Binocular Gaze Control Under Free-Head Conditions

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Accurate control of binocular gaze is fundamental to any behavior that requires visual information with high spatial and temporal resolution. Normally, such control has to be exerted under conditions of unrestrained head and body movements, in a richly structured and dynamically changing visual environment, containing a multitude of potential targets. The motions of subjects and targets consist of translations and rotations (each in 3 dimensions) and, moreover, translation of a subject is associated with configurational transformations of the optic stimulus array, known as optic flow. Obviously, a realistic assay of binocular gaze control under natural conditions is of great fundamental and practical importance, but at the same time technically and conceptually very demanding.

In contrast to the demands of everyday viewing, most of our knowledge of oculomotor control has been gathered under strongly simplified conditions, with a preference for monocular (often uni-dimensional) recording, fixed heads, and highly reduced and stereotyped stimuli. Such an analytical approach is customary and often very productive in science. Yet, some drawbacks of this approach can be pointed out in relation to oculomotor research: 1) eye movements are often studied under limiting conditions (*e.g.* solitary targets, isolated vestibular stimulation in darkness, pure vergence or pure version requirements) that are rarely encountered in nature and may not yield representative behavior; 2) characteristic behavior under standard laboratory conditions is often extrapolated as evidence for the existence of a dedicated, separate subsystem, mediating that particular behavior. (For further discussion, see Ref. 23).

We have recently recorded human binocular eye movements under conditions that were as "natural" as possible, and that required the integrated activity of all known smooth and saccadic oculomotor facilities. Specifically, we have studied the control of binocular eye movements while gaze was shifted between different targets or while a moving target was pursued. This was done under conditions where the head could be moved in all degrees of freedom, and for targets that were distributed or moving in three-dimensional space. For comparison, similar gaze movements were recorded while the head was immobilized by a bite-board.

Some aspects of this work were recently described.[10] The present report is limited to a discussion of the analytical framework and the practical results related to voluntary

gaze shifts between stationary, continuously visible targets, which were positioned in the horizontal plane of regard and which differed either only in direction, or in direction and distance. It will be demonstrated that such gaze shifts, with the head free, are made with great accuracy, and with superior dynamical performance compared to similar gaze shifts made while the head is fixed.

ANALYTICAL CONSIDERATIONS

For the study of the metrics of binocular saccades, it is important to reflect on the contributions of conjugate eye movements (version) and disjunctive eye movements (vergence), and their relation to the spatial arrangement of the stimuli. The simplest case is a pure difference in the direction of stimuli, in which no change in vergence is required. For the study of such conjugate saccades, it is obviously essential that the targets between which gaze is shifted subtend equal vergence angles. The locus of such targets is a circle through the rotational centers of the two eyes, as shown in Fig. 1 and described previously.[7] Targets T_1 and T_2, positioned on such an iso-vergence circle, subtend different directions but equal target vergence angles at both eyes ($V_1 = V_2$). Gaze-shifts between these targets require equal rotations (G_L and G_R) by the two eyes, but such targets generally are not located at equal distances from the eyes. Targets on a smaller iso-vergence circle, such as T_3 in Fig. 1, subtend a larger target vergence at the eyes, and require a larger ocular vergence. When the family of iso-vergence circles is rotated around the base-line connecting the rotational centers of the two eyes, a corresponding family of toroid iso-vergence surfaces is formed, extending the iso-vergence locus in the vertical dimension. Clearly, targets positioned on a flat screen or on a circle centered on the head are not isovergent, unless their position intersects with an iso-vergence circle, which is the case only for targets arranged symmetrically about the median plane.

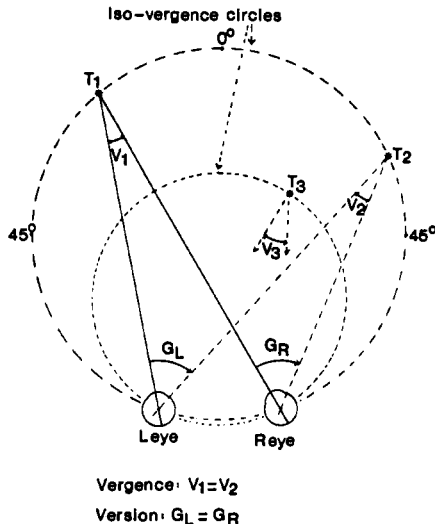Implicitly, the description of target positions in relation to the two eyes, as just

Fig. 1. Iso-vergence circles as loci of targets subtending equal vergence angles. Only gaze shifts between pairs of targets on a same iso-vergence locus can be expected to be strictly conjugate. See text.

introduced, conforms to Helmholtz's coordinate system for the description of eye position (see Ref. 1). This system is particularly transparent when dealing with binocular gaze, because vertical angles are measured about a fixed axis through the rotational centers of the two eyes. As a result, horizontal angles, and thus vergence, are invariant with vertical eye position, unlike the situation in Fick's system.

As a reference for free-head gaze shifts, and as an extension of previous work,[7,8,13] we first recorded voluntary, conjugate or disjunctive binocular gaze shifts without head movements. For this purpose we positioned stationary, permanently visible targets (pairs of LED's) on the same or on different iso-vergence circles subtending between 5 and 25 deg of target vergence, and fixed the head of the subject on a bite-board in an appropriate position.

As long as the head and targets remain stationary according to the geometric principles described above, the geometric relations between targets and eyes can be expressed in a straightforward manner by simple angular (Helmholtz) coordinates. Because iso-vergence surfaces are defined with respect to the head, however, they essentially lose their special relation to earth-fixed targets as soon as the head can move freely. Thus, under natural conditions, iso-vergent targets are an unusual, limiting case. Virtually all gaze shifts in normal life require unequal displacements of the two eyes.

