Testing the three-dimensional reference frame transformation for express and memory-guided saccades

Denise Y.P. Henriques, J. Douglas Crawford*

Medical Research Council Group for Action and Perception, Centre for Vision Research and Departments of Psychology and Biology, York University, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3

Abstract

The geometry of eye rotations necessitates an internal reference frame transformation between retinocentric visual codes and headcentric displacement commands for saccades. Here, we ask if this eye position-dependent transformation is bypassed in "express saccades" or degraded in "memory saccades", perhaps to favor a more direct visuomotor transformation. The answer to both was no: quantification of the behavioral data against simulated predictions revealed a correct biological transformation common to all saccades. This is discussed in terms of our "conversion-on-demand" model, wherein target representations are stored and updated within an early visual frame, but then transformed into appropriate motor frames for action. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Spatial vision; Reference frame transformation; Eye orientation; Three-dimensional; Retinal geometry

1. Introduction

Rapid eye movements, known as saccades, are responsible for producing abrupt shifts in gaze direction, usually to aim the fovea toward peripheral stimuli. The first step in generating visually guided saccades involves locating the target in space. When the eye fixates an object, light from the target stimulates the fovea, while other peripheral targets stimulate different sites on the retina, giving rise to an orderly retinotopic map of space. Retinal error (RE) can be defined as the distance and direction of these retinally stimulated sites from the fovea, and refers to the distance

---

*Corresponding author. Tel.: + 1-416-736-2100, ext. 88621; fax: + 1-416-736-5814.
E-mail address: jdc@yorku.ca (J.D. Crawford).

between current gaze direction and desired gaze direction. In this way, one receives information regarding the displacement of the target in visual space with respect to initial eye position. From this information, the oculomotor system must compute the motor error (ME) command required to activate the eye muscles and—hopefully—bring gaze onto the target.

One computational problem in this process lies in the lack of geometric correspondence between RE and ME, when their three-dimensional geometry is considered. When modeled as two-dimensional (2-D) displacements, these vectors seem to have the same characteristics [8,24,17]. However, in real three-dimensional (3-D) space RE is a 2-D eye-fixed entity, whereas an eye movement (and therefore the motor signal required to control it) is a 3-D displacement in head coordinates. (Although oculomotor scientists have a tendency to think of displacement vectors as coordinate system free, this simply is not the case.) As a result of this built-in geometry, RE does not project trivially onto ME. Thus, a model with realist 3-D geometry that does so produces simulated saccades that miss their goal, depending on the relationship between RE and initial eye position [3].

The necessity of transforming a 2-D retinal signal into a headcentric motor command is related to the fact that visual stimuli in space do *not* project on the retina in the manner that has traditionally been assumed. That is, due to properties of retinal geometry, a target that is displaced horizontally from the fixation point in space coordinates is not necessarily displaced horizontally in retinal coordinates. This discrepancy depends on eye position [3].

The consequences of this can be demonstrated by the simulation in Fig. 1 showing various peripheral targets of varying eccentricities ($30°, 60°, 90°$) on a horizontal ring
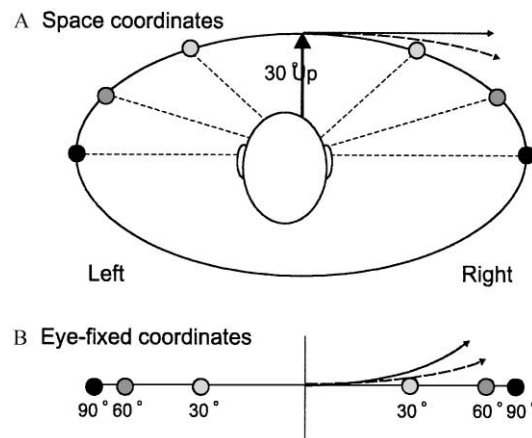

Fig. 1. Projection of peripheral targets on the retina and the resulting eye movements as a function of the axis used to rotate the eye from a behind view. Targets are displaced $30°, 60°$ and $90°$ (circles) both left and right from the midpoint of a "ring" rotated $30°$ upward with respect to the head. Eye direction is also rotated upward $30°$ so that the ring projects directly onto the horizontal meridian of the retina. (A) Space/head coordinates. (B) Retinal coordinates. While a rightward rotation along an eye-fixed axis would cause gaze to sweep around the ring, a similar rotations around a head-fixed axis (— $\equiv$) or an axis adhering to Listing's law (- - - $\equiv$) would produce gaze shifts that deviate away from the ring for both coordinate frames.

rotated $30°$ up. Gaze is also rotated $30°$ upward along the mid-line so that the targets fall along the horizontal meridian of the eye/retina, which is tilted with respect to the head. Therefore, the ring connecting the targets indicates how the target images would project onto the horizontal retinal meridian in eye-centered or retinocentric coordinates. If the eyes were allowed to rotate horizontally along an eye-fixed axis, they would produce accurate eye movements that would trace the ring, but the eye cannot move like this [22]. In contrast, rotating the eye horizontally along a head-fixed axis would produce inaccurate, straight gaze trajectories (—) away from the ring. But in reality, the eye does not move like this either. Rather it rotates about an intermediate axis. Thus, a rightward rotation of the eye along an axis rotated by half the angle of eye position as dictated by Listing's law [2,22], would produce a somewhat intermediate but still inaccurate trajectory (- - -).

