

# Effect of Freeing the Head on Eye Movement Characteristics during Three-Dimensional Shifts of Gaze and Tracking

Han Collewijn, Robert M. Steinman, Casper J. Erkelens, Zygmunt Pizlo,  
and Johannes van der Steen

Accurate control of binocular gaze is fundamental to any behavior that requires visual information with high spatial and temporal resolution. It is for this reason that we have sought, in recent years, to study the control of the binocular direction of gaze under conditions that are as likely as possible to encourage natural oculomotor behavior. Basically, this involves two principles: (1) the development of techniques that allow accurate recording of the direction of binocular gaze during unrestrained eye and head movements, and (2) a preference for using visual stimuli that are real, tangible objects. These objects are located in three-dimensional space within a visual context that is representative of arrangements and events likely to be encountered in everyday life. Most current knowledge of oculomotor function has been derived from experiments performed under highly restricted conditions in which the head was immobilized, and stimuli were highly artificial and abstract compared to stimuli in the real world. Some of this simplification and artificiality was dictated by technical limitations inherent in available recording, stimulation, and analysis techniques. Simplification and artificiality was also inspired by the traditional, compartmentalized concept of the oculomotor system as an assembly of separate, independent subsystems controlling voluntary and reflexive saccades, smooth pursuit, vergence, the vestibulo-ocular reflex (VOR), and the optokinetic response (for critical evaluations of this concept see Steinman, 1986; Collewijn, 1989a, 1989b).

We began the current line of research several years ago by developing an improved revolving magnetic field sensor-coil technique that allowed recording of gaze angles in a subject who was moving in a relatively large region of space, without contaminating our angular measurements with translation artifacts. Using distant, stationary targets, we showed that the stability of gaze of an unrestrained subject was considerably less than the stability of gaze recorded with the head restrained by a bite board, particularly when the subject was required to move his head voluntarily rather than to sit as still as possible (Steinman and Collewijn, 1980; Collewijn et al., 1981; Steinman et al., 1982; Ferman et al., 1987). The standard deviations of the gaze of each of the eyes and of vergence were on the order of 30 minutes of arc, with retinal image slip velocities reaching about 2°/s. Such oculomotor "imperfection" was subsequently shown to be well tolerated by the visual system without degradation of contrast sensitivity, stereopsis, or stereoacuity (Steinman et al., 1985; for review see Collewijn et al., 1990; Collewijn and Erkelens, 1990; Steinman and Levinson, 1990).

More recently, we used real targets to study the dynamics of saccades and vergence over their entire functional range. The main results of these studies were that: (1) saccades were more accurate than expected, (2) vergence was faster than expected, and (3) disjunctive saccades mediated substantial changes in vergence with targets off the median plane (Collewijn et al., 1988a, 1988b; Erkelens et al., 1989a, 1989b). When these data were collected, it was only possible to make measurements with the subject's head on a bite board because the targets were relatively close and translations of the head relative to these nearby targets could not be measured.

Techniques were implemented recently that allowed recording of the head translations in the three cardinal directions. This

allowed us to study the binocular control of gaze while an unrestrained subject viewed nearby target objects. In this chapter we describe the general method we employed and present the first comparative analysis of two types of oculomotor performance: performance in a head-free condition was compared to performance in a "bite board" (head-fixed) condition while the subject: (1) made saccades between two stationary targets and (2) tracked a target that moved both in a lateral direction and in depth. It will be shown that: (1) head-free saccades are faster than saccades made with the head on a bite board, and that their difference cannot be explained by "suppression of the VOR"; and (2) head-free three-dimensional pursuit does not differ significantly from such pursuit with the head on a bite board. This result demonstrates a rather effective interaction between the control of movements of the eyes and movements of the head.

## Methods

### Angular measurements

All experiments were done in the revolving magnetic field instrument situated in our laboratory at the University of Maryland. The general properties of this instrument have been described before (Collewijn et al., 1981, 1988a; Erkelens et al., 1989b). Briefly, homogeneous AC magnetic fields, rotating in the horizontal and median planes (frequencies 976 and 1,952 Hz) were generated by field coils (diameter 244 cm) in a cubic space measuring about 1 m on an edge, centered around the subject's head. Within this space, horizontal and vertical angles were measured with an accuracy of 1 minute of arc by phase detection of signals induced in sensor coils attached to each eye (by suction) and to the head (Collewijn et al., 1975) (sensor coils manufactured by Skalar, Delft, Holland). Each of the six digital outputs was sampled and stored at a frequency of 488 samples/s (effective bandwidth 244 Hz). The values obtained represented the angular orientations of the eyes ("gaze") and the head in space, that is, with reference to the earth-fixed coordinates of the field coils. These angles were insensitive to translation of the subject's head throughout the range of motion employed in our experiments.

Because of the configuration of the fields, the output values represent rotations about fixed vertical and transverse axes. These axes correspond to longitude ( $\phi$ ) in Fick's coordinates and elevation ( $\lambda$ ) in Helmholtz's coordinates. Helmholtz's coordinates have a distinct advantage for descriptions of binocular gaze because a vergence angle in this coordinate system corresponds to the true angle between the lines of sight in the plane of regard, independent of the vertical gaze angle, whereas in Fick's coordinate system this angle is projected on a horizontal plane. Therefore, we converted the horizontal longitude ( $\phi$ ) into azimuth ( $\mu$ ) values, according to the relationship:

$$\mu = \arctan(\tan \phi \cos \lambda) \quad (64-1)$$

### Translational measurements

The position of the head in space was measured with an acoustic ranging system (a very highly in-house modified SAC Associates