The new aspect in our current experiments was to free the head and compare the control of gaze with free-head *vs.* fixed head, taking into account the dynamic changes in the geometry of target-eye relations accompanying the free motion of the head. In previous investigations in which head movements were allowed to some degree, the topographic relations have usually been simplified, for instance by constraining the rotational freedom of the head to fixed axes,[20] and by neglecting the spatial complexities caused by the eccentric position of a rotating vantage point (the eye) on a rotating and translating platform (the head). Even when head motions are constrained to rotation, the relations are far from simple. For such conditions, the motions of the line of sight with respect to the target have been often approximated by adding the angle of the head in space and the angle of the eye in the head to obtain the gaze angle. While this gaze angle, as such, is mathematically correct, this procedure neglects the fact that the horizontal eye and head rotations are made about different vertical axes, which are about 10 cm apart. This means that gaze angles, obtained by adding eye and head angles, are not commensurate with the target angles, which are profoundly affected by the ocular translations, associated with even the simplest head rotations. These changes are non-linear, asymmetrical about the straight position, and strongly dependent on the distance and eccentricity of the target (see Appendix). Although this source of error becomes small for distant targets, this is only a mild relief, because the majority of behaviorally relevant visual targets are located nearby, in the working space close to the subject, not only in the laboratory, but also in daily life.

These, highly non-linear, effects of head rotation in the yaw direction on target angle will be further compounded by head rotations in the pitch and roll directions, and by head translations, which are certain to occur in random, as well as systematic ways, once the head motions are not constrained. For instance, the head will swing sideways towards a target when part of the head rotation in space is absorbed by the torso. Even 1 cm of lateral head translation will change the angle of a target 25 cm in front of the eye by 2.3 deg. The position of the rotational centers of the eyes in 3-D Cartesian space is determined by the compounded effects of 3-D rotations and 3-D translations. Thus, study of gaze control with the head free requires the measurement of all translations (3 D) and rotations (3 D) of the head, plus the rotations (at least 2 D) of the eyes. Once

the instantaneous linear position of a reference point on the head and the angular position of the head are known, the 3-D Cartesian coordinates of the rotational centers of the eyes can be computed, provided that the linear distances between the reference point and the centers of the eyes have been determined in advance. The appropriate rotational matrix was developed by one of us (Pizlo). For the data presented here, a simplified version of this matrix was used (see Appendix), because we failed to measure head-roll (rotation about the sagittal axis) in our current measurements. This incompleteness, which will be remedied in future experiments, leads to some uncertainty about the position of the eyes in space. Our conclusions are not likely to be affected by the absence of head roll information because gaze control, calculated with head roll included, is not likely to be less accurate than the results we will report.

TECHNICAL ASPECTS

The recording of all angular coordinates was achieved with the Maryland Revolving Magnetic Field implementation of the scleral sensor coil technique, which allows the recording of eye and head angles with unrivalled accuracy and precision, over a large spatial range through which the magnetic field is homogeneous.[7,9] Scleral annuli[5] were placed on both eyes, and an additional coil was attached to the head.

We measured 3-D head translations (X, Y, Z) with an acoustic ranging system (a very heavily, in-house modified SAC Associates 3-D Grafpen). An ultrasonic pulse emitter (sparker), mounted on the head with Velcro strips, emitted 60 kHz ultrasonic pulses, the acoustic wavefronts of which were picked up by 3 microphones located at the 3 corners of a right triangle on a horizontal plane about 1 m above and about 2 m away from the head (near 3 corners of the field coil assembly). The pulse frequency (sampling frequency of head position) was 61/s. Times of arrival of the wavefronts were converted to distances, with an overall accuracy of about 1 mm. The effective bandwidth of 30 Hz was more than sufficient to describe the head movements adequately; no energy was detected in the linear position signals above 10 Hz. Initial calibration measurements with the sparker and the head in standard positions served to determine the relative XYZ positions of eyes and sparker.

The XYZ positions of each eye was computed from the XYZ position of the sparker, the distances between the sparker and the eyes, and the angular position of the head. In addition, the XYZ positions of the targets were known. From the linear positions of the targets and the eyes, the instantaneous angles subtended by the targets at the eyes could be computed by arctangent relations. Finally, we obtained the gaze angles directly from the eye coil angles. Thus, instantaneous target and gaze angles for each eye could be compared to evaluate the accuracy of free-head gaze control (see Appendix).

SOME BASIC PROPERTIES OF BINOCULAR COORDINATION

To put the findings on binocular gaze-control with the head free in the right perspective, it is desirable to briefly recapitulate some basic properties of oculomotor control as measured in our conditions with the head fixed, which have been described elsewhere.

1)   Voluntary gaze shifts between stationary, permanently visible targets are relatively accurate, with little undershoot.[7,18] This contrasts with the responses to flashing or jumping targets, usually employed to study saccadic control, for which undershoots by about 10% are described as typical.[3]

2)   A fundamental property of all horizontal, binocular saccades is the occurrence of

a transient divergence. The abducting eye accelerates faster, and reaches a higher and earlier peak velocity than the adducting eye. This difference in velocity can amount to 100–200 deg/s in the early part of the saccade; later in the saccade the velocity difference inverts in the advantage of the adducting eye. As a result, both eyes land approximately on target at saccadic offset, with equal saccadic durations for both eyes.[7,10]

3) Shifts in gaze between non-isovergent targets is accomplished by saccades rather than by smooth vergence movements.[11,12,14] The saccadic vergence is not explained by a simple addition of a conjugate saccade with ongoing (slower) vergence. This is at variance with narrow interpretations of Hering's law, and also with traditional schemata of the trajectory of the binocular fixation point in disjunctive eye movements, such as the popular diagram by Yarbus[26] (Fig. 94). Another violation of Hering's law of conjugacy in the strict sense occurs in asymmetric adaptation of saccadic sizes, as induced, for instance, by anisometropic spectacle corrections.[13,17]

