

Primate Head-Free Saccade Generator Implements a Desired (Post-VOR) Eye Position Command by Anticipating Intended Head Motion

J. DOUGLAS CRAWFORD¹ AND DANIEL GUITTON²

¹Centre for Vision Research and Departments of Psychology and Biology, York University, Toronto, Ontario M3J 1P3; and ²Montreal Neurological Institute and Department of Neurology and Neurosurgery, McGill University, Montreal, Quebec H3A 2B4, Canada

Crawford, J. Douglas and Daniel Guitton. Primate head-free saccade generator implements a desired (post-VOR) eye position command by anticipating intended head motion. *J. Neurophysiol.* 78: 2811–2816, 1997. When we glance between objects, the brain ultimately controls gaze direction in space. However, it is currently unclear how this is allocated into separate commands for eye and head movement. To determine the role of desired final eye position commands, and their coordination with intended head movement, we trained three monkeys to make large gaze shifts while wearing opaque goggles with a monocular 8° aperture. Animals eventually developed a new set of context-dependent eye-head coordination strategies, in particular expanding the head range and compressing the eye-in-head range toward the aperture (while wearing the goggles). However, when we shifted the location of the aperture to a different subsection of the normal head-free oculomotor range (by covering the original aperture and creating a new one), eye-head saccades failed to acquire visual targets, because they continued to drive the eye ultimately toward the now occluded original aperture. Even when a head-stationary saccade acquired the new aperture, subsequent head-free saccades drove the eye eccentrically toward a point that anticipated the intended head movement, such that the subsequent vestibuloocular reflex slow phase brought the eye onto the location of the original aperture. Animals could only acquire the new aperture consistently after several days of retraining. These results suggest that 1) eye-head coordination is achieved by a plastic, context-dependent neural operator that uses information about initial eye/head position and intended movement to compute desired combinations of final eye/head position and 2) acquisition of these positions involves sophisticated anticipatory compensations for subsequent movement components, akin to those observed previously in complex oral and manual behaviors.

INTRODUCTION

By studying eye-head coordination during large gaze shifts, we hope to gain fundamental insights into the general mechanisms of motor coordination and the specific neural mechanisms of visual orientation. Gaze shifts typically consist of 1) at least one rapid eye movement (saccade), 2) a slower head movement in the same general direction, and 3) vestibular-driven slow phases that stabilize gaze between saccades until the head comes to rest. Most recent models suggest that both the eyes and head are ultimately driven by a gaze error command that guides the visual axis onto target (Freedman et al. 1996; Galiana and Guitton 1992; Goossens and Van Opstal 1997; Guitton and Volle 1987; Guitton et al. 1990; Lauritis and Robinson 1986; Robinson and Zee 1981; Tomlinson 1990; Tweed 1997). However, the mecha-

nisms that distribute this command into separate but coordinated control signals for the eye and head remain in dispute.

The highly coupled eye-head gaze saccades of cats have been adequately modeled by essentially parsing gaze error to the eye and head as a matter of different weightings (Galiana and Guitton 1992; Guitton et al. 1990). However, additional *position* signals appear to be required to account for the gaze behavior of primates and humans. These signals may come into play in determining both the behavioral limit of the size of the saccade (Guitton and Volle 1987), and determining the initial proportion of drive to the eye and head (Becker and Jürgens 1992; Freedman and Sparks 1997; Fuller 1996; Goossens and Van Opstal 1997). To account for such observations, Guitton and Volle (1987) proposed that eye motor error was computed by comparing initial eye position to a saturating desired eye position within a gaze feedback loop. A further position-related problem arises in coordinating the initial eye saccade with the subsequent vestibuloocular reflex (VOR) slow phase, where the direction of the latter depends only on concurrent *head* movement. This becomes a nontrivial problem in multidimensional gaze shifts, because the eye and head do not rotate in exactly the same direction (Freedman and Sparks 1997; Glenn and Vilis 1992; Guitton and Crawford 1994). In this case, for the eye to come to rest at an intended final eye-in-head position, the ocular saccade would have to be “preprogrammed” to compensate for slow-phase eye movements linked to the *intended head movement* (Crawford and Vilis 1991; Guitton and Crawford 1994; Tweed et al. 1995). A recent three-dimensional (3-D) model (Tweed 1997) incorporates all of these features, but has yet to be tested.