3-D Grafpen). A sparking device, attached to a band on top of the head with Velcro strips, emitted 60-kHz ultrasonic pulses whose acoustic wavefronts were picked up by three microphones located at the three corners of a right triangle on a horizontal plane about 1 m above and about 2 m away from the head (near the three corners of the field coil assembly). The pulse frequency (sampling frequency of head position) was 61/s. The effective bandwidth of 30 Hz was more than sufficient to describe the head movements adequately; no energy was detected above 10 Hz in a Fourier analysis. The instrument determined the distance of the sparker from each of the microphones on the basis of the propagation times of the sound pulses. Software based on the known locations of the microphones and simple geometry was developed to convert these distances to a three-dimensional Cartesian coordinate system (Fig. 64-1) with an anteroposterior  $x$  axis (forward positive), a transverse  $y$  axis (rightward positive), and a vertical  $z$  axis (upward positive). The overall accuracy of these coordinates (including all of the various sources of imprecision) was about 1.0 mm.

### Stimuli

Stationary targets consisted of small red light-emitting diodes (LEDs) (diameter 2 mm) positioned: (1) on different isovergence circles (vergence  $5^\circ$  to  $25^\circ$ ) and (2) on isodirection lines when the subject was on the biteboard in a standardized head position (see Collewijn et al., 1988a, for the definition of an isovergence circle). Target positions were defined in Helmholtz's coordinates. Two different LEDs were continuously lit in any trial, and the subject was asked to change gaze between these targets accurately, at a self-determined, comfortable pace. Usually the subject made eight to ten saccades in any one trial. Trials, which lasted 10 seconds, were started by the subject when he felt ready.

The moving target consisted of a single LED mounted on the pen-holder of a Houston X-Y plotter. The target was moved at linear speeds of 6.35, 12.7, or 25.4 cm/s through a circular or square trajectory with a diameter of either 15.3 or 25.4 cm. The X-Y plotter was mounted vertically. It could be rotated around a vertical axis in the median plane of the subject from the frontoparallel plane (maximal horizontal version and minimal vergence stimulus) to the sagittal plane (maximum vergence and minimal horizontal version). When a subject was on the bite board in the standardized head position, the midpoint (M) between the rotational centers of his eyes was positioned 43.5 cm posterior to the center of the stimulus plane. Recordings were made while the subject tracked square and circular trajectories with the moving target in the frontoparallel, sagittal, and  $30^\circ$  or  $60^\circ$  intermediate planes. Each of these four planes required greater or lesser version and vergence tracking components. The vertical version stimulus was almost independent of the orientation of the stimulus plane. The diameter of the circle or square amounted to either  $20^\circ$  or  $33^\circ$  of visual angle when the stimulus trajectory lay in the frontoparallel plane.

### Experimental procedure

At the beginning of each session, subjects were aligned on an individually fitted bite board in such a way that the rotational centers of the eyes (assumed to lie 13.5 mm behind the anterior pole of the cornea) were in standard positions on the isovergence circles (see Fig. 64-1). The midpoint (M) between these centers then coincided with the origin of the  $x,y,z$  coordinate system, which was fixed relative to the stimuli. In initial calibration trials, subjects viewed the center of the image of their own pupil monocularly in a frontoparallel, flat mirror that was removed after these calibration trials (one for the right and one for the left eye). The horizontal and vertical gaze angles recorded in these trials represented straight-ahead gaze (zero gaze angles). These angles were subtracted from all values recorded during the session in order to obtain the absolute angles of gaze.