CONJUGATE GAZE SHIFTS WITH THE HEAD FREE

Figure 2 illustrates gaze shifts with the head free made between targets that were horizontally separated by about 80 deg, subtending a vergence of about 5 deg. These targets were stationary, but due to eye translations associated with head rotations, and due to the head translations themselves, the position of the targets relative to the eyes was variable. The horizontal and vertical head rotations, and the calculated linear translations of the left eye arising as a consequence of head movements (rotation or transla-
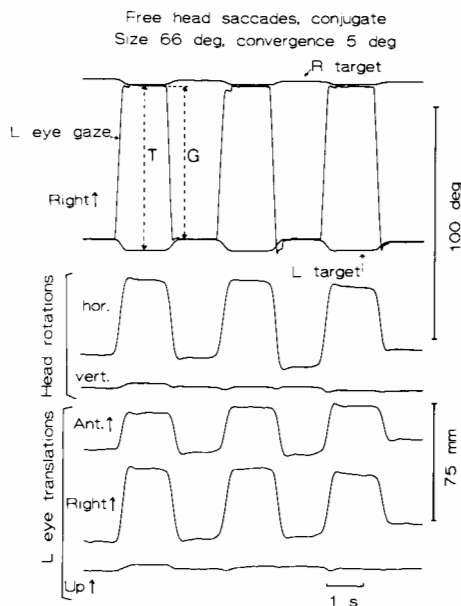

Fig. 2. Recordings of gaze-shifts with the head free (subject Z.P.). The upper panel shows the changes in the gaze angle of the left eye, in relation to the positions of the targets. These targets were earth-fixed, but underwent relative motion with respect to the eye, due to the eye translations associated with head rotations. As a result, the appropriate gaze-shifts (G) were smaller than the angular distance between the targets (T), as observed by the subject before making the saccade. The middle panels show the angular rotations of the head and the lower panels show the linear translations of the left eye, resulting from head rotations and translations.

tion), are shown in the lower panels of Fig. 2. These signals were used to reconstruct the angles, subtended by the two targets at the eye, as a function of time (see Appendix). These target angles, together with the gaze angle of the left eye, are shown in the upper panel of Fig. 2.

The results shown in Fig. 2 are typical for a subject who made large horizontal head rotations. The most salient point of Fig. 2 is the excellent correspondence between the directions of gaze and the two targets (either of which was fixated alternatingly for about 1 s). It should be stressed that the relations between target and gaze, as plotted, are veridical, and have not been improved by any arbitrary shifting of traces. Thus, we can conclude that the accuracy of gaze control with the head free is good. Saccades landed near the targets, with little systematic under- or overshoot, despite the complex kinematic conditions.

COPING WITH THE RELATIVE TRANSLATIONS OF THE TARGET

As can be seen in Fig. 2, horizontal head rotations were made in phase with the gaze-shifts. (Vertical motions were very small). As a result, a gaze shift to the right was accompanied by a translation of the eyes to the right, *i.e.*, a relative displacement of the targets to the left. These relations will generally occur with a freely moving head, and thus the angular size of the gaze saccade (G in Fig. 2), in a natural situation, has to be smaller than the angular distance of the targets (T in Fig. 2), as observed by the subject before starting the gaze-shift. This is very different from the situation with the head fixed, and it is interesting to compare the free and fixed situations with regard to the programming of the gaze-shift.

In Fig. 3, the same gaze shifts as in Fig. 2 are replotted (right panel), along with gaze shifts obtained (in the same session) while the subject was on the bite-board (left panel). The measurement on the bite-board was selected for a similar size of the effective gaze-shift; the target separation was actually larger in this measurement than in the one with the head free. The motions of the left eye are plotted, and the target angles also represent the viewing angles for the left eye. The two targets were positioned symmetrically about the median plane of the subject at 40 deg left and 40 deg right, at a convergence angle of 5 deg; therefore, they were displaced to the right by 2.5 deg when viewed with the left eye, as can be seen in Fig. 3 (and also in Fig. 4). Horizontal head rotations are also plotted in Fig. 3, as well as the rotation of the eye in the head.

With the head fixed, this subject did not shift his gaze accurately between two targets, positioned 80 deg apart (symmetrical about the median plane). This was probably a genuine limitation, as gaze holding in the extreme positions was disturbed by centripetal drift, and secondary saccades did not overcome the deficit in ocular excursion. This restricted oculomotor range may have been one reason why this subject chose to make substantial head rotations when the head was free. In the latter case, saccades were quite accurate. The eye-in-head deflections were much smaller than in the head-fixed situation, and partly of a transient nature, because the head rotation eventually accomplished part of the gaze shift. Most of this head rotation occurred during the later part, or even after, the completion of the gaze shift.