If we look at the same configuration in eye coordinates (Fig. 1B) the same effect is observed, but one's definition of straightness and curvature reverse. The retinocentric peripheral targets now look straight (the ring is viewed edge-on), but an eye movement resulting from a rightward rotation along a head-fixed axis (—) or an axis compatible with Listing's law (- - -) would curve obliquely, with larger deviations from the retinal meridian occurring for greater target displacements. The magnitude of the retinal curvature of visual space increases in a non-linear fashion for more eccentric initial eye positions and for points located more peripherally along the horizontal lines. Consequently, the retinal site that the target image projects onto is a product of both target displacement in space and 3-D eye orientation.

These eye-position dependent curvatures of visual space as it projects on the retina have been described in previous experiments by Klier and Crawford [12] and Crawford et al. [4]. By having subjects make visually guided movements between horizontal pairs of targets, these authors looked to see whether subjects made movement trajectories that mimicked the distorted/curved retinal projections as a function of initial eye position. These studies showed that subjects did not make position-dependent systematic errors in locating the target. These results suggest that the brain does overcome this reference frame problem by taking into account initial 3-D eye position and combining this information with RE in a non-linear manner for both regular saccadic eye movements and for pointing movements [12,4]. In other words, it performs the correct 3-D *reference frame transformation* (RFT).

So far, this RFT has been investigated in "regular saccades"—saccades that were made directly to a visual target at a regular latency with no delay or special priming. However, due to certain constraints in processing time of coordinate frames, certain types of eye movements might be expected to circumvent some of the steps involved in the RFT.

One example is short-latency saccades. Saccadic latency or saccadic reaction time, the time it takes to initiate a saccadic eye movement in response to the onset of a visual target, is approximately 200 ms in humans. Since these latencies surpass the conduction time of the shortest neural pathways from the retina to the extraocular muscles, it is assumed that the necessary computations for localizing the target with respect to the fovea and the motor command to direct the eye to this location occurs

within this time. However, saccades with reaction times of less than 200 ms tended to be evoked in both humans and monkeys in greater frequency during tasks where a 200 ms "gap" is inserted between the offset of a fixation light and the onset of the target. This reduction in saccadic reaction time is also known as a gap effect and is sometimes accompanied by a sub-population of eye movements, called express saccades, which in humans have latencies between 80 and 120 ms [6,14,18]. Due to reduced processing time, it is possible that short-latency saccades bypass the eye-position dependent RFT necessary for regular latency eye movements [12]. Instead, shorter latencies for saccades under these conditions might result in a more simplified computation of the motor command to drive the eyes.

Saccades to remembered targets following a memory time delay are also associated with different neural activities, as well as different behavioral responses, when compared to saccades made without such delay. These memory-guided eye movements show systematic errors in target acquisition that vary with eye position and target location [7,21,25]. These same studies found greater variable errors (larger scatter) were produced as the memory delay interval increased. Studies have suggested that the memory-linked representations of spatial targets are stored in an intermediate stage within the visuomotor transformation process occurring between the initial retinotopic spatial frame and final motor frame representing desired change in eye position. Some researchers attribute errors following a memory delay to inaccuracies in retaining a retinotopic registration of the remembered target site [7]. The goal of this paper is to determine whether different types of eye movements, such as short latency (express) saccades and memory-guided saccades, circumvent the computationally demanding eye-to-head RFT, in preference for a more simplified and direct visual-to-motor transformation. Could this account for some of the position-dependent errors observed previously in memory-guided saccades?

2. Theory

To calculate the motor displacement of the eye for regular visually guided saccades the brain computes an eye-to-head RFT that take 3-D eye orientation into account [12]. However, other algorithms for computing motor commands from 2-D retinal signals have been proposed, including a model that simply maps components of RE onto an equivalent saccadic ME.

The model for a direct RE-to-ME mapping is shown in Fig. 2A, and is referred to as the look-up table (LUT) model because it approximates the mathematical steps that would be involved in an eye-to-head RFT with a visuomotor look-up table [12,3]. The potential advantage of this approximation is that the LUT model provides a more direct and possibly faster process in computing ME, which we model here as "change in eye position" (ΔE), as compared to transformations that take eye position into account.