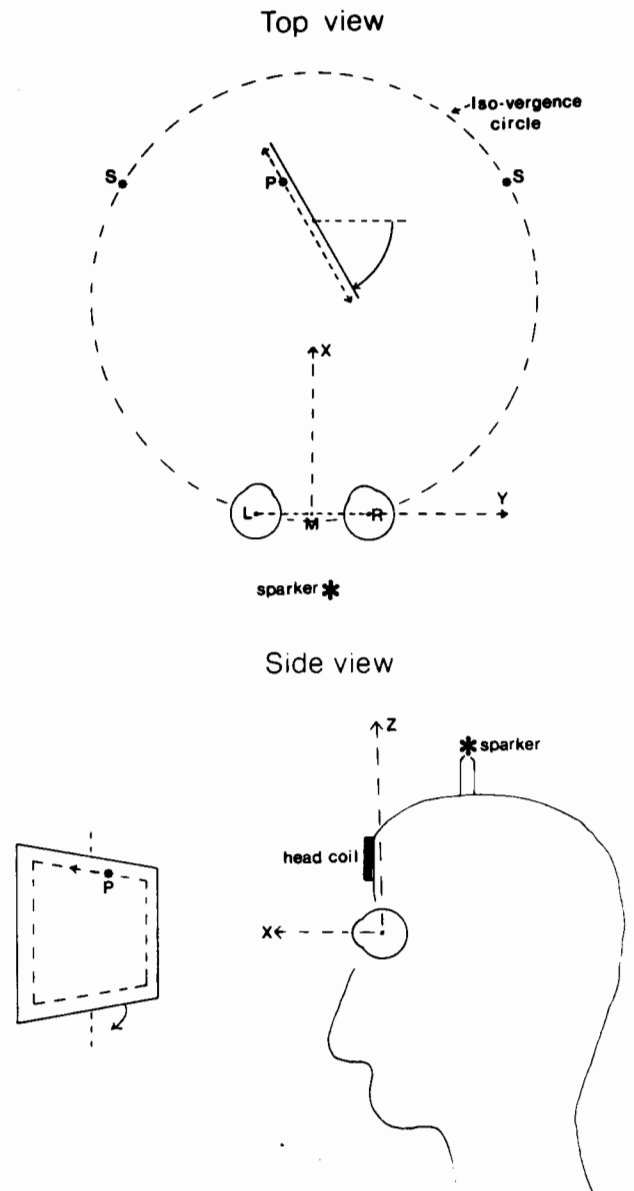


Fig. 64-1. Diagram showing the experimental conditions (not to scale). (Upper panel) View from above, with the subject's eyes aligned on a bite board in the standardized initial position. L, R, centers of rotation of the left and right eye; M, midpoint of the line connecting the centers of rotation of the eyes, which in the standard position coincides with the origin of the  $x,y,z$  coordinate system; P, pursuit target, consisting of an LED moved by an X-Y plotter, that can be rotated around a vertical axis (the plotter is shown rotated  $30^\circ$  with regard to the subject's median plane); S, stationary targets, subtending equal target vergence. (Lower panel) Side view showing the locations of the head coil and the sparker. The X-Y plotter, in front of the subject, shows the pursuit target (P), rotated  $30^\circ$  out of the median plane and thus moving sideways, vertically, and in depth as it follows a square trajectory.

Head-free sessions started with a calibration trial during which the sparker was positioned at the origin of the  $x,y,z$  coordinate system. The values obtained in this initial calibration were subtracted from all  $x$ ,  $y$ , and  $z$  values obtained during the session, in order to standardize them to the origin of the  $x,y,z$  coordinate system. Subsequently, the sparker was mounted on the head of the subject when he was aligned on the bite board. A recording

made in this position represented the  $x$ ,  $y$ , and  $z$  positions of the sparker with the head in the standard position (i.e., with M at the origin of the  $x, y, z$  coordinate system). This procedure measured the actual distances between M and the sparker. The centers of the eyes in the standard position would have the coordinates  $y = d/2$  and  $y = -d/2$ , where  $d$  is the interocular distance. The angular positions of the head coil with the head in this standard position were also set to zero.

Pure translations of the head (i.e., without rotations) would displace the eyes over similar  $x$ ,  $y$ , and  $z$  distances. When the head rotates as well as translates, the  $x$ ,  $y$ , and  $z$  locations of the center of each eye can be calculated by considering the position of the sparker as the instantaneous pivot point around which the head rotates. For this purpose, trigonometric relations were worked out that describe the  $x$ ,  $y$ , and  $z$  positions of the eye as a function of the horizontal and vertical head angles, the distances between the sparker and M,  $d$ , and the  $x$ ,  $y$ , and  $z$  position of the sparker. Actually, this description was an approximation, because it assumed the absence of head torsion about the occipito-frontal axis, (which we did not measure). In the future we plan to measure head torsions because the present, incomplete description leads to some uncertainty about the lateral ( $y$ ) position of the eyes (failure to measure head torsion means that oculomotor compensation of head movements may be better, but not worse, than our incomplete observations indicate).

In addition to the momentary  $x$ ,  $y$ , and  $z$  positions of the eyes, the instantaneous positions of the target(s) were calculated. As a final step, we calculated the instantaneous angles subtended by the target(s) at each eye. These angles should be matched by the gaze angles; that is, fixation should be "on target" or accurate. We compare target angles and gaze angles (fixation accuracy) in the following section.

## Results

### Three-Dimensional Pursuit

We illustrate our typical findings with a case in which the target moved in three dimensions (horizontal, vertical, and depth) and thus required three-dimensional binocular eye tracking. Figures 64-2, 64-3, and 64-4 show representative three-dimensional pursuit of a square trajectory (15.3 cm on a side; target velocity 25.4 cm/s; cycle frequency 0.42 Hz). The plane of the target trajectory was rotated 30° with regard to the subject's median plane, in which the orientation of the horizontal, vertical, and vergence components of the target subtended angles of about 10°, 25°, and 3°, respectively. Composite binocular gaze movements are shown. That is, version was calculated as (left eye gaze + right eye gaze)/2, and vergence as left eye gaze - right eye gaze.

As shown in the upper panels of Figures 64-2 and 64-3 (subject R.S. on a bite board), there was a satisfactory overall correspondence between the trajectories of the target and the trajectories of the horizontal and vertical version gaze movements. There were episodes, especially toward the end of a side of the square trajectory, when gaze position matched the position of the target almost perfectly. Saccades were frequently made, especially near the corners, but the smooth gaze movements were markedly rounded; that is, they were anticipating target motion. Such behavior, including the anticipation of the corners by smooth eye movements, is characteristic of the pursuit of square trajectories (Collewijn and Tamminga, 1984).

The lower panels of Figures 64-2 and 64-3 show pursuit of the same stimulus by the same subject, but in a different session with the head free. Head rotations and the calculated translation of the left eye are shown in the lower traces. Appreciable, although modest, head movements were made in all directions. Nevertheless, gaze movements, and their relation to the target, were strikingly similar to those recorded with the head fixed. This similarity includes all the peculiar details characteristic of this subject