To put these ideas to the test, we employed a recently developed technique (explained in METHODS) whereby the useful visual/oculomotor range relative to the head is dramatically reduced during head-free gaze shifts (Tweed et al. 1993). Whereas this technique evoked only moderate parametric changes to movement metrics in acutely trained humans (Tweed et al. 1993), we added two new variations: chronic training in monkeys, and suddenly imposed post-training shifts in the functional oculomotor range. The question is, can primates learn to utilize different oculomotor ranges during head-free gaze shifts? Moreover, if so, can simple parametric changes in motor error and eye/head gating account for the new ranges? Or, does the brain require information on initial and desired final eye position to coordinate saccades with intended head movements, such that

the eye ultimately lands within a neurally predetermined range of final desired positions?

METHODS

Three primates (*Macaca fascicularis*) underwent aseptic surgery under general anesthesia (isoflurane, 0.8–1.2%) during which they were fitted with an acrylic skullcap and scleral search coils (described below). Animals were trained to sit upright, head-unrestrained, and facing forward in a Crist Instruments primate chair, modified to remove encumbrances to head movement. Other than gaze directions $>50^\circ$ downward (which we did not explore), vision and head movement were unobstructed. Animals were then trained to fixate “primate treats” held at 80–100 cm distance, throughout a large range of the remaining visual field. In these controls, animals were allowed to make self-paced gaze shifts between targets using an eye-head coordination strategy of their own choosing. This was designed to emulate a biologically “natural” pattern of gaze shifts.

When this initial training was completed, animals were fitted with a pair of opaque plastic goggles that attached (via wing nuts) to screws implanted in the skullcap. These goggles were shaped to the contour of the monkeys face with the addition of soft flanges at the edge, so as to completely occlude vision in both eyes. A single round aperture was drilled (off-line) into the front of the goggles, such that the right eye was given a useful visual range of $\pm 4^\circ$. This first aperture was placed at our best estimate of the center of the eye’s mechanical range (which is not necessarily the same as the behavioral center) (Tweed et al. 1990), such that the visually estimated line between the center of the aperture and the center of the eye was above and parallel to the Frankfurt plane. A second aperture was placed at 16° above the first, but was initially occluded. The exact aperture locations with respect to the oculomotor range were measured anatomically in stereotaxic coordinates and confirmed by measuring visual fixations through the aperture with the head fixed.

Forty-five-minute per day training sessions with the goggles then commenced. Initially, animals were trained to visually follow slow movements, and then as the speed of their gaze movements increased, targets were displaced rapidly over a wide range until they easily made rapid searching head movements to visually acquire the target. Invariably, animals mastered horizontal gaze shifts first, then vertical gaze shifts, and finally oblique gaze shifts. Between training periods, the goggles were removed, and the animals were returned to their normal housing area. As judged subjectively, the total training time required for rapid, accurate, and discrete movements in all directions and throughout the entire range required ~ 4 wk in *animal 1*, ~ 10 days in *animal 2*, and ~ 6 wk in *animal 3*. However, *animal 3* was excluded from quantitative measurement because it exhibited an array of general behavioral abnormalities and refused to adopt an upright body or head posture during experiments.

The remaining animals were placed within three orthogonal magnetic fields during the experiments. Signals were recorded from two 5-mm-diam coils implanted subconjunctivally in the right eye (Crawford and Vilis 1991) and from two orthogonal 1-cm “head” coils embedded in plastic. During head-free experiments, the head coils and wire leads for the eye coils were secured with nylon screws to the skullcap. Gaze directions, three-dimensional orientations, and angular velocities of the eye and head were measured and quantified using the quaternion technique (Glenn and Vilis 1992; Tweed et al. 1990). These were computed for the eyes relative to head, head relative to space, and eyes relative to space, henceforth referred to as eye, head, and gaze. To select a subjective reference position, animals repeatedly fixated a target straight ahead (in magnetic field coordinates), and a fixation at the center of the variable eye-head distribution was chosen.

