Preview control of gaze saccades: Efficacy of prediction modulates eye–head interaction during human gaze saccades

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Healthy human subjects made orienting saccades towards visual target stimuli, either with the head fixed or during intended time optimal head movements. Four experimental paradigms were used to study the influence of target predictability on eye-head coordination. They represented different sequences of horizontal target steps, that were varied in amplitude, direction and frequency. In some subjects midflight perturbations of the active head movements were applied to examine the intrasaccadic vestibulo-ocular reflex (VOR). In coordinated gaze saccades, latencies and dynamics of the eye saccade and the additional head trajectory demonstrated specific task-related changes with respect to the head fixed condition. Highly predictable target steps result in the relatively earlier onset of the head movement and an increase of the intrasaccadic head contribution to the overall gaze displacement. Differences in the level of VOR suppression became significant when gaze amplitudes exceeded 60°. Consequently, an effective speed up of large gaze saccades was found with increased target predictability. We concluded, that eye–head coordination during human gaze saccades underlies high level preview control mechanisms. A parametric modulation of the intrasaccadic VOR maintains gaze accuracy, although the actual contribution of the more flexible head motor system varied, depending on gaze amplitude and prediction. The efficacy of preview control depends on interaction of these factors. [Neurol Res 1993; **15**: 417–432]

Keywords: Coordinated gaze saccades; vestibulo-ocular reflex; prediction; preview control; human

INTRODUCTION

A coordinated gaze saccade is an orienting movement of the eyes in space to fixate an object of interest. It is performed by a fast saccade and a synkinetic head movement. When the visual axis is in line with the new target position, a counter-rotatory eye movement compensates for further head movements to stabilize the target image on the retina[1]. In the first experiments on monkeys by Bizzi and coworkers, the accuracy and the kinematics of these combined eye–head gaze shifts were similar to those of a corresponding saccade when head was restrained. They proposed, that the vestibulo-ocular reflex (VOR) plays a dominant role in the maintenance of gaze accuracy during saccades and the following CEM[2–4]. In a natural environment, human saccades without additional head trajectories are generally limited to amplitudes of 15° or less[5]. Beyond that range, head movement contribution increases progressively with target amplitude.

In most of the studied species, the saccade generally precedes the synkinetic head movement, when natural gaze shifts are triggered by randomized sequences of target steps within the oculomotor range[6–10]. The delay of head is caused by the different dynamic properties of eye and head. Saccades require a simple effort of the very fast extra-ocular muscles, whereas the head rotation lags due to its large visco-inertial load for the comparatively slow-moving neck muscles[2,11–14]. However, as demonstrated by Stark[14] and later studies, head fixed saccades underly the influence of target predictability. Bizzi *et al.*[7] described a lead of the head trajectory with respect to the saccadic eye movements, when a gaze saccade anticipated highly predictable target steps. Zangemeister and Stark[11–13,16–19] obtained variable onset times of eye and head movements in human gaze saccades, depending on several interacting factors, such as target step predictability and frequency, target step amplitude, the subject's intention, verbal and visual feedback and given neurological deficits. They found, that head contribution to the resulting gaze shifts varied depending on these factors. On the contrary, Barnes[6] reported a constant linear correlation between gaze amplitude and concomitant head velocity, when randomized target patterns were exclusively used.

In the following time, two closely related questions were of major interest in research on underlying mechanisms of eye–head coordination: Does the VOR provide a reflexive control mechanism during the gaze saccade (intrasaccadic VOR) and do eye and head motor systems share a common neuronal control signal, so that they are always tightly coupled during saccadic gaze movements?

Based on the oservation of Morasso *et al.*[3], it was orignally presumed, that gaze velocity depends on the saccadic controller signal, because a VOR gain, operating close to unity, is compensating for the

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head motor system was recently observed by Ron and Berthoz[41] when they used gaze shifts in response to double-step target patterns. The influence of tightly coupled control signals of eye and head premotor circuits on brainstem level may be overridden by the output from high level preview control circuits, when prediction becomes more effective.