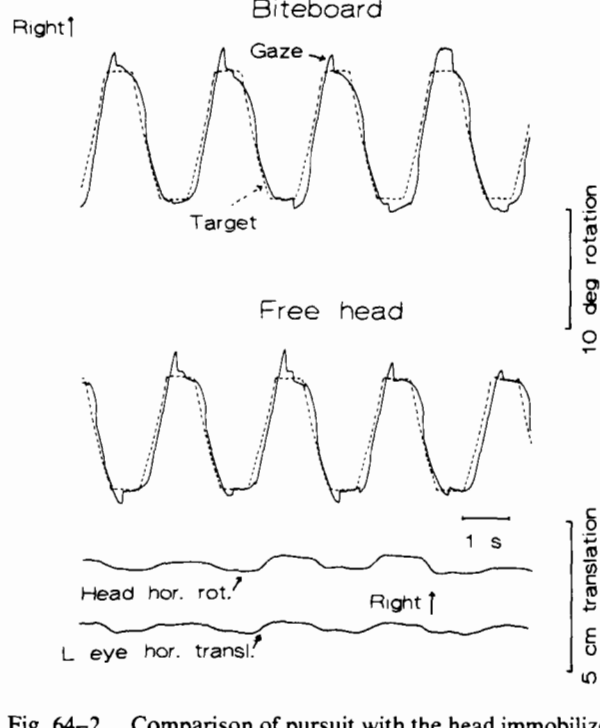


Fig. 64-2. Comparison of pursuit with the head immobilized on the bite board (top panel) or with the head free (bottom panel) in subject R.S. The target followed a square trajectory in a vertical plane, rotated 30° with regard to the median plane (see Fig. 64-1). This figure shows composite binocular horizontal version movements (continuous lines) of the eyes, that is, (left eye gaze + right eye gaze)/2 (the average direction of the combined lines of sight). Horizontal rotations of the head and translations of the left eye are also shown when the head was free. The interrupted lines show target version—the angle subtended by the target at M, the midpoint between the eyes.

pursuing this particular target trajectory. The similarity between the performance with the head fixed and that with the head free demonstrates two important points: (1) our methods of recording and data processing do not contain any gross errors and (2) eye-head coordination during pursuit is quite good.

Figure 64-4 shows a similar comparison for the vergence. Once again, the performance is virtually identical for the head-free and head-fixed conditions, including all the fine details. These details are idiosyncratic and are a very reproducible characteristic of each subject's three-dimensional tracking performance. The other four subjects who served in these experiments also showed very similar performance in the head-fixed and head-free conditions, but a direct comparison of performance between these conditions was sometimes complicated by the fact that, unlike subject R.S., they tended to move their head somewhat backward when they got off the bite board. This reduced the amplitude of the target motions at their eyes and, correspondingly, it reduced the amplitude of the required gaze movements.

All subjects reported that they found pursuit with the head free easier than when the head was clamped on the bite board despite the fact that they made rather small head movements when their heads were free from restraint. In all subjects, the horizontal and vertical rotations of the head were essentially in phase with motions of the target. The calculated vertical, lateral, and forward-backward translations of the eye were generally small, but these linear movements tended to track the target in all dimensions so as to contribute to the required changes in gaze.

Our conclusion that pursuit is equally good with the head free or fixed is obviously limited to the dimensions of the target move-

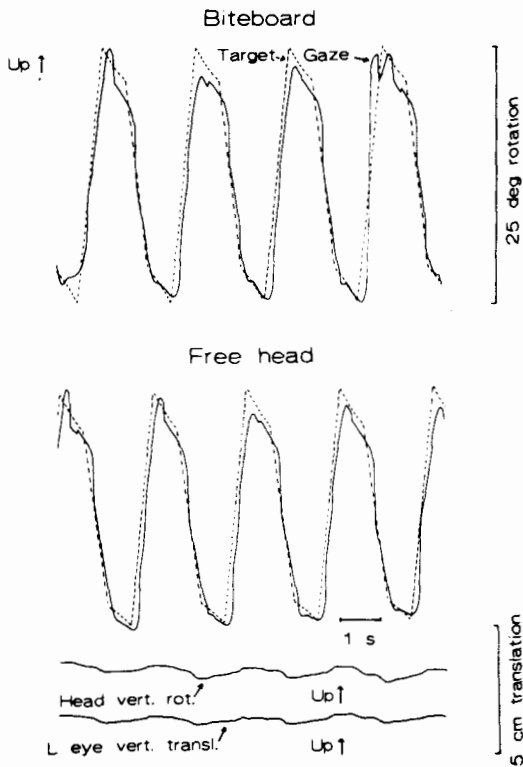


Fig. 64-3. Same comparison as in Figure 64-2, but showing the composite vertical version movement of target and eyes for the same pursuit episode for subject R.S. For the head-free condition, vertical rotation of the head and vertical translation of the left eye are also shown.

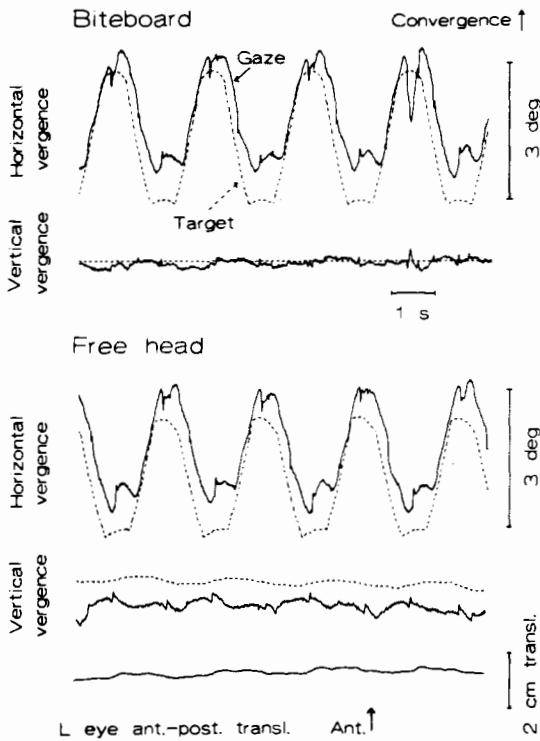


Fig. 64-4. Same pursuit episode shown in Figure 64-2 and 64-3 for subject R.S., but plotting vergence of the eyes (left eye gaze - right eye gaze) and of the target (difference between the angles subtended by the target at each eye). For the head-free condition, anterior-posterior translation of the left eye is also shown.

ments in our current experiments. We required movements well within the oculomotor range with the head fixed (the eyes were not required to make versions exceeding 33° or vergence changes exceeding 3°). For targets moving over larger version and vergence angles, differences between head-free and head-fixed performance may emerge. Also, a complete numerical analysis of our data may reveal subtle differences not obvious at this early stage of analysis. We consider this unlikely, however, because a previous analysis of one-dimensional pursuit in the frequency domain also demonstrated a great similarity between head-free and head-fixed conditions (Collewijn et al., 1982b) and we now know that vergence eye movements can be as fast and accurate as versions (Erkelens et al., 1989a, 1989b).