In contrast, the RFT model (Fig. 2B) rotates RE into desired gaze direction in head coordinates, and then subtracts current eye position to obtain the saccadic ME

A   Look-up Table (LUT) Model

RE → | Look-upTable | → ΔE → | Saccade Generator |

B   Reference Frame Transformation (RFT) Model

3-D eye position

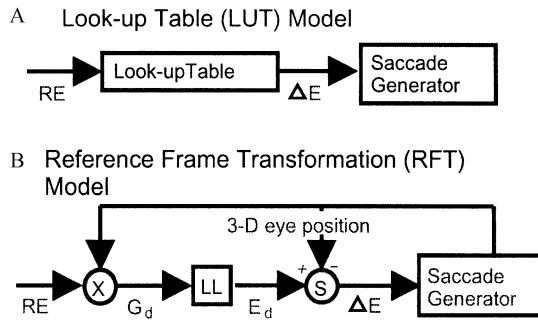RE → (X) G_d → | LL | E_d → (S) ΔE → | Saccade Generator |

Fig. 2. Two 3-D oculomotor models of how RE is transformed into ME. (A) The LUT model generates a displacement command to move the eye by simply mapping RE onto a desired change in eye position command (ΔE) using a look-up table. (B) The RFT model first uses 3-D eye orientation to rotate RE (in a non-linear fashion) from an eye-centered frame to a head-centered frame (G_d). Using a Listing's law operator, the model computes a desired eye position (E_d) vector in Listing's plane and then subtracts off the current eye position to derive ME (ΔE). Both models share the same saccade generator, equipped with pulley-like plant.

command. The result is that the RFT model correctly converts eye-centered 2-D RE into a head-centered 3-D ME command—providing saccades that are both accurate and obey Listing's law. Note that both these models shown in Fig. 2 share the same 3-D model of the downstream saccade generator, equipped with a "pulley-like" plant, i.e., eye muscles that help to maintain Listing's law by linearizing the oculomotor plant (see [3] for a more-detailed explanation).

Although the LUT model cannot compensate for the eye-position dependent distortions of RE described above (and demonstrated below), these retinal distortions of visual space are quite minor for the saccades with amplitudes of less than 25° that make up the majority of visually guided eye movements [11]. For this range of saccade amplitudes, the ME computed by both the LUT and RFT models differ only slightly, and consequently, the real RFT may tolerate potential errors of the computationally less demanding LUT model rather than perform these relatively complex position dependent transformations.

Thus, while the RFT model is more mathematically correct and most accurately describes what is occurring for regular visually-guided saccades, other types of saccades may not adhere to this model. Based on possible limitations in the reference frame that the target representation is stored for memory-guided saccades or due to a shorter processing time for express saccades, a quicker approximation provided by the LUT model may be used instead. To test this hypothesis and to get a better understanding of how the visuomotor transformation system works, we applied the test used by Klier and Crawford [12] (described in methods) for regular eye movements to determine if the brain does perform an eye position dependent RFT for memory-guided and express saccades.

3. Methods

3.1. Subjects

Five subjects (ages 23–44, with no known neuromuscular deficits) gave informed consent to participate in the experiment. Two subjects wore required corrective lenses, and only two subjects were aware of the nature and design of the study, while the rest were naïve.

3.2. Apparatus

Each subject was seated with their head fixed (secured by a bitebar) such that their right eye was at the center of three mutually orthogonal pairs of Helmholtz coils 2 m in diameter. Orientation of the right eye was measured using a 3-D search coil [23,12] and data were sampled at 200 Hz and converted off-line into quaternions. The stimuli consisted of ten light-emitting diodes (3 mm diameter LEDs) mounted on a matte black screen located 110 cm from the center of the subject's right eye. The LEDs were organized in horizontal pairs, arranged symmetrically across the midline such that the rightward target light was displaced horizontally by $60°$ in space coordinates from the leftward fixation light, at five different angular elevations: one at eye level, and the others $20°$ and $40°$ above and below this. Peripheral electronic modules, computers, an oscilloscope for monitoring eye movements, and the experimenters were located in an adjacent closed room during the experiment. Details regarding the magnetic fields, calibration procedures and accuracy were as described previously [12].