As the head rotation and the associated shift in target location began at about the same time as the saccade, one might anticipate that the gaze shift would initially overshoot the position of the target, and then return to the less eccentric target position. This was not, however, the dominant pattern. Overshoots did occur sometimes, as well as undershoots. On the whole, however, the size of the gaze-shifts was remarkably
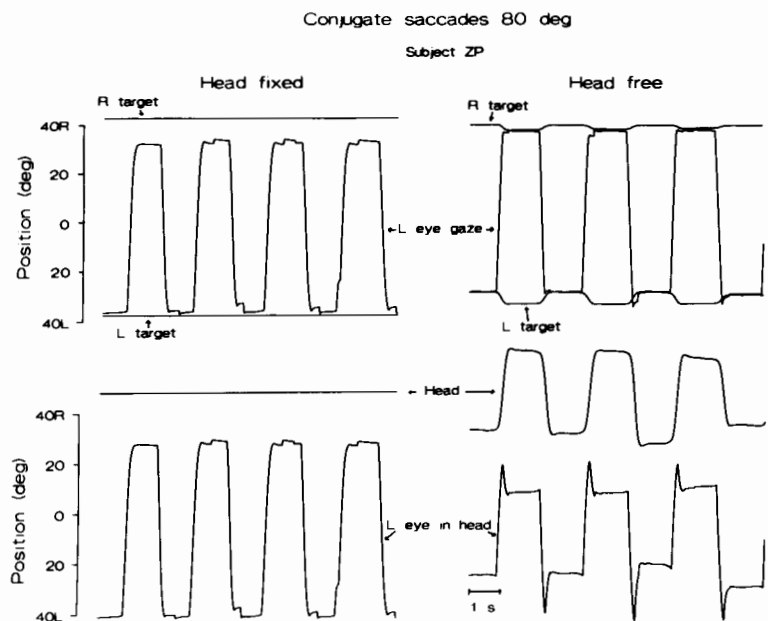
Fig. 3. A comparison of saccades between targets that were separated by 80 deg with the subject on the bite-board (left panels) and with the head free (right panels). Effective target separation was slightly decreased in the free condition, because the subject (Z.P.) leaned somewhat back. Upper panels show gaze and target positions; middle panels show horizontal head rotation (absent in left panels); lower panels show eye-in-head position (identical to gaze in left panels).
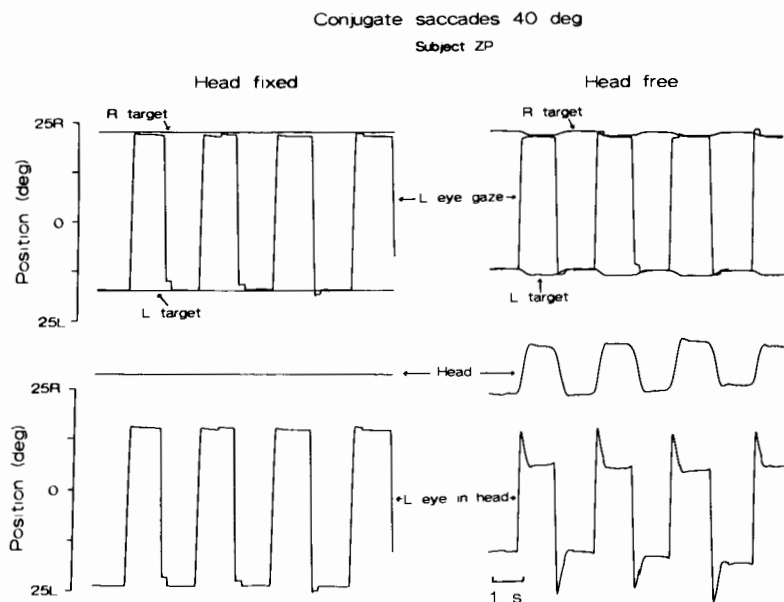

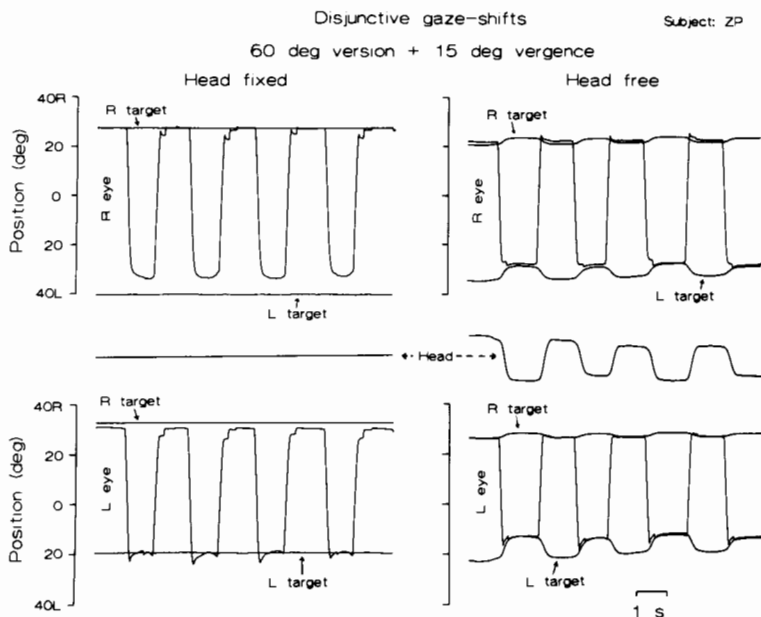**Fig. 4.** Similar to Fig. 3, for gaze-shifts of about 40 deg.

Fig. 5. Similar to Figs. 3 and 4, for disjunctive gaze-shifts. The targets were located 30 deg left and 30 deg right of the median plane. The right and left targets subtended convergence angles of 5 and 20 deg, respectively.

accurate. This was also the case when smaller gaze shifts were required, as is shown in Fig. 4 for saccades of about 40 deg.

The remarkable quality of gaze-control with the head free is even better illustrated in the more general case shown in Fig. 5 for non-isovergent targets. The two targets were positioned 30 deg to the right at 5 deg convergence, and 30 deg to the left at 20 deg convergence. This means that for the right eye the targets were viewed at $30-2.5$ deg to the right and $30+10$ deg to the left of straight-ahead, while for the left eye the viewing angles were $30+2.5$ deg to the right and $30-10$ deg to the left, as shown in Fig. 5, left panels.