**Saccades between stationary targets**

Saccades made to shift gaze between targets when the head was free are illustrated in Figure 64-5. It should be emphasized that subjects used their own preferred combination of eye and head movements. They were told that they were free to move their heads, but they were not instructed to use any particular strategy of coordinated eye-head movement. The subject whose typical performance is illustrated in Figure 64-5 (Z.P.) consistently made substantial head rotations, as well as head translations, in the horizontal plane. Such motions obviously affect the angles the targets subtended at each of the eyes. First, the angle between the two targets (which was 80° with the subject in the standardized position on the bite board) was reduced to about 66° because the subject leaned backward. Second, the target positions relative to each eye change as the head rotates or translates laterally. A saccade to shift gaze to the right was associated with a head rotation to the right, but also with a translation of the eyes to the right because the axis of head rotation is located posterior

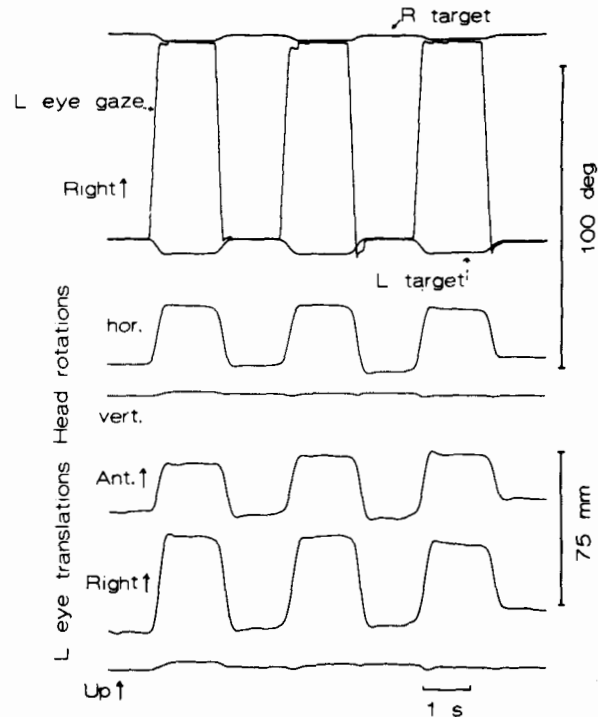


Fig. 64-5. Saccades between two stationary targets made with the head free (subject Z.P.). The upper panel compares the horizontal angle of gaze of the left eye with the instantaneous angles subtended by each of the targets at this eye. The middle and lower panels show the head rotations and translations of the left eye. The saccades have an amplitude of about 66° and are essentially conjugate (vergence was constant at about 5°).

to the eyes, as shown in the traces representing the calculated translations of the left eye in Figure 64-5. The overall result of such head motions is that the relative position of each target shifts in the direction opposite to the direction of the gaze shift, thus reducing the amplitude of the saccade required for accurate fixation.

The important result shown in Figure 64-5 (upper panel) is the excellent match between the (self-paced) saccades and the instantaneous angular positions of the continuously visible targets. This was true for conjugate saccades as well as for disjunctive saccades used for gaze shifts between targets differing in distance as well as in direction. This finding further corroborates the robustness of gaze control with the head free, and also the validity of our measurement and analysis techniques. Note that all our tracings represent absolute angles as calculated. No arbitrary offsets have been introduced anywhere to improve the match between the direction of gaze and the direction of the target.

The accuracy of saccades used to shift gaze between stationary targets with the head free parallels the accuracy of three-dimensional pursuit with the head free (described above). However, an important advantage of having the head free emerges when the microstructure of the saccades used to shift gaze is examined.

Velocity profiles of horizontal, rightward saccades for the head-free and bite board conditions are shown in Figure 64-6 for subject R.S. In making such comparisons, it is obviously essential to choose saccades that match in actual size, not just in nominal target separation, because the latter is affected by the extent of head movement. The upper panel of Figure 64-6 shows velocity profiles characteristic of horizontal saccades of such amplitudes made with the head stabilized on a bite board (similar