3.3. Experimental paradigms

Subjects performed two experimental paradigms in complete darkness, as illustrated in Fig. 3. Trials began with subjects fixating the leftward LED (F), followed by a saccadic eye movement toward the remembered location of paired rightward LED (T). The duration and horizontal angular location of both fixation (solid bars) and target (open bars) LEDs and a schematic of the horizontal eye trace (solid line) is plotted as a function of time for one trial. In the memory delay task (Fig. 3, top), F was illuminated for a total of 2400 ms, and T was briefly flashed for 200 ms half-way into F duration, producing a memory delay of 1000 ms before the subject made the required eye movement. In the gap task (Fig. 3, bottom), F is illuminated for a random period of 1000–2000 ms, followed by a gap of 220 ms where no LEDs were illuminated. T was flashed for 100 ms, cueing the subject to make the required open-loop saccade toward its location. A 1 s pause followed each trial. The pairs of LEDs were presented serially from top to bottom, a total of 20 times for the memory delay task and 40 times for the gap task. To ensure that subjects were not making mere stereotypical or rote cognitively-guided horizontal saccades, in 20% of the trials the standard rightward paired targets were substituted with non-standard oblique-rightward LEDs that were $20°$ above or below the standard target site. The data for trials using these non-standard pairs were not included in the data analysis. In a control
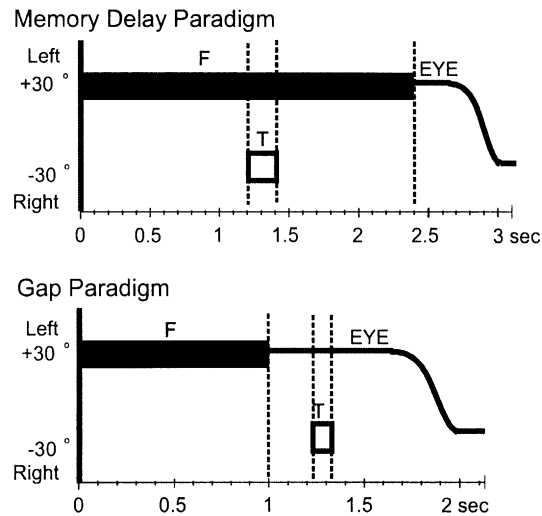
Fig. 3. Horizontal eye traces (——), and the horizontal location and duration of fixation (F, solid bar) and target (T, open bar) lights are plotted schematically against time for one trial. Vertical dotted lines represent LED onset and offset. Memory Delay paradigm (above): subjects maintain gaze on F until offset and then make a saccade to the remembered direction of T (briefly flashed one second earlier). Gap paradigm (below): subjects fixated F then immediately saccade toward T (flashed 220 ms after F offset).

task performed at the end of the experiment, subject fixated 15 continuously illumin-ated LEDs (each for 1 s; repeated 3 times) arranged in a grid pattern, including the 10 LEDs used in the experiment. From these recorded eye signals, reference eye positions and target directions in space coordinates were computed.

4. Results

4.1. Calculating retinal error

RE refers to the displacement of target image from the fovea, or the desired direction of gaze relative to current gaze direction. To test whether subjects make accurate eye movements between horizontal pairs of LEDs, we needed first to calculate RE in a geometrically correct manner in order to determine target direction with respect to the eye. As mentioned in the introduction, retinal projections of targets in space are somewhat curved as function of initial eye orientation due to the effect of eye rotation on retinal geometry. To calculate RE for each of the five pairs of horizontally displaced LEDs, we recorded the 3-D eye position vectors when subjects fixated each of the ten LEDs in space coordinates as shown by the diamonds and circles, joined by a dashed horizontal line (Fig. 4A). Rotating the mean right target vector by the inverse of the vector for initial eye orientation when the subject was fixating the leftward LED, we obtained the position of the target as it would appear on
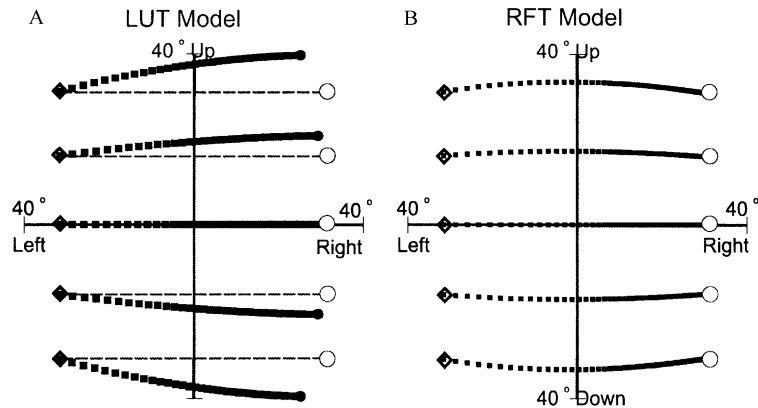
Fig. 4. Simulated 2-D eye trajectories for the LUT (A) and RFT (B) models viewed from behind. Initial gaze direction (diamonds) when subject fixated F is joined by a dashed line with gaze direction toward the paired T (open circle) 60° to the right for each horizontal pair of LEDs at 5 different vertical elevations. The eye traces predicted by the two models are shown by the dark squares (trajectories), with final saccadic direction indicated by the dark circles. LUT model produces systematic, eye-position dependent errors in final saccade direction, with larger vertical errors produced for more eccentric initial eye positions. RFT model predicts accurate saccades that land on the target site.

the retina when subjects foveated the leftward target of each pair. By this method, we calculated the RE of all the peripheral visual targets from each corresponding initial eye orientation.