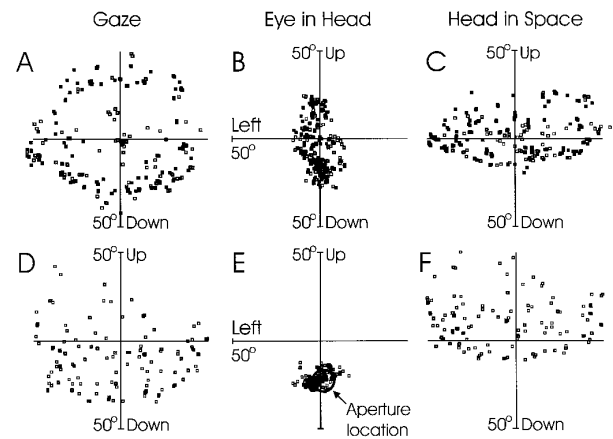


FIG. 1. Range of 2-dimensional (2-D) gaze (\sim eye + head), eye, and head positions before (A–C) and after (D–F) putting on the goggles, with original aperture (E, circle). Only positions at final fixations (gaze and head velocity $<10^\circ/\text{s}$) are shown. To be precise, the depicted positions are the tips of gaze, head, and eye direction vectors computed from 3-D quaternions, and projected from behind onto a pseudofrontal plane. The origin is the animal’s subjective reference position (defined in METHODS), not the anatomic center. The normal eye-in-head fixation range for this particular animal (B) was somewhat elevated within the overall oculomotor range, such that the anatomically central aperture (E, circle) fell within its lower extent. The eye-in-head excursions during saccades were considerably larger, but were largely reversed by vestibuloocular reflex slow phases. When the goggles were removed (not shown), animals immediately resumed the default ranges like those shown in A–C.

RESULTS

Figure 1 illustrates the 2-D position ranges of gaze, eyes, and head before (A–C) and 5 min after (D–F) placing the goggles on *animal 1* (after the 4-wk training regimen was complete). Only final fixation positions at the end of head movements are shown. In the controls a roughly equal distribution of final vertical-horizontal components of gaze directions (A) was subserved by a mainly vertical range of eye positions (B) and a mainly horizontal range of head positions (C), in agreement with most previous studies (Freedman and Sparks 1996; Glenn and Vilis 1992). However, our trained animals were able to rapidly switch from this normal strategy to a new strategy as soon as the goggles were set in place. Animals were still able to obtain a wide range of gaze (D), but this was now largely subserved by an increased range of head positions (F) that now closely resembled the range of gaze directions, except shifted upward. These changes were evidently necessary to accommodate the new fixation range in eye positions, which was shifted downward (relative to the normal subjective reference point, which was somewhat elevated within the overall oculomotor range of this animal). More importantly, the new range was greatly reduced, particularly in the vertical dimension (toward a subset of the lower normal range). We quantified this range as the standard deviation of final vertical eye-in-head position. This measure was reduced from $14.13 \pm 1.21^\circ$ to $4.36 \pm 0.29^\circ$ in *animal 1* and from $13.00 \pm 0.58^\circ$ to $3.87 \pm 0.26^\circ$ in *animal 2* (mean \pm SE across 5 experiments). This range reduction clearly served to align the eye-in-head fixation range with the aperture location (Fig. 1E, circle), as will be illustrated further below.

The key question is, what sort of neural control signals

account for these alterations in the eye and head fixation ranges? While wearing the goggles, trained animals showed an array of modifications to the normal relations in eye-head coordination (Freedman and Sparks 1997; Guitton and Volle 1987), including increased “head gain” (particularly in the vertical dimension) leading to increased alignment of eye and head trajectories during oblique gaze shifts, and a reduction in the final contribution of the eye-in-head position to the gaze shift (Guitton and Crawford 1994). Two hypotheses could account for these observations. First, the observed parametric changes could directly reflect similar internal parametric changes. In particular, increased gain in the internal mapping from the gaze error vector to the head motor vector (Galiana and Guitton 1992), such that the two would be equal. This would automatically bring the aperture into alignment with the target for all gaze shifts, whereas concomitant increases in VOR slow phases (compensating for the larger head movement) would tend to counterrotate the eye into alignment with the aperture after each initial saccade. With this hypothesis, the altered final eye/head position ranges would be trivially emergent effects. However, the reverse was also possible: the parametric adjustments in movement trajectories could have been an emergent effect of adapting an internal control signal for final desired eye position, such that the eye was ultimately driven toward an internally selected reduced range (Guitton and Volle 1987; Tweed 1997).

