VISUAL-MOTOR TRANSFORMATIONS ACCOUNT FOR THREE-DIMENSIONAL EYE POSITION

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INTRODUCTION

The ability to simplify complex sensorimotor transformations is both attractive and advantageous when investigating intricate brain functions. But simplicity has its own pitfalls. For example, psychophysicists and neurophysiologists have long treated the retina as a flat surface and have largely treated eye movements as if they were two-dimensional (2-D) translations of this surface. However, although the retina is a 2-D surface, it is curved along the back inner wall of the globe and, for the most part, the eyes do not translate – they rotate. This changes the way objects in space project onto the retina, especially when the eye is oriented at secondary positions (i.e. positions with non-zero horizontal and/or vertical components) (3, 4). Furthermore, the eyes move with three degrees of freedom – horizontally (about a vertical axis), vertically (about a horizontal axis) and torsionally (about a naso-occipital axis). Thus, at tertiary positions the eyes are rotated torsionally by various amounts about their line of sight (so called false torsion) and these rotations, though small, also affect the pattern in which targets project onto the retina and consequently complicate the visuomotor transformations that follow (9, 10).

The differences between retinal errors induced by certain targets, and the motor commands necessary to foveate these targets, are outlined in figure 1. In the most basic example, fovea position A, the eye is looking straight ahead, and we equate this with primary position. A target that causes a horizontal retinal stimulation of 40° right necessitates (as shown on the screen) a purely rightward eye rotation of precisely 40°. Similarly, a horizontal retinal error of 80° to the right requires a rightward eye rotation of 80°. The equivalence between sensory input and motor output at primary position seems trivial and supports a simple one-to-one correspondence between input and output structures. However, the relationship is quickly complicated when the eye is oriented toward other positions in space.

With the four remaining foveal positions (B-E), the eye has been rotated vertically by various amounts and identical retinal stimulations have been applied – either 40° or 80° right. But now, a glance at the corresponding trajectories on the screen outlines a non-trivial mapping. The trajectories required to foveate either the 40° or 80° retinal errors are not just horizontal, but oblique – with the amount of curvature

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dependent on two factors. First, as the eye is deviated further eccentrically from primary position the amount of curvature in the trajectories increases (compare screen trajectory at position B vs. position C). Second, at each eye eccentricity, larger retinal errors are associated with highly convergent paths while smaller retinal errors require smaller, less convergent paths (compare the patterns of 80° and 40° trajectories).

From this simple picture it becomes evident that, except at primary position, there is a non-linear relationship between sensory retinal inputs and the corresponding motor outputs (i.e. gaze shifts). Thus, targets causing horizontal retinal errors cannot simply be foveated by purely horizontal gaze shifts. This further implies that purely horizontal retinal errors are not caused by purely horizontally displaced targets in space; and conversely, that horizontal lines in space do not produce purely horizontal retinal errors. The purpose of our studies was to (1) determine if humans account for three-dimensional (3-D) eye orientation when programming movements to targets and (2) to reveal what stage of the visuomotor transformation is coded for in the superior colliculus (the most studied visuomotor nucleus).

METHODS

Psychophysics experiments – saccades.
Six subjects had to make large 60° saccades between horizontally displaced LED targets. The initial fixation target was located 30° to the left of the midline, at eye level, while the final fixation target was located 30° to the right of the midline (also at eye level). Similar pairs of LED targets were placed 20° and 40° both above and below the pair at eye level for a total of five light pairs. The subjects were required to fixate one of the initial LEDs (left) and saccade to its paired target after it was briefly flashed (right). This set-up was integrated using saccades with regular, express and delayed latencies. Express saccades were induced by disengaging fixation of the initial target 220 ms before the presentation of the final target (i.e. the gap paradigm). For memory-guided saccades a delay period was introduced by having subjects fixate the initial target for an additional 1000 ms after presentation of the final target. For methodological details see (11, 15).