4.2. Simulating predictions

Using these computed RE's, we then tested between the LUT and RFT models and determined how the ME, that guides the resulting eye movement, is calculated from this retinal information. We did this by inputing the calculated 2-D RE signals and actual eye positions produced by the subjects from the task involving the above targets into the two models.

If the oculomotor system uses a LUT model to generate ME, the resulting RE-to-ME vectors would appear as the dark simulated eye traces (squares from left to right) in Fig. 4A. Note that these vectors are not purely horizontal from the fixation points, but are instead tilted in different oblique directions relative to initial eye position as a function of eye rotation. For eye movements made between the highest or lowest elevated LEDs, the simulated endpoints of the saccade produced a large vertical error (and a smaller horizontal one) which progressively decreased non-linearly as initial eye position approached the horizontal meridian of the orbital center. However, if ME is calculated in a non-linear fashion by comparing these tilted RE's with 3-D eye orientation as predicted by the RFT model, the eye trajectories should look like the dark traces in Fig. 4B, and land accurately on target.

In summary, if the brain uses a simplified approximation to calculate a ME command to direct memory-guided saccades or express saccades as predicted by the
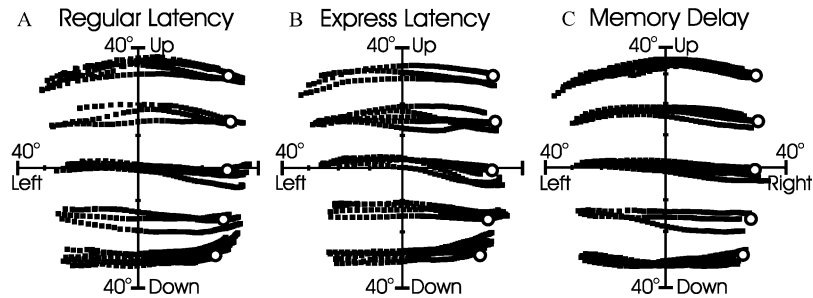
Fig. 5. Actual 2-D saccadic eye movements between the paired LEDs for saccades with (A) regular latencies (> 120 ms) and (B) express latencies (80–120 ms) produced in the gap paradigm, and (C) memory-guided saccades followed by a 1.0 s delay produced in the memory-delay task (behind view). The data shown are derived from 4 trials (per LED-pair) for each task from one typical subject. Circles indicate mean saccadic direction toward the continuous illuminated *T*'s in the control task. Vertical errors in the text refer to the difference between actual saccadic endpoints and control saccadic direction.

LUT model, then the resulting final eye movement should not be horizontal, but tilted as a function of initial eye position. Alternatively, saccades should accurately land on target if the correct eye position dependent RFT occurs (RFT model).

4.3. Performance

How do subjects making saccadic eye movements between these horizontally displaced LEDs at different eye elevations perform? Fig. 5 shows a behind-view of four actual eye trajectories (squares from left to right) made between each of the five horizontal LEDs for saccades made in the gap paradigm that had (A) regular latencies (> 120 ms) and (B) express latencies (80–120 ms), and for those saccades produced in the memory-delay task (C) for one typical subject. If the visuomotor transformation simply generates a ME command in the direction of the retinal target vector (or RE as computed above) as according to the LUT model, errors in final eye position would lie in a fanning out pattern as illustrated in Fig. 4A. The circles in Fig. 5 refer to the mean final eye position for the control closed-loop trials. These correspond to accurate final eye position in an open-loop condition if the brain implemented a RFT to account for the eye position-dependent distortion of RE as predicted by the RFT model. For most of our subjects, the final resting site of the eye showed little or no tendency to fan out as a function of initial eye position for any of the eye movement types.