With the head fixed, the subject had difficulty reaching the left target (at 40 deg eccentricity) with the right eye, and the right target with the left eye. In comparison, gaze control was excellent when the head was free (Fig. 5, right panels). To a small degree, this was achieved because the subject took advantage of the free condition by moving his head slightly backward, thus reducing the overall distance between the targets by a small amount. To a larger degree, gaze shifts were facilitated by the head rotations. As shown in Fig. 5, right panels, the ocular translations associated with these head-rotations affected especially the angle at which the left, closer target was viewed. Because this target was closer to the left eye than to the right eye, the modulations in left angular target position were even larger for the left eye than for the right eye. The modulation of the viewing angles of the right, more distant, target was much smaller for either eye. These highly complex spatial relations were taken into account with remarkable perfection in the execution of the gaze-shifts. The left eye, in particular, was very well on target, even during the rapid changes in position of the left target. In the interval between the main saccade and the successive, small corrective saccade, the gaze followed the trajec-
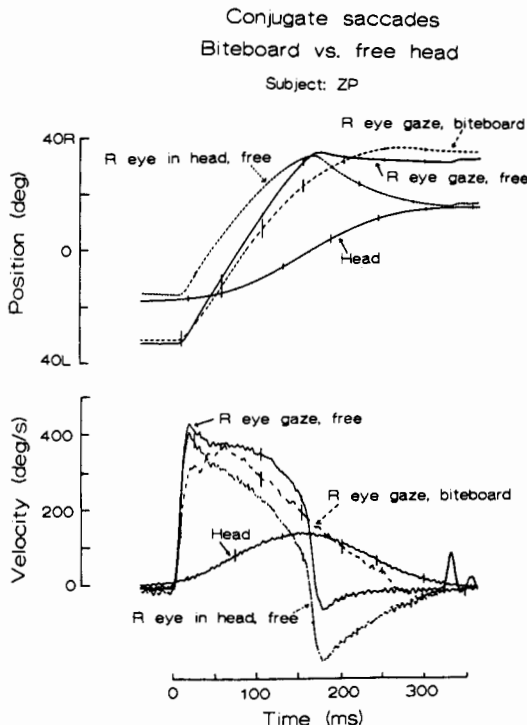
Fig. 6. Averaged position and velocity profiles of about 4 successive saccades. The small vertical bars represent 1 S.D. Saccades of similar size, made with the head free and fixed, are compared. For the free-head saccade, gaze, head and eye-in-head traces are shown. For the fixed-head saccade, only gaze is plotted. Subject: Z.P.

tory of the target faithfully, with only a small, constant, position error, as shown in Fig. 5, bottom of right panel.

This panel, as well as the upper panel in Fig. 6, also show a further effect of the head movements on the relative target angle. When gaze shifts are accompanied by large head movements, as in subject Z.P., the head continues to rotate after the gaze has reached the target, the eye continues to be translated laterally, and the eccentricity of the target continues to be reduced. Thus, in the late phase of such eye-head gaze shifts, gaze has not to be just stabilized, as is usually stated, but has to move back smoothly, to offset the relative, centripetal shift of the target. The accurate gaze shifts show that even during head movements, the gaze control system is continuously aware of the relative positions of the targets with respect to the eyes, and adapts the motor programs appropriately. Under normal behavioral conditions, this would usually require a smaller saccade than indicated by the initial angular separation of the targets, to a degree dictated by the vergence, subtended by the targets and by the pattern of ongoing head movements.

Closer scrutiny of Fig. 5 allows some speculations about how accurate gaze shifts were programmed when the head was free. This figure provides some evidence that, even when a subject is on a bite-board, gaze shifts are planned as if the subject's customary head movements and the associated translations of the target are expected to be part of the gaze shift. Some features of the gaze shifts (seen in the right panel), which are well tuned to the free situation, occurred similarly in the head-fixed situation (Fig. 5, left panels), where they were counterproductive. Note in this respect the undershooting of the right
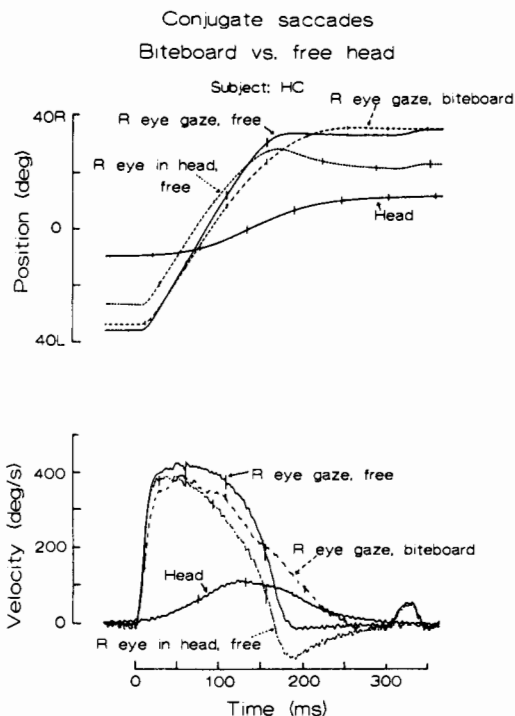
Fig. 7. As Fig. 6, for subject H.C.

eye when moving to the left target, the undershooting of the left eye when moving to the right target, and the rounding of the gaze of the left eye in the intersaccadic intervals near the left target.

If this undershooting represents the incorporation of planned (but unexecuted) head movements, two implications can be drawn. First, accurate control of gaze with the head free relies as much or more on pre-programming of what are expected to be effective eye-head routines, as on complex feedback control systems that attempt to modify programs on-line in order to minimize retinal error. Second, saccades made while the head is on the biteboard provide a distorted picture of normal oculomotor capacities because the saccadic programs take into account head movements that cannot actually be made.