Psychophysics experiments – pointing.
The experimental design for the human pointing task was similar to that of the saccade paradigms. The five initial pointing targets were located on the midline – one at eye level, two ± 15° and two ± 30° (vertically), while the five final pointing targets were displaced 60° horizontally to the right, one paired with each of the initial five targets. The subjects began by fixating one of the initial LEDs. When its paired LED to the right was briefly flashed, the subjects would point with their index fingers to its location. All human studies were head-fixed. For methodological details see (4).

Neurophysiological experiments.
Two monkeys were simply required to move their eyes and heads freely as desired. They were encouraged to look throughout their oculomotor ranges by the presentation of novel toys and food rewards (to obtain a large range of initial eye/head positions). Stimulations trains (50μA, 500Hz.) of 200 ms. were delivered every 3.3 seconds to a total of 77 sites on both sides of the SC. These primate experiments were conducted with the head free and in all experiments eye (and head) movements were measured via the magnetic search coil technique. For methodological details see (16).

RESULTS

Psychophysics experiments.

Many believe that information on current eye position is a key factor to understanding the visuomotor transformation; and this information is available to saccade-related circuitry from either efference copies or proprioceptive inputs (1, 13). If retinal error signals can be internally compared with 3-D eye position signals, then the correct trajectories (Fig. 1) may be computed. We compared subjects' performances with the predictions of two theoretical models – a look-up table model (LUT) which directly maps retinal errors onto motor errors and a reference frame transformation (RFT) model which uses efference copies of 3-D eye position from the neural integrator to modify incoming retinal error signals (15). Because both of these models predict quite accurate movements in the peri-primary range, the experimental design incorporated relatively large saccades that tested the visuomotor system at its limits. Here the more complex RFT model predicts high levels of accuracy for all initial eye positions and all trajectory sizes. In contrast, the LUT model predicts a pattern of errors that increase both as a function of initial vertical gaze eccentricity and as a function of gaze amplitude.

We then proposed that eye movements such as express saccades (which have extremely low latencies of between 80 and 120 ms.) and memory-guided saccades may not be as accurate as normal saccadic eye movements (11). For the very rapid express saccades (5, 14, 18) inaccuracies might occur because in its haste, the saccadic system may bypass the eye position dependent steps of the spatial model (15). Memory-guided saccades (also known as remembered saccades) have been shown to be less accurate and more variable than regular saccades (8, 23, 26). It is believed that these errors may arise because either the initial retinal input or the internal representation of eye orientation slowly decays as it is held in memory (8). However, no one had ever determined if these errors are systematic and whether they are due to a failure of taking 3-D eye position into account.

While performing normal 60° saccades, the six subjects tested were remarkably accurate. Although some undershot and others overshot the final targets, the directional errors in the saccade trajectories made were minimal compared to those predicted by the LUT model. In addition, both the express and memory-guided saccades behaved like normal saccades. Subjects did not make the systematic errors predicted by the LUT model, but instead were accurate as the RFT model predicted. Thus, none of the three saccade types favored the simplicity of the LUT model over the accuracy of the RFT model.