Relative to controls, subjects made average (absolute) vertical errors in final saccadic direction in the magnitude of 2.82° for saccades in the memory-delay task and 3.644° for express saccades and 4.040° for regular latency saccades (across subjects). Subjects showed only small amounts of variance (greater precision) in final gaze directions, with mean standard deviations (across subjects) of 2.63 for memory-guided saccades and 3.26 and 3.43 for short-latency and regular-latency eye movements, respectively.
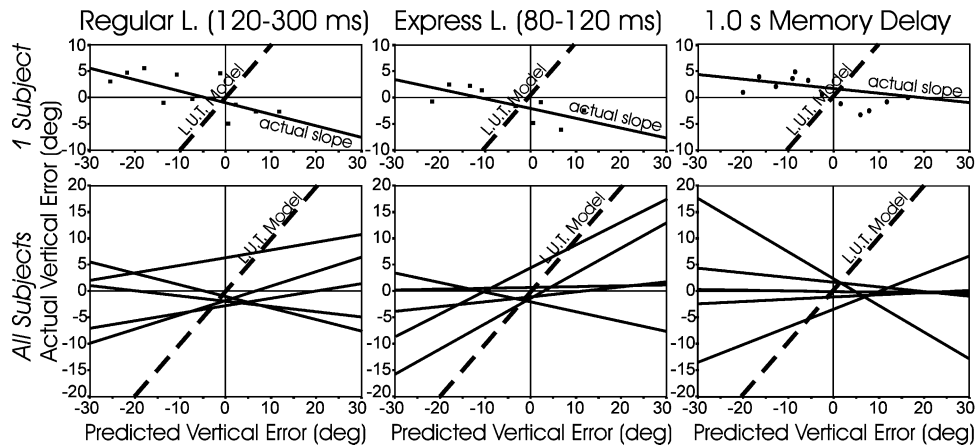
Fig. 6. Actual vertical saccade errors plotted as a function of vertical errors predicted by the LUT model for regular latency saccades (left), express saccades (center) and memory-delay saccades (right). Upper row: data for one subject. Since both paradigms were separated into two segments with a rest in between, each point (▦) represents the mean for the trials for each LED pair in each paradigm segment (thus producing a total of 10 points—2 means per pair—rather than 5). Solid lines indicate slopes fitted to the data while dashed-lines indicate unit slope predicted by the LUT model. Lower row: Slopes for all 5 subjects for each of the saccade types.

To quantitatively determine whether these saccadic errors were related to eye-position dependent distortions of RE, we compared the vertical errors predicted by the LUT model with the actual vertical errors in saccadic endpoints relative to controls made by the subjects. Predicted vertical errors refer to inaccuracies in final vertical eye position that the subject would make if they failed to account for initial eye orientation on retinal curvature when computing target location or the vertical component of the computed RE.

Fig. 6 shows vertical errors plotted along the abscissa as a function of predicted errors, for one subject (above), for regular latency saccades (left), express saccades (center) and memory-delayed eye movements (right). Slopes fitted to the data are indicated by solid lines, while dash-lines represent the predicted unit slope of the LUT model. Slopes for all five subjects for the three types of eye movements are shown below. Overall, slopes across subjects did not significantly differ for different saccade types ($p > 0.05$). This absence of differences imply that saccades with short latencies or saccades followed by a 1000 ms memory storage period do not appear to implement a different computational strategy in calculating ME for aiming the eyes on target as compared to regular latency, non-delayed, eye movements.

Average slopes across subjects (and standard deviations) for regular latency saccades (0.167 ± 0.282), express saccades (0.048 ± 0.200), and memory-delay saccades (0.070 ± 0.353) were quite small and did not approach the unit slope predicted by the LUT model. This suggests that the RFT for express and memory-delay saccades make the correct compensations for the complex geometry of RE produced by eccentric 3-D eye orientation.

5. Discussion

Despite the potential simplicity that a LUT model offers in calculating ME commands for driving goal-directed saccades, the oculomotor system does not appear to utilize this approximation in any of the situations that we have tested. In the current study, regular-latency, express, and memory-guided saccades showed roughly equal accuracy in terms of accounting for components of eye position orthogonal to the main direction of RE. In other words, for all three saccade types, the brain employed a RFT that took 3-D eye orientation and retinal geometry into account, as predicted by the RFT model.

Surprisingly (to us anyway) the accuracy and precision of eye movements in our study were quite good despite large saccadic amplitudes. Overall, saccadic errors made towards remembered targets in the current study were smaller than those results in similar memory-delay tasks performed by monkeys. Both White et al. [25], Standford and Sparks [21] and Gnadt et al. [7] found that monkeys produced systematic upward-biases for memory-guided eye movements when compared with visually-guided ones (no delay). Moreover, vertical saccadic errors varied by approximately $8°$ for a memory delay of 800 ms, with variability increasing for longer delays [25]. Gnadt et al. [7] also found similar magnitude in vertical error for varying memory-delays in monkeys, although their human subjects produced smaller errors in the order of approximately $5°$ for more eccentric targets. Thus, humans in general, and particularly those in our study, showed greater accuracy when producing eye movements toward remembered targets than do monkeys.