THE DYNAMICS OF SACCADES

Having shown that saccades, made with the head free, are at least as accurate as saccades made with the head fixed, and more accurate when the separation between targets approaches or exceeds the mechanical range of the eye in the orbit, we next looked at the dynamics of the saccades, which should preferably be fast, as well as accurate. We found that free-head saccades were faster and shorter in duration than fixed-head saccades of a similar size. This difference between free- and fixed-head saccades could not be explained by the simple addition of the velocity of the eye-in-head and head-in-space (*i.e.*, cancellation of the VOR) as has been proposed in the past.[15,16,22]

This point is illustrated for 5 subjects in Figs. 6-10, in which the position and the velocity of gaze-shifts of matching sizes (about 70 deg) for the head-fixed and head-free condition are shown. Each profile represents the average of about 4 successive saccades
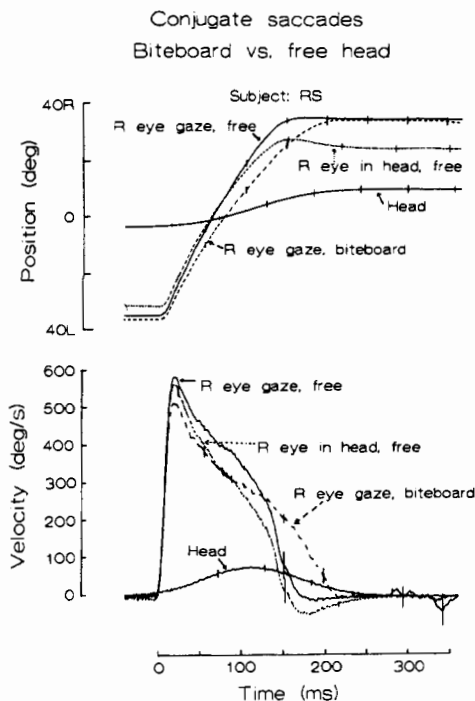
Fig. 8. As Fig. 6, for subject R.S.

in the same direction. The average functions are representative of the individual trials, as shown by the small standard deviations (vertical bars).

It should be emphasized, that we left our subjects entirely free to choose their own preferred combination of eye and head movements. In particular, no instruction was given to maximize the velocity or amplitude of the head movement. Under these conditions, the eye-head synergies used to produce accurate gaze-shifts differed markedly among the subjects. Nevertheless, in all cases the gaze-shifts with the head free were faster and shorter in duration than the gaze-shifts with the head fixed, irrespective of whether head movements were small or substantial. Figures 6–10 show our subjects in decreasing order of magnitude of the head movement they made as a part of their gaze shifts.

Figure 6 shows the position and velocity profiles of the same gaze shifts of subject Z.P. that were shown in Fig. 3. The amplitude of the head rotation was about half that of the gaze shift; only about half of this head movement was accomplished before gaze reached the target.

The relatively large head rotation made it interesting to plot as well the difference between gaze and head movements, *i.e.*, the eye movement with respect to the head. As shown in the top panel of Fig. 6, this signal showed no evidence of saturation, as has been described by others for gaze-shifts with very forceful head rotations.[15] Therefore, the velocity profiles (Fig. 6, lower panel) are not perturbed by any saturation.

These profiles reveal some important trends. A new observation emerging from our material is that the initial acceleration of gaze was substantially higher with the head free than with the head fixed. In the example of Fig. 6, peak gaze velocity with the head free was reached after about 20 ms, while a (lower) peak velocity was reached only after about 60 ms with the head fixed. This difference can not be attributed to the addition of
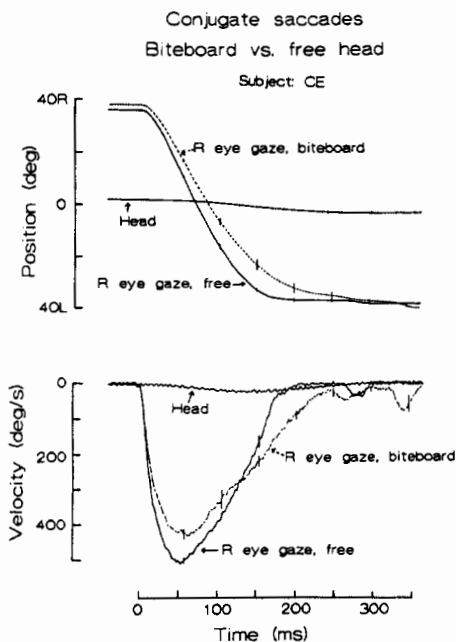
Fig. 9. As Fig. 6, for subject C.E.

the velocity of the eye in the head to the velocity of the head in space (*i.e.*, VOR cancellation) because the velocity of the eye in the head also shows the same early, high velocity peak. The fact is that the head velocity at this early stage of the gaze shift is small and insignificant. Therefore, the increase in peak gaze velocity after freeing the head can not be accounted for by suppression of the vestibulo-ocular reflex. Instead, the saccade dynamics depend on whether the head is free or fixed. It is tempting to say that freeing the head gives an extra boost to saccadic velocity, but it is surely more reasonable to look upon matters in the opposite way, namely, that keeping the head fixed creates an aberrant and unnatural pattern of activation. The oculomotor system does not work naturally, or near capacity, when the head is prevented from moving—the condition employed in most prior oculomotor research.

These trends are seen in the recordings of the other subjects. Subject H.C. (Fig. 7) shows the same increased initial acceleration and higher peak gaze velocity that was found for Z.P. (Fig. 6). Gaze shifts of both subjects were shorter in duration when the head was free. Subject R.S. (Fig. 8) made smaller head movements than the other two subjects, but his peak gaze velocities were once again considerably higher with the head free. And, once more, initial acceleration of the eye in the head was higher in the free than in the fixed condition. Figures 9 and 10 illustrate similar gaze shifts for subjects C.E. and A.P., whose head movements were quite small. Despite the small size of their head movements, the higher initial acceleration and higher peak velocity of gaze in the free condition, compared to on the biteboard, was particularly clear.

