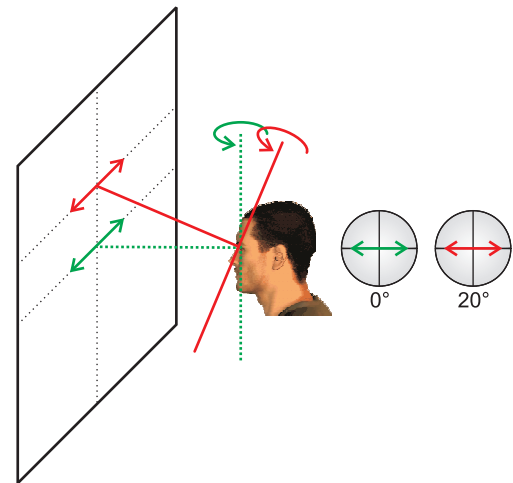


Fig 1: Effect of the retinal projection geometry on the visuomotor velocity transformation.

Second, our model predicts that the brain must account for “false torsion”, i.e. the apparent misalignment of visual and spatial axes during oblique eye orientations. Fig 2 shows how cardinal movement directions in space (as represented by arrows on the screen in Fig 2) project in a rotated fashion onto the retina. Therefore, in order to initiate smooth pursuit in the spatially accurate direction, the brain has to rotate the visual velocity input back into the correct reference frame. This compensation for false torsion is dependent on the eccentricity and “obliqueness” of eye orientation.

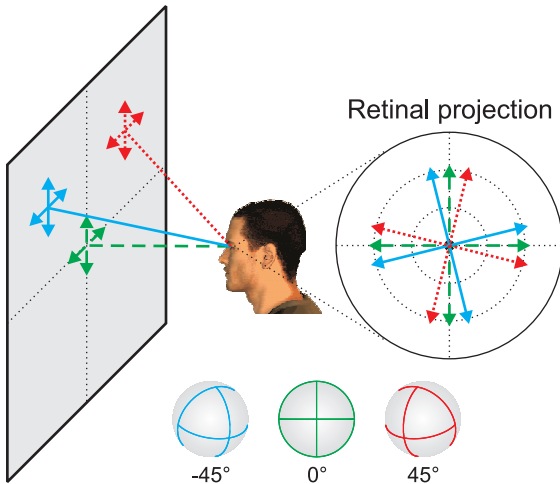


Fig 2: "False torsion" due to Listing's law.

Third, our model predicts that the brain must compensate for real torsional angles of the eyes. Those can occur for example when the head is tilted sideward (roll movement). In this situation, the eyes counter-rotate due to the vestibulo-ocular reflex (VOR), as shown in Fig 3. As a consequence, the visual input is rotated with respect to the required motor output. In order to generate pursuit eye movements into the correct direction, the brain must take these torsional eye orientations into account and compensate for them.



Fig 3: Effect of ocular torsion (here due to ocular counter-roll) on the visuomotor velocity transformation.

Experimental results (not shown) demonstrate that the direction of smooth pursuit initiation did not follow the retinal (no transformation) hypothesis. Rather, pursuit initiation is spatially accurate in all three situations and regression slopes show that initial pursuit direction was not dissociable from spatially perfect behavior ($p < 0.01$).

IV. CONCLUSIONS

Our model and experimental results demonstrate that the brain indeed uses information about 3D eye-in-head

orientation in order to correct for the misalignment between the retinal input and required motor output for smooth pursuit initiation.

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