Finally, we tested whether this kinematically correct transformation holds for other motor modalities – specifically pointing (4). In this case, comparing retinal inputs with eye position information is the first in a series of steps which is required to transform initial visual inputs, relative to the eye, into a coordinate system relative to the head. Subsequently, these head-related signals can be transformed into body coordinates and arm coordinates necessary for pointing. However, if the initial eye-to-head transformations are not calculated correctly, one would expect to see a
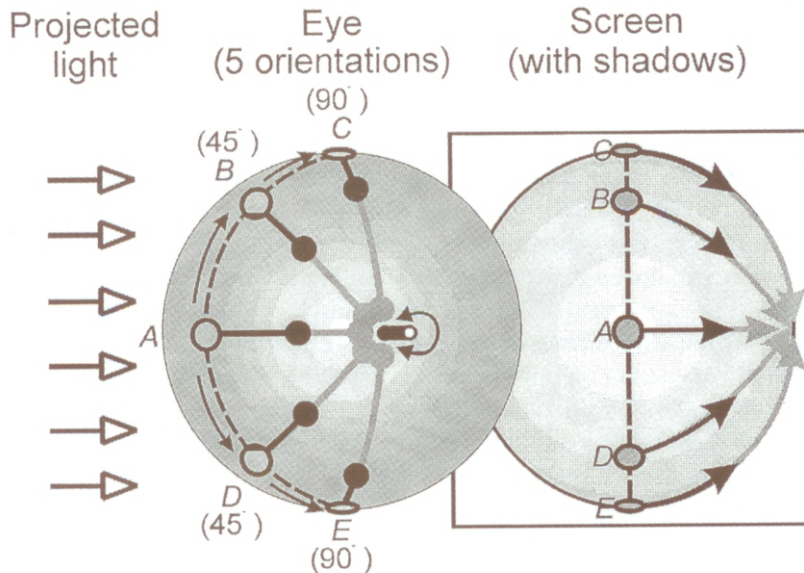
Fig. 1. - *The non-linear relationship between retinal stimulation and motor commands.*
A spherical globe (the eye-left) is illuminated by a light source from behind. This imaginary eye is semi-transparent and so objects within it cast shadows onto a flat screen in front of it (right). The fovea (open circle) is identified at five different positions which correspond to five different eye orientations: when gaze is directed straight ahead (A), when gaze is directed ± 45° vertically (B and D), and when gaze is directed ± 90° vertically (C and E). The eye can reach these new orientations by simply rotating about a horizontal axis through the center of the eye (dark bar). The dark circles represent purely horizontal retinal stimulations of 40° from each of the five foveas, while the grey circles represent horizontal retinal stimulations of 80°. Thus, the ten points of stimulation on the retina represent induced retinal errors and their corresponding points on the screen identify the trajectories that gaze (i.e. the eye-in-space) must follow in order to foveate these targets.

systematic pattern of errors in pointing similar to those predicted by the LUT model for saccades.

Similar to the saccade experiments, the data from the pointing paradigm did not show the LUT model's predicted errors. As the RFT model predicted, subjects accurately localized the final LEDs irrespective of the initial vertical elevation. See Crawford et al. (4) for details. Thus, kinematically correct visuomotor transformations also hold for motor modalities other than saccades.

Neurophysiology experiments.

Although the human data presented above can indicate whether or not the brain uses 3-D eye orientation to compute accurate trajectories, it would be even more compelling to identify neural structures that encode the steps in this transformation. Using stimulation techniques, we focused our attention on the superior colliculus (SC) (16). The SC receives visually-related sensory information both directly from the retina as well as from cortical centers like the striate cortex and the frontal eye fields (22, 27). The SC is then believed to output a gaze-related signal to down-

stream burst neurons for further processing (6, 7). Our rationale was to stimulate sites throughout the primate SC, with the head free, in order to produce gaze shifts of various eye and head amplitudes and directions. We then wanted to examine the coordinate system in which the resultant movements are organized. We hypothesized that the SC may operate in early retinal coordinates while other steps of the visuomotor transformation occur downstream. Such a coordinate system must be based on how incident light rays fall on a retina that is bound to a 3-D oriented eye.

Until now, one theory has been dominant in explaining how SC outputs are coded. The displacement model (19, 21, 25), which was initially suggested by David Robinson (19), states that SC outputs are fixed-vector commands. For example, if a locus on the SC motor map encoding 60° leftward gaze shifts is stimulated, then a 60° leftward gaze shift will be executed. Eye position information is not considered when the movement is programmed. In contrast, a less popular model known as the spatial model (17, 20, 24) serves to explain certain SC stimulation-evoked movements, especially larger ones, that the displacement model cannot. It holds that the SC encodes target directions in space. Thus, when a locus encoding 60° left is stimulated, a gaze shift will be produced that drives the eyes to the location 60° left in space coordinates. Both of these models complement one another. The displacement model explains fixed-vector movements found when stimulating the SC anteriorly and with the head fixed, while the spatial model describes larger movements evoked by posterior SC stimulation and data found in head-free animals.