The velocity of the eye in the head remained faster when the head was free instead of fixed for about 50–100 ms into the gaze shift. After that time, free- and fixed-head functions reversed so that the velocity of the eye in head was faster when the head was on the biteboard. For the 3 subjects who made significant head movements (Figs. 6–8),
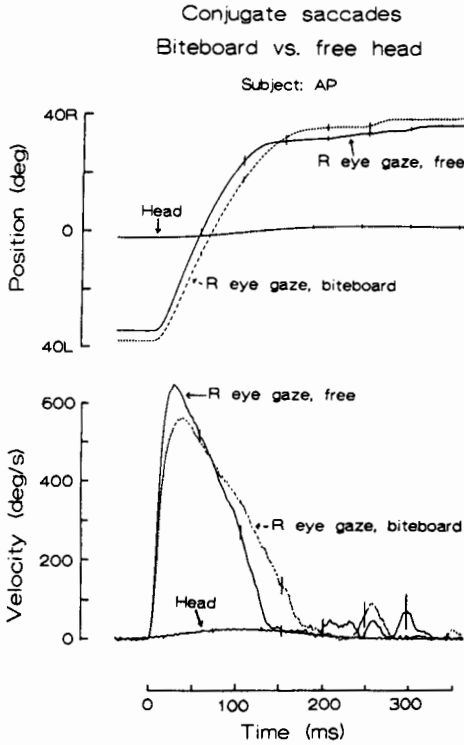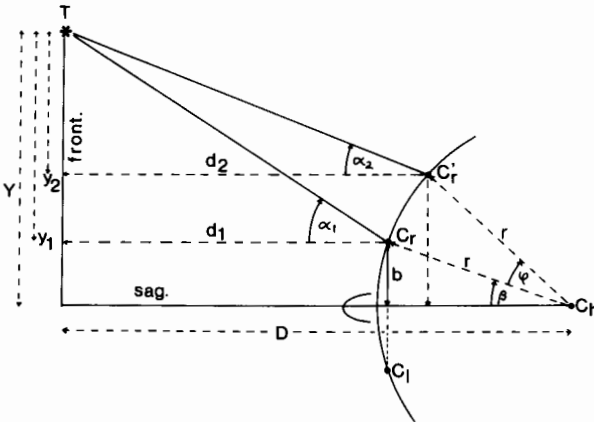
Fig. 10. As Fig. 6, for subject A.P.

Fig. 11. Diagram of the changes in geometric relations between eye and target, associated with horizontal rotations of the head around an earth-fixed center of rotation. See text.

gaze shifts with the head free continued to be faster than gaze shifts with the head fixed due to the contribution of the head movement itself.

The decrease of the velocity of the eye in the head when the head was free appeared to be particularly rapid just after the peak head velocity was reached, when the eye was

still several degrees (5–14 deg in the examples shown) from its final position. This coupling of changes in head and eye velocity profiles illustrates the excellent coordination of these two types of movements that underlies the accurate control of gaze.

What accounts for the near simultaneous reduction in the velocity of both the eye and the head movement during the gaze shift? One possibility is that a mechanism keeping track of the current position of the target directs the eye and the head to slow down as gaze approaches the target. Such a process would be expected to produce accurate gaze shifts because both eye and head movements would stop when the target was reached. Models of eye movement control based on this general idea have been proposed in the past.[15,16,22] In these models the current position of the target is computed, not by analysis of visual signals (believed to be too slow to affect rapid, saccadic, shifts in gaze), but rather by taking into account both the initial retinal position of the target and the non-visual signals coding angular position of the eye in the head and angular position of the head with respect to the body. But the models of this sort that have been proposed would be unable to account for our results because, as noted earlier, an accurate representation of target position in space requires taking into account target translation, which we already pointed out depends on translations of the eye (caused by both head rotation and translation) and on target distance. How such computations might be performed rapidly and accurately, and the sources of information about translations and target distance, are unknown.

An alternative reason why eye and head velocity both decrease as gaze approaches the target is that the decreases were pre-programmed to occur at a fixed time after the start of the gaze shift. Since gaze shifts were of about the same size for a given subject in these examples, the time since the start of the gaze shift and the current gaze-position error are highly correlated. As a result we cannot determine which of these two variables—position error or time—is more important. (See Nachmias[21] for an analogous argument to explain why the probability of making a saccade during fixation is predicted by the time since the last saccade rather than by position error.)

GENERAL CONCLUSIONS

The main result of the present investigation is the demonstration that a complete numerical analysis of binocular gaze in relation to targets can be achieved under conditions in which head movements are entirely unrestrained either by mechanical devices or by instructions. Our subjects shifted their gaze voluntarily, at their own pace, between real, continuously visible targets, much as they would do in normal behavior. Under these conditions, gaze-shifts of about 70 deg were accompanied, in various subjects, by head rotations amounting to between 5 and 50% of the gaze-shift. We looked at both the accuracy and the speed of these gaze-shifts.

We found that free-head saccades were surprisingly accurate. This was true for conjugate, as well as disjunctive, gaze shifts. This accuracy is remarkable once it is appreciated that in a free-head situation target angles are affected by the gaze shifts. When the head can move freely in translation and rotation, the ocular centers of rotation are not fixed in space. In general, a combined eye-head movement will translate the eye towards the target, and as a result the effective angle of gaze rotation to reach the target becomes smaller than the initial retinal eccentricity of the target, as perceived before the gaze-shift. Our results show that natural gaze control takes such effects into account very effectively.

We also found that gaze-shifts with the head free were appreciably faster, and shorter

in duration, than gaze shifts of the same size with the head fixed. The magnitude and timing of this enhancement of gaze velocity, as well as its lack of correlation with the actual head velocity, preclude an explanation of this phenomenon in terms of an inhibition of the VOR.

The enhancement of gaze acceleration when the head is freed may be best stated by saying that saccades made with the head restrained tend to be slowed because the natural tendency to move the head along with the eye must be inhibited. This natural tendency has been demonstrated by the co-activation of eye and neck muscles during saccades in cat,[24] monkey[19] and man.[2] Human subjects become acutely aware of this co-activation when they experience the strain of neck muscles while making saccades on the biteboard —a phenomenon particularly apparent when subjects try to make rapid sequences of saccades.[27] It seems plausible, given the natural coupling of head and eye, that attempts to resist the natural tendency to move the head and the eye together could inhibit saccadic commands to some degree. We found evidence for such inhibition in the enhancement of gaze velocity of the two subjects who made only very small head movements during gaze shifts with their heads free, showing that it is indeed the effort made to keep the head firmly in place, rather than the magnitude of the commands generated for moving the head, that is responsible for the inferior velocity characteristics when the head is restrained mechanically.