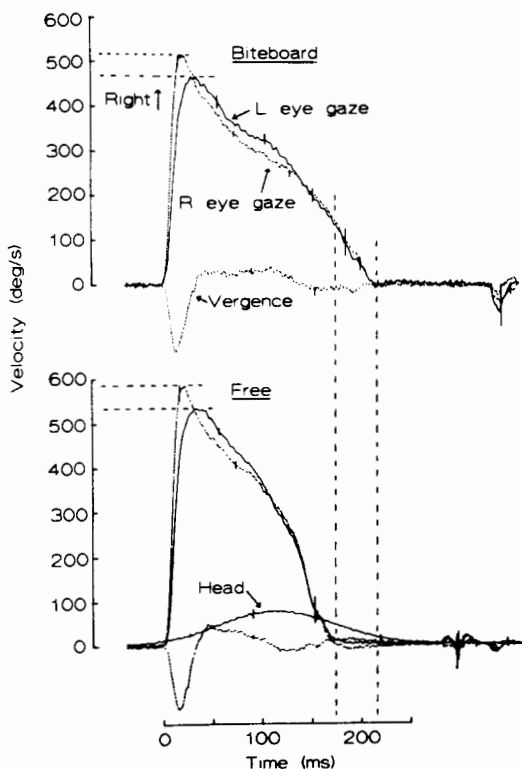


Fig. 64-6. Velocity profiles of conjugate saccades with the head immobilized on a bite board (top) or free (bottom) (subject R.S.). The size of the saccades in the two conditions is matched at  $70^\circ$ ; vergence is constant at  $5^\circ$  convergence, except for the initial transient divergence (a well-known characteristic of all horizontal saccades). Each panel shows the average of four to five consecutive saccades made in the same trial. Short vertical bars represent  $\pm 1$  S.D.

to results reported previously by Collewijn et al., 1988a). Saccades made under both conditions illustrated in Figure 64-6 were of about  $70^\circ$  as can be seen in the corresponding position traces in Figure 64-7 (below).

In Figure 64-6, the temporally-moving right eye accelerated faster and reached a higher and earlier peak velocity (about  $520^\circ/\text{s}$ ) than the nasally moving left eye (peak velocity about  $470^\circ/\text{s}$ ). As a result, the eyes diverged at about  $150^\circ/\text{s}$  in the beginning of the saccade, but converged again (at a lower velocity) later in the saccade. The total angles of displacement, as well as the duration the saccades, were similar in each eye. Freeing the head (Fig 64-6, lower panel) did not change these basic characteristics, but it improved the dynamics of the saccade appreciably. Peak velocities of both eyes were increased by about  $60^\circ/\text{s}$ , and duration was reduced from about 230 ms in the fixed condition to about 175 ms in the free condition. It is tempting to attribute these changes to the contribution of the head movement, but closer analysis of the data excludes any simple addition of head and eye velocities.

This fact is illustrated in Figure 64-7, in which the data of Figure 64-6 for the right eye and head have been replotted (left panels) along with matched saccades from another subject (Z.P.). The position traces in the upper panels of Figure 64-7 show that the saccades in the head-free and bite board conditions had similar amplitudes and that the saccades made when the head was free were faster and shorter than the saccades made when the head was on the bite board. Z.P. made much larger head movements than R.S. The data from Z.P. show that even relatively large and fast head movements do not add to eye velocity.

Two important observations can be made with regard to the interaction between head and gaze movements in the recording reproduced in Figure 64-7. First, the corresponding velocity profiles (lower panels) demonstrate that the increase in peak eye velocity occurred very early, only about 20 ms after the beginning of the saccade. At this time, head velocity was much too low to account for the increase in eye velocity. Second, the moment of peak head velocity virtually coincided with the time at which the velocity profiles of head-free and head-fixed saccades crossed over. This means that at the time of maximal head velocity head-fixed and head-free saccades had identical velocities. Head velocity *did not add anything* to eye velocity. The crossover also occurred relatively late, near the end of the head-free saccade. This means that saccades when the head was free were faster than their head-fixed counterparts for almost the entire duration of the saccade. The cutoff of gaze velocity at the end of the head-free saccades was sharp. Accordingly, their velocity profiles were more square and less skewed than those of head-fixed saccades (see also Chapter 71, this volume). These two observations show that the improvement in dynamics of saccades after freeing the head has causes other than the simple addition of the head and eye movement velocities in combination with the suppression of compensatory eye movements such as the VOR. Central factors are more likely to be involved.

A systematic illustration of these findings is shown in the peak velocity-amplitude and duration-amplitude relationships plotted in Figure 64-8. At all amplitudes above  $10^\circ$ , peak velocities with the head free were higher than with the head fixed (Fig. 64-8, upper panel). The peak velocities of the head have also been plotted (triangles). It is obvious that these instantaneous head velocities can account only for a small part of the increase in gaze velocity, even if it is assumed that vestibular responses are completely absent. The marked reduction of saccadic duration (Fig. 64-8, lower panel) after freeing the head is obviously related to increasing eye velocity without increasing the amplitude of the saccade. It cannot be related quantitatively, in any straightforward manner, to the velocity of the head movement.

The characteristic differences between conjugate saccades made with the head free or fixed were retained when the two targets were located at different distances, requiring disjunctive