In an attempt to unify all the existing data we suggested a retinal model of SC encryption which does not ignore the geometrical facts illustrated in Figure 1 (16). The model holds that if each point on the SC encodes a point of retinal stimulation, then these signals must be mapped onto different gaze displacements depending on the eye's initial 3-D orientation in space when the stimulation is delivered (or the target presented). Thus, while a 60° leftward movement evoked when gaze is around primary position will be mostly horizontal; stimulating the same SC site when the gaze is rotated upward or downward will induce a more oblique movement. The predictions of this "retinal" model, when stimulating three different sites on the SC (30° left, 60° left and 90° left), from five different initial gaze positions, are shown in Figure 2a-c. (Note the relationship to the geometry illustrated in Figure 1).

One outstanding difference between these three models is the extent to which their predicted movements, elicited from various initial gaze positions, converge. The displacement model produces fixed-vector movements in space coordinates that never converge, while the spatial model predicts gaze movements that converge perfectly at one location in space. The retinal model predicts a pattern of elicited gaze shifts that converges minimally for small gaze shift amplitudes, but then predicts progressively larger convergence patterns for larger gaze shift amplitudes (Fig. 2a-c). Therefore, for the retinal model, the amount of convergence depends on the amplitude of the gaze shift.

Our actual stimulation-induced movements were highly variable in the amount of convergence observed (Fig. 2d-f). Anterior SC sites produced fixed-vector movements, while posterior SC sites produced more convergent movements. These data
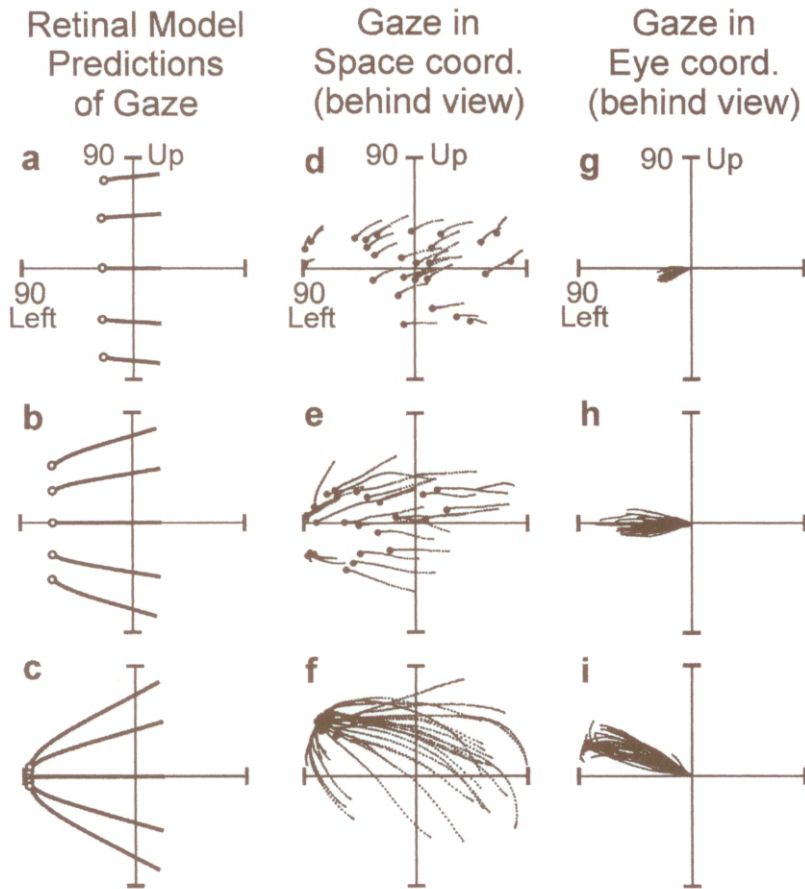
Fig. 2. - *Predicted and actual gaze movements evoked by stimulating the superior colliculus at three sites.*
The superior colliculus was simulated (or stimulated) at an anterior site (top row), an intermediate site (middle row) and a posterior site (bottom row). *a-c*: The retinal model is simulated at three SC sites which encode 30° (*a*), 60° (*b*), and 90° (*c*) leftward movements. This new model predicts trajectory paths which, unlike previous models, are based on the initial 3-D orientation of the gaze. Each simulated trajectory begins on the right and final endpoints are indicated by open circles on the left. *d-f*: Actual stimulation-evoked gaze shifts in space coordinates. These stimulation sites are not identical, but somewhat match the simulation sites. Final endpoints are indicated by filled circles. *g-i*: Actual stimulation-evoked gaze shifts rotated into eye coordinates. At the origin, one is looking down the initial gaze line from behind the fovea (i.e., where gaze was pointing when the stimulation was delivered). Each trajectory proceeds from the origin in a direction and distance proportional to the gaze shift.