Nor were express saccades induced by the gap paradigm any less accurate than memory saccades—at least in terms of vertical error in horizontal saccades, as a function of vertical eye position. It is difficult to make comparisons with respect to saccadic accuracy in the current study with those gap paradigms in other studies since errors in saccade direction for express saccades are rarely reported and the required saccade amplitudes are usually quite small (typically only $10°$). Nevertheless, given the general superiority of monkeys in simple, visually guided eye movements, we would expect them to be equally good at this aspect of the task.

The lack of eye-position dependent errors for express and memory-delay saccades may not be surprising given recent evidence regarding the neurophysiological location of the 3-D visuomotor transformation for saccades. In a microstimulation study with monkeys, Klier and Crawford [13] concluded that the superior colliculus codes 2-D RE and that the RFT occurs downstream in the brainstem. While it may be possible to program motor behaviors that circumvent certain cortical processing, it is unlikely that visuomotor programming could avoid these lower motor-oriented brain structures [9,15]. In light of this recent finding, it may not be surprising that express saccades and memory-delay saccades use the correct RFT in humans. On the other hand, if this brainstem RFT did go awry in monkeys during the memory-delay paradigm, this would still be consistent with the conclusion of Standford and Sparks [21] that the problem was arising downstream from the superior colliculus.

At this point we deem it important to distinguish between the eye-to-head RFT that we have been discussing and the one that has been posited as a potential mechanism
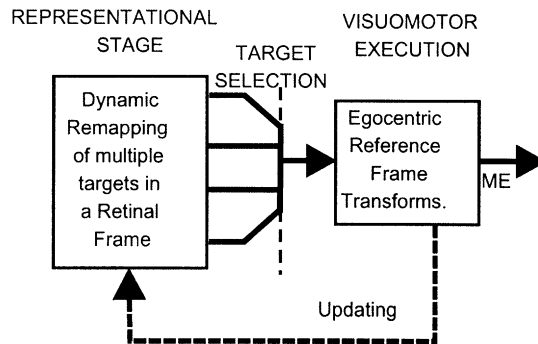
Fig. 7. Computation-on-Demand scheme of visuomotor representation and visuomotor control. Target representations are initially held in a eye-centered frame, and can be shifted in this frame to compensate for intervening eye movements through dynamic remapping (left). Once a target has been selected for action, its final retinal representation is put through a RFT to generate an accurate 3-D motor signal in motor reference frame (right).

for space constancy in headcentric or spatial coordinates [1,16,20]. A number of authors have pointed out that such a scheme is inconsistent with the largely retinocentric organization of visuomotor areas of the cortex (for review, see [17]). While the current results imply that an eye position-dependent visuomotor transformation is necessary for the execution of saccadic movements, it does not necessitate that all stimuli that fall in our visual field need to go through this complex algorithm to produce a 3-D motor command. After all, not every single, perceivable object will precipitate action. A more efficient scheme is to maintain multiple visual stimuli in the same eye-centered frame used to initially code the visual input, and then only perform the RFT discussed in the current study on those particular representations chosen for action [10,12].

To reflect the selection process that precipitates the egocentric transformation, we call this dual-stage process the "conversion-on-demand" model [10]. A schematic model of the conversion-on-demand hypothesis is shown in Fig. 7. The first stage or process (left) pertains to the visual representation of object location that occurs in an eye-centered frame, while the second process (right) relates to the visuomotor aspect of movement execution, which includes the RFT discussed in this study. Thus only the targets chosen for action are converted—on demand as it were—into the coordinate systems required for action.

In this model, the accuracy of movements and the apparent constancy of targets in space would occur through a combination of this transformation and updating of the upstream retinocentric targets across saccades—where the latter refers to the shifting of short-term visual representations of objects across retinotopic maps in the brain to compensate for movements of the eye [5,17,24]. Since the RFT occurs downstream from the latter representations and only as an executional process, it does not require its own spatial map. Indeed, a recent investigation utilizing artificial neural networks has shown that the 3-D eye to head transformation explored in the current study can be performed simply by modulating vectorial signals as a function of eye position

signals [19]. Thus, this conversion-on-demand scheme amounts to a type of virtual representation, where the minimum number of spatial computations is performed on any given point in space, but the system interacts with seamless accuracy with objects that are chosen as the targets for action.

Acknowledgements

References

[1] R. Andersen, G. Essick, R. Siegel, Encoding of spatial location by posterior parietal neurons, Science 230 (1985) 456–458.

[2] J.D. Crawford, T. Vilis, Axes of eye rotations and Listing's law during rotations of the head, J. Neurosci. 65 (1991) 407–423.

[3] J.D. Crawford, D. Guitton, Visual-motor transformations required for accurate and kinematically correct saccades, J. Neurosci. 78 (1997) 1447–1467.

[4] J.D. Crawford, D. Henriques, T. Vilis, Curvature of visual space under vertical eye rotation; implications for perception and visuomotor control, J. Neurosci. 20 (2000) 2360–2368.