Subject: RS

Subject: ZP

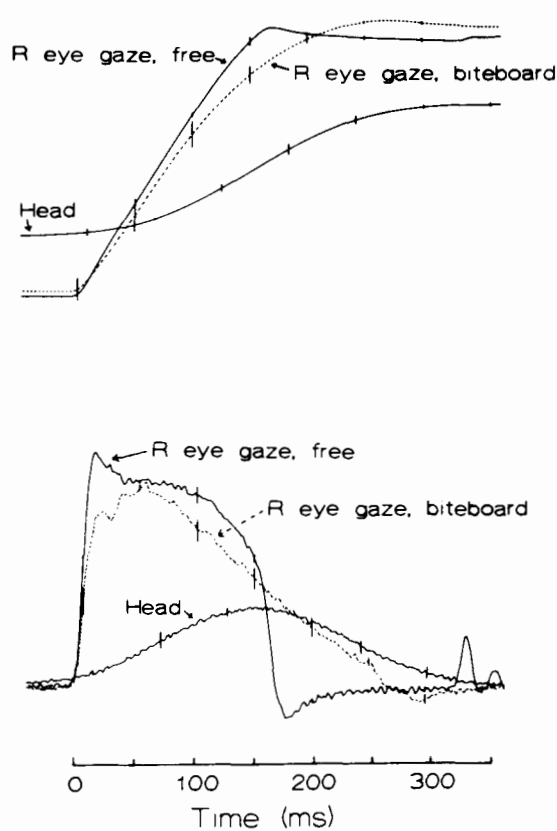
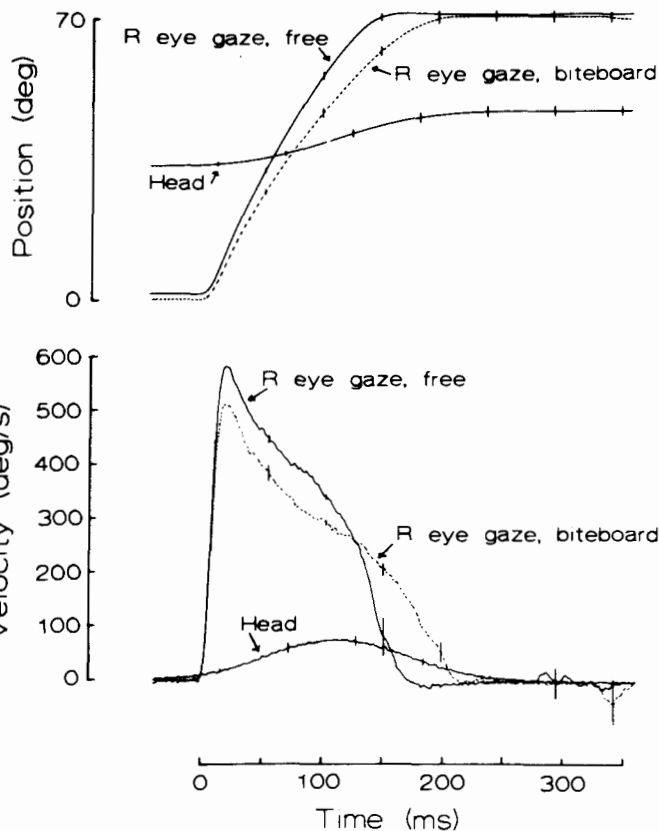


Fig. 64-7. Direct comparison for two subjects (R.S. and Z.P.) of the trajectories of the right eye and the head (top row, position; bottom row, velocity) of conjugate saccades (matched in size) made

with the head immobilized on a bite board (interrupted lines) or with the head free (continuous lines).

saccades. Examples of matched, leftward, disjunctive saccades, mediating 60° of version and 10° of divergence in the head-free and head-fixed conditions, are shown in Figure 64-9. In this example, the left, temporally moving eye maintained a higher velocity than the right eye during the entire saccade. It also continued to move slightly longer than the right eye. As a result, virtually all of the required divergence was accomplished during the disjunctive saccade. Very little postsaccadic smooth vergence correction was required. Freeing the head had the same

effect as for conjugate saccades: velocities were increased and durations were shortened. This was true of the vergence as well as of the versional saccadic component. Note that the compression in time preserved the idiosyncratic features of the performance of subject R.S. He makes a transient convergence toward the end of his saccades. Note also that head velocity was particularly low in this trial, almost zero at the time of peak eye velocity. Eye velocity was enhanced by about 50°/s when the head was freed.

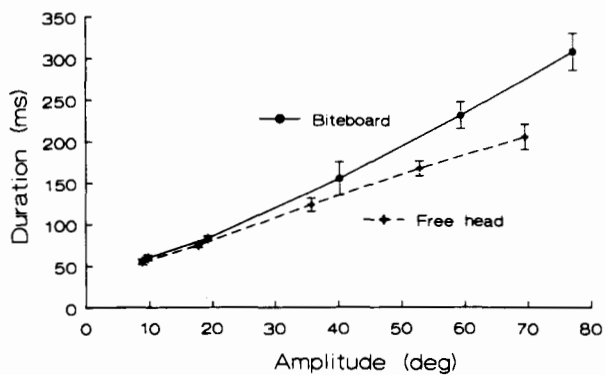
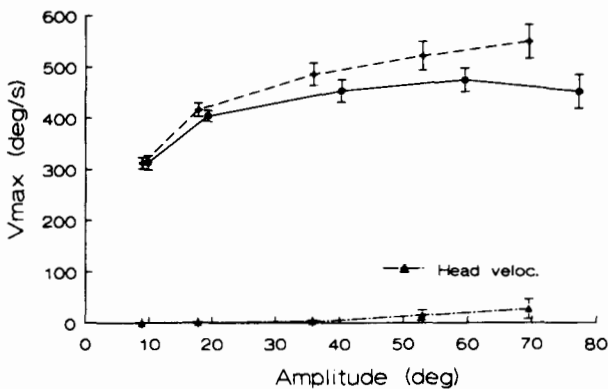


Fig. 64-8. Comparison of peak velocity (Vmax; left) and duration (right) as a function of the amplitude of horizontal saccades used to shift gaze between stationary targets separated by different amounts (10° to 80°) when the head was immobilized on a bite board (continuous lines) or when it was free (interrupted lines). Each datum point

represents the mean of 10 to 20 saccades of subject R.S. Vertical bars represent ± 1 S.D. Equal numbers of temporally and nasally directed saccades were pooled. In the top panel, head velocity at the moment of peak gaze velocity is also shown (triangles).