APPENDIX

1. The relation between head-yaw and target angle

Simplified solutions, amounting to a correction-factor between eye and head angles, to make them commensurate with respect to targets at a constant distance, have been used previously.[4,6,25] Although such approximations may offer empirical solutions in specific situations, they do not deal adequately with the problem of linear displacements (translations) of the eyes. Because the eyes are located about 10 cm anterior to the rotational axis of the head, each horizontal head rotation results in a sideways and antero-posterior translation of the eyes. These translations, and the concomitant changes in target angle, are not simply proportional to head rotation.

From the diagram shown in Fig. 11, the correct relations can be easily derived for a (fictitious) situation in which the head rotates only in the horizontal plane around a center of rotation C_h, which is fixed in space. We take this point as the origin of a 2-D Cartesian coordinate system in the horizontal plane. As a result of head rotation, the ocular centers of rotation, C_l and C_r, describe a circle around C_h, with radius r. With the head straight, the spatial and head sagittal planes coincide; C_r lies at distance b (half the baseline) lateral to the sagittal plane, and the position of target T in space is described by a distance D anterior to C_h, and a distance Y lateral to the spatial sagittal plane (rightward positive). The angle subtended by C_r at C_h with respect to the head sagittal plane is β; the angle through which the head rotates from the straight position is ϕ (rightward positive), and the angle subtended by T at C_r (with respect to the spatial sagittal plane) is α. The gaze angle of the right eye is also measured with respect to the spatial sagittal plane, and should, of course, equal α for foveation. With the head

straight, C_r is located at $b = r \sin \beta$ to the right of C_h, and $r \cos \beta$ anterior to C_h. Thus, we can write for the target angle α_1:

$$\tan \alpha_1 = \frac{Y - r \sin \beta}{D - r \cos \beta} \tag{1}$$

With the head rotated through ϕ, the general solution becomes:

$$\tan \alpha = \frac{Y - r \sin (\beta + \phi)}{D - r \cos (\beta + \phi)} \tag{2}$$

2. Calculation of target angles with free head movements

The following solution was worked out by one of the authors (Pizlo). An earth-fixed 3-D Cartesian coordinate system is defined with its origin in M, the midpoint between the ocular rotation centers (assumed to lie 13.5 mm behind the front of the cornea) when the subject is in the standard position on the biteboard. The positive z axis points upward; the positive y axis points to the right; the positive x axis points straight ahead (from the subject's viewpoint). These coordinates are measured with the sparker system (in mm); the arbitrary offsets in the measured values are removed by subtracting values obtained, in a first calibration measurement, with the sparker positioned at the position of M, from all measurements. In a second calibration measurement, the subject is on the bite-board in standard position, with the sparker mounted on his head. In this position, we call the coordinates of the eye: xe_0, ye_0, ze_0; the coordinates of the sparker point are: xh_0, yh_0, zh_0. The distances from the sparker to the eye are defined as:

$$x_0 = xe_0 - xh_0$$
$$y_0 = ye_0 - yh_0$$
$$z_0 = ze_0 - zh_0$$

Because of the standard alignment, xe_0 and ze_0 are equal to zero, while ye_0 is $+b$ for the right eye and $-b$ for the left eye (b being half the baseline, or interocular distance). Thus, $x_0 = -xh_0$; $z_0 = -zh_0$; y_0 (right eye) $= b - yh_0$; y_0 (left eye) $= -b - yh_0$. These parameters have to be determined separately for each session.

To calculate the ocular xe_1, ye_1, ze_1 positions during free head movements, the instantaneous xh_1, yh_1, zh_1 position of the sparker point is taken as the (fictitious) center of rotation about which the head is rotated by the measured head angles. Then, the coordinates calculated from this rotation are added to the instantaneous coordinates of the sparker xh_1, yh_1, zh_1. By doing this we reconstruct both translational and angular components of the head position in space. We do not need to know the parameters of the *actual* center of rotation of the head.

In the Maryland phase-sensitive angular measurement system, vertical angles are measured as elevation (λ), following Helmholtz's convention, while the horizontal angles are measured as longitude (ϕ), following Fick's convention. In the current measurements we neglected head roll (assuming that it was zero) and we treated the head rotations in Fick axes. For this purpose, elevation (λ) is converted to latitude (v) by the following relation:

$$\tan v = \tan \lambda^* \cos \phi \tag{3}$$

The spatial coordinates of the eye are then calculated from the following equations:

$$xe_1 = x_0{}^* \cos v^* \cos \phi - y_0{}^* \sin \phi - z_0{}^* \sin v^* \cos \phi + xh_1 \tag{4}$$
$$ye_1 = x_0{}^* \cos v^* \sin \phi + y_0{}^* \cos \phi - z_0{}^* \sin v^* \sin \phi + yh_1 \tag{5}$$
$$ze_1 = x_0{}^* \sin v + z_0{}^* \cos v + zh_1 \tag{6}$$

Notice, that y_0 is different for the right and left eye.

The spatial coordinates of the target(s), xt_1, yt_1 and zt_1 are measured in the same

Cartesian coordinate system. The angles of elevation (λt_1) and longitude (ϕt_1) subtended by the target at the eye can then be calculated from the following tangential relations:

$$\lambda t_1 = \arctan\frac{zt_1 - ze_1}{xt_1 - xe_1} \tag{7}$$

$$\phi t_1 = \arctan\frac{yt_1 - ye_1}{xt_1 - xe_1} \tag{8}$$

Notice, that these target angles are commensurate with the gaze angles, as measured in the Maryland system, and can thus be directly compared.

The calculations described above were done off-line, by software developed by another of the authors (Van der Steen).

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