To test between these hypotheses, we simply occluded the old aperture and abruptly unmasked a new aperture, deviated (in angle of gaze) by 16° upward and 2° leftward. (This placed it right at the central subjective reference point for *animal 1*). According to our “parametric adjustment” hypothesis, this should not pose any special problem for the trained animal. The animal should simply redirect the eye toward the new aperture and then continue with the same strategy. However, with this shift in the aperture location, both animals showed a marked inability to acquire visual targets using rapid gaze shifts. Their initial behavior was dominated by halting and slow head movements with prominent 3-Hz oscillations. Analysis of the eye position data revealed the central problem. Figure 2 shows the final 2-D eye-in-head fixation range (following eye-head gaze shifts) of *animal 1* immediately before (A), and immediately after (B) moving the aperture (large open circle). Remarkably, after the aperture shift, the animal continued to drive its eye almost exclusively toward the behaviorally eccentric location of the original aperture (dark disk). Note that this occurred despite the fact that this aperture was now completely occluded, and that visual information was only available (open circle) at the preferred *center* of the normal head-free fixation range of the illustrated animal (Fig. 1B).

A more detailed analysis of the eye-in-head movement trajectory revealed the reasons for this unusual result. Two natural questions came to mind. First, why would saccades not drive the eyes toward the real aperture during head-free gaze shifts? The answer is that sometimes they did (Fig. 2C), but then subsequent VOR slow-phase eye movements (which counterrotate the eye until the head comes to a stop) drove the eye away from the aperture (Fig. 2D), toward some pseudorandom final fixation position (small open circles). Thus this was an ineffective strategy and was observed

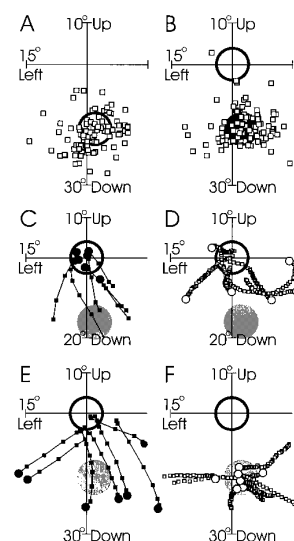


FIG. 2. Effect of shifting the aperture location (*animal 1*). A and B: final eye-in-head fixations (gaze and head velocity $< 10^\circ/s$) after gaze shifts where the head obtained a minimum velocity of $100^\circ/s$. A: tested with goggles on with original aperture location (large open circle). B: immediately after occluding the original aperture (filled disk) and opening a new aperture (open circle). C: several eye-in-head saccades toward new aperture (accompanied by head movements $\geq 100^\circ/s$). Filled squares: data points recorded at 100 Hz. Filled circles: final positions of saccades. D: slow-phase eye movements immediately following the saccades illustrated in C. Open squares: data points recorded at 100 Hz. Small open circles: final eye positions when head motion stops. E: typical head-free saccades that followed head-stationary saccades to the new aperture. F: slow-phase eye movements immediately following the saccades in E.

only occasionally. Second, why would the animal not simply make a corrective saccade toward the new aperture when the head had stopped, and then somehow maintain the eye near that position during eye-head gaze shifts? Animals did occasionally aim head-stationary saccades (not shown) toward the aperture, setting up the initial conditions shown in Fig. 2E. However, when subsequent head-mobile gaze shifts occurred, the saccade then drove the eye downward (Fig. 2E), although neither in the direction of the head movement (which can be inferred here from the subsequent slow phases in Fig. 2F) nor directly toward the location of the original aperture. Instead, these saccades aimed the eye toward a point such that the subsequent slow phase (in opposition to the head) drove the eye toward a *final* fixation position at the location of the original aperture (Fig. 2F). Although seemingly complicated, this is the only way the eye *could* return to this location in the presence of a functioning VOR. Thus there were two mechanisms at play here: one visually guided, but *not* coordinated with head movement (Fig. 2, C and D) and one internally guided and *coordinated* with the head (Fig. 2, E and F). From the perseverant behavior illustrated in Fig. 2B, it is clear that exposure to the first aperture had adapted the latter mechanism, and that this dominated the initial behavior following the aperture shift.

Figure 3 quantifies this adaptive effect in both animals with the use of a fixation frequency histogram in 2° bins for *vertical* eye position relative to the center of the original aperture, following eye-head gaze shifts. The control figure (A) confirms that animals still utilized a relatively broad vertical range after training when the goggles were *not* in