seemed to cover the whole range of behaviors previously described in both cats and monkeys (17, 19, 20, 21, 24, 25). We quantified the data by calculating a convergence index (see Methods in (16)) which indicated to what extent the data converged (0 = no convergence; -1 = perfect convergence). Rather than finding a narrow range of indices (the displacement model predicts indices of 0, while the spatial model predicts indices of -1), we found that the convergence indices were low for small gaze

shifts and became progressively larger for bigger gaze shifts (16). These results follow the pattern outlined in figure 1 and thus clearly favored the retinal model.

If the different gaze shifts elicited from each SC site were in fact due to different initial gaze positions at the time of stimulation, then the elicited gaze shifts (in space coordinates) must appear fixed-vector when rotated into retinal coordinates. This coordinate transformation was achieved by mathematically projecting the elicited gaze trajectories (in space) back onto the retina using the initial 3-D orientation of the eye when the stimulation was delivered. The results were very impressive (Fig. 2g-i). When transformed into retinal coordinates, the wide variety of gaze trajectories produced at each site essentially overlapped, like soldiers falling in line. These neurophysiological findings nicely support the ideas presented Figure 1 which stress that retinal errors and motor commands are not identical.

DISCUSSION

The only way in which the extremely large saccades, performed in the human experiments, could have been so accurate was if the saccadic system actively compared the retinal inputs with current eye position signals. Some might argue that such comparisons are only made in extreme conditions such as the ones found in this experimental set-up, but that in the normal saccadic range a more simple and direct mapping of sensorimotor information is used. However, it is very unlikely that evolution would develop two separate saccadic systems, including one that is highly complex and used solely for rare, large amplitude saccades, when only one correct model will do.

The neurophysiological data takes these findings a step further. Not only is eye position taken into account when programming gaze shifts, but one of the most important gaze-related nuclei – the SC – encodes its gaze output command in a retinal coordinate system. That is, a coordinate system based on a fixed point of retinal stimulation. Consequently, subsequent steps of the visuomotor transformation (which take into account 3-D eye and head orientations) are likely processed downstream. This remarkable finding highlights the importance of an eye-based coordinate system in the brain. We have previously suggested a "conversion-on-demand" (12) model in which we argued that the vast amount of visual information received by the brain is held in this early encoding stage until one specific object is selected to be acted upon. Only then do the reference frame transformations necessary for action proceed. This type of set-up would be both economical in terms of the amount of information that requires processing and efficient in terms of processing time. This theory is also in agreement with Bernstein's original concepts for simplifying control systems for complex sensorimotor transformations (2).

SUMMARY AND CONCLUSION

We have shown theoretically, behaviorally and physiologically the indispensable role of eye position information in the visuomotor transformations of the brain. Despite the attractive simplicity of models which directly map inputs onto outputs, more complex models are required to describe the kinematically correct saccades observed in both humans and monkeys. These models must be equipped to perform the rigorous steps required of reference frame transformations. Specifically, the brainstem must compare retinal signals with 3-D eye orientation in order to generate accurate gaze shifts.

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