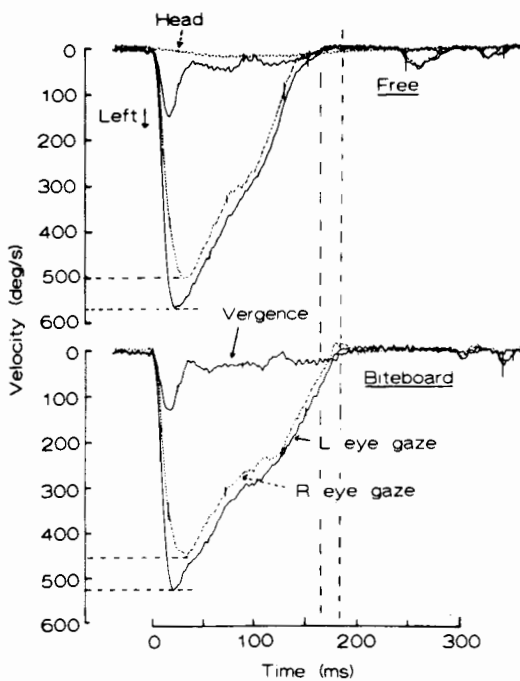


Fig. 64-9. Velocity profiles of disjunctive saccades made with the head free (top) or immobilized on a bite board (bottom) (subject R.S.). The size of the saccades selected was matched for each of the two conditions at about  $60^\circ$  version and about  $10^\circ$  vergence. Each panel shows the average of four to five consecutive saccades made in the same trial. The short vertical bars represent  $\pm 1$  S.D.

## Discussion

Two main conclusions emerge from our present work. First, we have demonstrated the feasibility of recording binocular gaze behavior in subjects who are totally unrestrained and who view visual configurations that are representative of real-world conditions, including three-dimensional structure and three-dimensional motion. Second, the performance of oculomotor control under such relatively natural conditions is excellent.

Our results in three-dimensional pursuit emphasize the unity of function in the oculomotor system. Appropriate, binocular tracking of a target moving simultaneously horizontally, vertically, and in depth was mediated by a mixture of smooth and saccadic eye movements, each of which contributed to both version and vergence of the eyes. There was no obvious partitioning between the performance of a conjugate smooth pursuit (version) system and a disjunctive, smooth vergence system. Although the unity in performance between these traditionally distinguished subsystems will have to be confirmed in a complete numerical analysis, recordings such as those shown in Figures 64-2 through 64-4 strongly suggest that vergence and version operate in an indistinguishable manner when artificial, limiting conditions are avoided. The kind of stimulus used in our present experiments (i.e., a target moving over stretches of about 15 to 25 cm in all directions, at an average distance of about 40 cm) appears reasonably representative of targets encountered in natural tasks. The excellent performance of vergence, as well as the integrated generation of conjugate and disjunctive components by the saccadic system, have been demonstrated previously (Erkelens et al., 1989a, 1989b). Our present findings encourage us further to em-

phasize the holistic nature of gaze control, including head control, because three-dimensional pursuit was as accurate with the head free as with the head stabilized on a bite board, and the dynamic properties of saccades were even appreciably improved by freeing the head.

Saccades made with the head free were as accurate as, but faster and shorter than, saccades made with the head on a bite board. This included disjunctive components. It has been noticed before that human saccades become faster when the head is moved (e.g., Lauritis and Robinson, 1986; Guitton and Volle, 1987; Pélisson et al., 1988). Similar effects have been described for cats (Fuller et al., 1983). Contrary to these findings, Tomlinson and Bahra (1986a) reported that, in monkeys, head-free saccades had lower peak velocities and longer durations than saccades made with the head fixed.

In all prior discussions, the interaction between head and eye movements in gaze control has been dominated by a subsystem-oriented approach. The main issue considered has been whether the VOR does or does not continue to operate during a saccade. In other words, concern centered around whether any increase in saccadic velocity with the head free should be attributed to some kind of summation of head-in-space and eye-in-head velocities. The inhibition of the VOR required for this summation to take place has been supported in some experiments (Lauritis and Robinson, 1986; Tomlinson and Bahra, 1986b; Pélisson et al., 1988) but has been inconsistent and idiosyncratic in other experiments (Guitton and Volle, 1987). Our findings suggest that these prior discussions about the operation of the VOR during saccades are actually tangential to the important effects produced by freeing the head. We have clearly shown that the instantaneous differences in velocity between head-free and head-fixed saccades are in no way matched by the simultaneous head velocity. Other, central processes must be at work.

It is appropriate to emphasize that two of the organizers of this conference (P. P. Vidal and A. Berthoz) have been among the protagonists showing a strong coupling between the horizontal component of eye position and ipsilateral dorsal neck muscle activity [e.g. Vidal et al. (1982) in the cat; Lestienne et al. (1984) in the monkey; André-Deshays et al. (1988) in man]. Anyone who has been a subject in an oculomotor experiment on a bite board will confirm this coupling from first-hand experience. The strain on the teeth exerted by the neck muscles is felt very keenly in such experiments when any but the smallest eye movements are made. Zingale and Kowler (1987) discussed the implications of such strain in their experiment on saccadic patterning. It seems highly likely that human subjects (and animals as well) whose heads are restrained will adjust their motor commands in such a way as to avoid uncomfortable strain on their teeth or skull. As commands to the eye and neck muscles are programmed in close synergy, it is plausible that inhibition of neck muscle activity will lead to some parallel inhibition of the commands to the eye muscles. Thus, the better dynamics of saccades with an unrestrained head are more likely to be caused by the uninhibited expression of natural commands to shift gaze, rather than by a direct contribution of the motion of the head. Once this is appreciated, the main sequence parameters observed with a subject's head held on a bite board (or bolted to a metal frame) may be considered to reflect subnormal performance caused by the partial inhibition of the natural commands for shifting gaze.

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