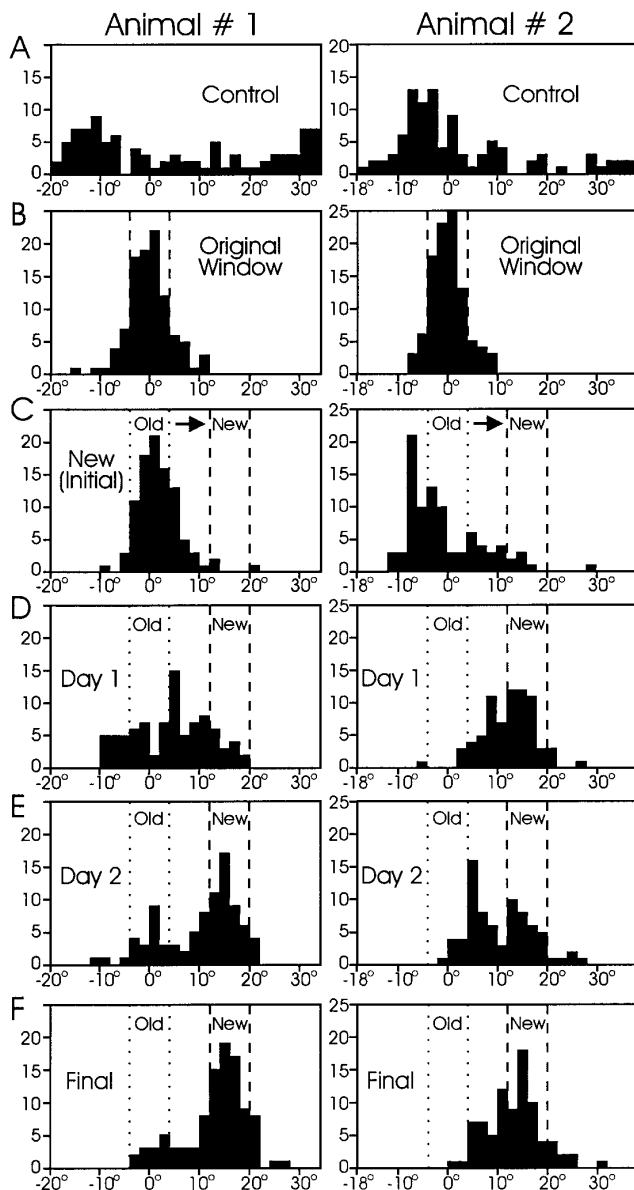


FIG. 3. Oculomotor performance of 2 animals on the original aperture task, and progressive retraining with new aperture. Each vertical bar gives the frequency of fixations within a 2° bin for vertical eye position relative to the center of the original aperture, following gaze shifts where head velocity exceeded $100^\circ/\text{s}$. A: controls, without goggles but after training (which may have influenced the distribution: note peak in animal 2). B: final performance with original aperture (dashed vertical lines). C: performance on 1st exposure to new aperture (dashed vertical lines). Dotted lines indicate the original aperture location. D: performance after 1st 30 min of retraining. E: performance after 2nd day retraining. F: final retrained performance, after 11 days in animal 1 and 13 days in animal 2.

place. Figure 3B then shows the final performance with the original aperture, and Fig. 3C shows performance immediately after shifting the aperture location. Neither animal acquired the new aperture with any consistency. (The performance of animal 1 was virtually unchanged, whereas animal 2 showed a preponderance of slow upward head movements after gaze shifts, driving the eye-in-head even further down: perhaps a maladaptive search strategy.) To ensure that this was not due to some trivial constraint, we then retrained the animals with the new aperture. Figure 3, D–F, shows the

results at the end of the first, second, and final day of retraining, respectively. Their performance with the new aperture gradually improved (which agreed with our subjective observations), but with considerable perseverance of fixations toward the original aperture (Fig. 3E). Even after 10 days of retraining (Fig. 3F), they never quite attained the degree of performance observed after initial training (Fig. 3B).

DISCUSSION

This study does not directly address the existence of a gaze-feedback loop in the brain, but rather the means by which eye and head movements might be coordinated within such a loop. In 1987, Guitton and Volle noted that the human eye position range (at the end of head-free saccades) is limited behaviorally, not mechanically, and Fuller et al. (1983) have further suggested that such a range might also be adaptable. The current paper shows, moreover, that the final fixation range of eye-in-head positions at the end of head movements/slow phases is also defined neurally, such that it can be retrained and even alternated for different contexts. By corollary, the same is likely true for the desired final head range (Fig. 1F).

Our result supports the idea that, given the right training conditions, the gaze control system shows the same kind of adaptive flexibility (Lisberger 1988; Melvill Jones et al. 1988; Optican and Miles 1985) that one normally assumes to be the domain of sophisticated manual and oral control. Thus the somewhat stereotypical nature of normal gaze behavior does not appear to be the product of a hard-wired, machinelike control system, but is more likely the optimal solution for relatively constant mechanical and task constraints. If so, then the differences between the details of orienting behaviors in various species, i.e., cats, monkeys, and humans (Freedman and Sparks 1997; Fuller 1992; Guitton et al. 1990) is probably more related to day-to-day constraints (particularly in the mechanical oculomotor range) than the underlying neural substrates.