[5] J. Duhamel, C. Colby, M. Goldberg, The updating of the representation of visual space in parietal cortex by intended eye movements, Science 255 (1992) 9092–9094.

[6] B. Fischer, H. Weber, M. Biscaldi, A. Franz, P. Otto, V. Stuhr, Separate populations of visually guided saccades in humans: Reaction times and amplitudes, Exp. Brain Res. 92 (1993) 528–541.

[7] J. Gnadt, R. Bracewell, R. Anderson, Sensorimotor transformation during eye movements to remembered visual targets, Vision Res. 31 (1991) 693–715.

[8] M. Goldberg, C. Bruce, Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal, J. Neurophysiol. 64 (1990) 489–508.

[9] V. Henn, K. Hepp, T. Vilis, Rapid eye movement generation in the primate: physiology, pathophysiology and clinical implication, Rev. Neurol. 145 (1989).

[10] D. Henriques, E. Klier, M. Smith, D. Lowy, J.D. Crawford, Gaze-centered re-mapping of remembered visual space in an open-loop pointing task, J. Neurosci. 18 (1998) 1583–1594.

[11] I. Howard, Human Visual Orientation, Wiley, New York, 1982.

[12] E. Klier, J.D. Crawford, Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades, J. Neurophysiol. 80 (1998) 2274–2294.

[13] E. Klier, J.D. Crawford, The superior colliculus encodes two-dimensional commands for head-free gaze shifts in oculocentric coordinate, Soc. Neurosci. Abstracts 26 (2000) 292.

[14] A. Kingstone, R. Klein, What are human express saccades? Percept. Psychophys. 54 (1993) 260–273.

[15] E. Luschei, A. Fuchs, Activity of brainstem neurons during eye movements of alert monkeys, J. Neurosci. 35 (1972) 445–461.

[16] L. Mays, D. Sparks, Saccades are spatially, not retinotopically coded, Science 208 (1980) 1163–1164.

[17] A. Moschovakis, S. Highstein, The anatomy and physiology of primate neurons that control rapid eye movements, Ann. Rev. Neurosci. 17 (1994) 465–488.

[18] P. Reuter-Lorenz, H. Hughes, R. Fendrich, The reduction of saccadic latency by prior offset of the fixation point: An analysis of the gap effect, Percept. Psychophys. 49 (1991) 167–175.

[19] M. Smith, J.D. Crawford, Self-organizing task-modules and explicit coordinate systems in a neural network model for 3-D saccades, J. Computational Neurosci. 10 (2001) 127–150.

[20] D. Sparks, The neural encoding of the location of targets for saccadic eye movements, J. Exp. Bio. 146 (1989) 195–207.

[21] T. Standford, D. Sparks, Systematic errors for saccades to remembered targets: Evidence for a dissociation between saccade metrics and activity in superior colliculus, Vision Res. 33 (1993) 2631–2644.

[22] D. Tweed, T. Vilis, Geometric relations of eye position and velocity vectors during saccades, Vision Res. 30 (1990) 111–127.

[23] D. Tweed, W. Cadera, T. Vilis, Computing three dimensional eye position quaternions and eye velocity from search coil signals, Vision Res. 30 (1990) 97–110.

[24] D. Waitzman, T. Ma, L. Optican, R. Wurtz, Superior colliculus neurons mediate the dynamic characteristics of saccades, J. Neurophysiol. 66 (1991) 1716–1737.

[25] J. White, D. Sparks, T. Stanford, Saccades to remembered target locations: An analysis of systematic and variable errors, Visual. Res. 34 (1994) 79–92.

Doug Crawford completed his Ph.D. in physiology at the University of Western Ontario in 1993, working in the area of 3-D eye movement control under the supervision of Tutis Vilis. He then spent 2 years working as a post-doctoral fellow with Daniel Guitton at the Montreal Neurological Institute, working on the modeling and neurophysiology of 3-D eye-head coordination. In 1995 he joined the faculty of York University, Toronto, where he established his current laboratories within the York Centre for Vision Research. He has since won numerous awards for his work on the computational and physiological mechanisms of visual-motor transformations, including an A.P. Sloan Fellowship, Governer General Gold Medal, Polanyi Prize, MRC Scholarship, and Premiers Research Excellence Award. Currently, he is Associate Professor of Psychology, Biology, and Kinesiology and Health Science at York.

Denise Henriques completed her M.A. in psychology in 1997 and is currently working towards a Ph.D. under the supervision of J.D. Crawford at York University, Toronto. The topic of her dissertation is the examination of visual-motor mechanisms involved in the coordination of the eye, head and arm. She has completed several (published) studies in this area of research and expects to complete her dissertation within a year. Denise is supported by an E.A. Baker Foundation CNIB-MRC Doctoral Research Award.