In particular, our original training procedure effectively shifted the primate's normal eye-head coordination strategy toward a strategy that more resembled that of the cat: the effective oculomotor range was reduced in favor of a larger range of head motion, and both segments would have to rotate in the same direction to maintain fixation on the original aperture. This in itself is readily modeled by simply parsing gaze motor error to the eye and head as a matter of different weightings (Galiana and Guitton 1992; Guitton et al. 1990). However, our aperture-shift test (Figs. 2B and 3C) revealed an underlying set of computations that would otherwise have been missed: the perseverant behavior of the animals revealed that the trained gaze-control network was actively selecting a final head-free oculomotor fixation range that aligned with the original aperture location.

Note that this process involved more than computation of saccade endpoints. After the aperture shift, eye trajectories that ultimately landed at the original fixation zone (Fig. 2, E and F) were clearly distinct both from trivially visual saccades (i.e., guided directly toward a visual target, Fig. 2C), and trivially vestibular movements, i.e., in the same direction as head movement (this can be inferred by comparing the saccades and slow phases in Fig. 2, C and D, E and

F). To compute the final fixation positions of the eye (after the head stops moving) the gaze-control system had to (in effect) compute both desired *final* eye position, and account for intended head movement, so that saccades would compensate for subsequent slow phases in an anticipatory fashion and ultimately land the eye on target (Fig. 2, E and F). This shows an intriguing resemblance to the sophisticated anticipatory maneuvers observed in trained pianists (Engel et al. 1997), and the phenomenon of *coarticulation* in speech (Daniloff and Moll 1968). Indeed, if even the “lowly” gaze-control system can generate anticipatory compensations for intended sequential movement components, then neural networks must be constitutionally capable of such sequencing when it is dictated by the spatiotemporal demands of the task (Engel et al. 1997).

The question remains whether this motor strategy reflects a fundamental mechanism for eye-head coordination, or something created a nova by our training procedure. The latter seems unlikely: i.e., that the brain would create such a complex algorithm (that leads to errors when the aperture is shifted!) when a simpler combination of parametric changes would seem to satisfy the basic task requirements. Moreover, although this algorithm was internally driven in our task, similar algorithms have been proposed (Tweed 1997) to compute desired final 3-D eye and head positions from visual inputs. These algorithms are necessary in nontrivial multidimensional movements where the directions of saccades and slow phases generally differ (Freedman and Sparks 1997; Tweed et al. 1995), and where slow phases routinely violate Listing’s law (Crawford and Vilis 1991; Guitton and Crawford 1994). Interestingly, when the head is immobilized, the Tweed-style algorithm (Tweed 1997) “collapses” to our 3-D algorithm (Crawford 1994; Crawford and Guitton 1997) for goal-directed, torsion-correcting saccades (Crawford and Vilis 1991; Van Opstal et al. 1996). Thus there is no apparent need to evoke fundamentally different control systems for the currently described adaptive behavior, normal head-free gaze saccades, or head-fixed saccades.

The ultimate question we need to address is where and how these processes are implemented in the brain. The superior colliculus is clearly involved in orienting movements of both the eyes and head (e.g., Cowie and Robinson 1994; Harris 1980), but most recent studies suggest that it encodes an undifferentiated gaze error command (Freedman et al. 1996; Munoz et al. 1991). Furthermore, the colliculus appears to encode a 2-D signal, independent of the control mechanism for torsional quick phases (Van Opstal et al. 1991). These factors would suggest that the position-coordinating mechanisms under study here are located functionally downstream, in the brain stem reticular formation, vestibular nuclei, and/or cerebellum. The brain stem saccade generator and vestibular system clearly possess the gaze, eye movement, head movement, and 3-D position signals required as the substrate for these processes (e.g., Crawford 1994; Cullen and Guitton 1997; Phillips et al. 1995; Tomlinson and Brance 1992), but the mechanisms that coordinate these signals have remained obscure. However, by further employing our training paradigm in conjunction with classical neurophysiological techniques, we hope to provide a key tool for sorting out the details of these coordinating mechanisms.

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Address for reprint requests: J. D. Crawford, Dept. of Psychology, York University, 4700 Keele St., North York, Ontario M3J 1P3, Canada.

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