Guitton *et al.*[27] examined the effects of prediction during gaze saccades in trained cats. The hungry cats made orienting gaze shifts towards visible or expected food targets (predictive gaze saccades). The expected targets occasionally did not appear, so that the intention to predict was influenced by negative feedback effects. Their results on predictive saccades of cats were different to our findings in humans. In cats, the relative contribution of eye and head to the overall gaze displacement remained independent from prediction. It was only determined by gaze amplitude. Peak velocity of visually guided saccades always exceeded those of predicted saccades with head fixed as well as free to move. They also found a close covariance of eye and head latencies, irrespective of the level of prediction. From these observations we can infer that the efficacy of preview control of coordinated gaze saccades appears to be highly variable between different species; in particular, it seems to differ between laboratory animals and humans for seemingly comparable conditions. The dominance of proposed gaze control neurons in the superior colliculus[27,37] and the ponto-medullary reticular formation[31,34] in the cat may be less affected by previous control in these animals than it does in man.

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saccades remains a matter of discussion. The linear summation hypothesis[3,8,49] failed when gaze amplitudes exceeded about 30° in humans, for passive as well as active head movements[9–11,16,17,20,26].

Evidence of an intrasaccadic VOR suppression in larger gaze saccades were also found in cats and monkeys[21–24]. Some authors proposed a complete inhibition of the VOR using the saccadic eye movement[20,23]. Roucoux *et al.*[40] found an inactive VOR during combined eye–head shifts, that were triggered by electrical stimulation of the cat's superior colliculus. However, in most previous experiments and in our study, some compensatory slowing of the saccade occurred during active head movements, whether the head was perturbed or not. Thus, some counteractive short latency mechanism was still working during saccades and kept up the gaze accuracy.

Zangemeister and Stark[26] proposed that the intrasaccadic VOR gain was gradually modified depending on the underlying gaze strategy. Lisberger[51] made analogous observations in monkeys, while he examined the effect of head or target perturbations during smooth pursuit. He found evidence for a short latency VOR suppression and introduced the concept of a parametric modulation of the VOR. McKinley and Peterson[52] reported, that VOR gain during smooth pursuit underlies predictive control mechanisms. Saccades, however, present a completely different type of eye movement. In Lisberger's experiments, short latency VOR suppression became most evident when target velocity reached the upper limits of the smooth pursuit system. He noted that the similarity of conditions that elicit suppression of the VOR during smooth and saccadic gaze shifts suggested a common principle of organization. Parametric modulation of the intrasaccadic VOR appears to be linked to the underlying prediction control mechanisms of gaze saccades.

Preview control of gaze saccades

Humans are capable of suppressing their VOR by mental effort in darkness while fixating an imaginary target[52–55]. These results demonstrated the high level, predictive control of the VOR. Although sinusoidal targets are predictive, McKinley and Peterson proposed that responses to sinusoidal head movements were independent of prediction. Head latency and velocity during coordinated gaze shifts are also modified by the subject's intention and vigilance[11–13,17,20,26]. In our experimental setting, we used verbal feedback to enforce the subject's intention towards time optimal gaze saccades. All our subjects confirmed, that they consciously recognized their changing ability to anticipate the target steps in the predictable target paradigm. Efficacy of prediction also depended on the subject's experience. When predictable target tasks were repeated, the adaptation interval that was required to switch from visually guided to predictive gaze saccades dropped markedly: from first to second run of predictable 80° steps, the time of the first predictive saccade dropped from 12.2 sec to 5.3 sec in a typical example. The parametrics of gaze saccades in response to highly predictable stimuli were obviously modified by the preprogrammed output of high level control systems.

The term 'preview control' refers to this aspect of coordinated gaze saccade control. In studies on optimal control of robots, Sheridan[56] used this term to describe models of a particular time window of early anticipation. More recently, Brown[57] tested robot simulation models of different types of gaze control systems, including coordinated 'rapid gaze shifts'. He found, that predictive control mechanisms were a key to overcoming the problems of stabilizing the interacting closed loop multi-rate control systems with different time delays. Our hypothesis of preview control of gaze saccades connects high level estimation and prediction of target dynamics, central preprogramming of feed-forward signals to lower motor control subsystems, and parametric VOR gain modulation. According to computer simulations of experimental data using a nonlinear sixth order reciprocally innervated model of the eye mechanical system, Winters *et al.*[25] showed two nonlinear mechanical interactions of saccades and VOR driven eye movements triggered by sinusoidal predictive head movements that depended on initial eye velocity and initial eye eccentricity. We found that initial eye velocity and relative peak eye velocity during gaze saccades increased with prediction. Further, Winter *et al.*[25] postulated a partial inhibition of the VOR controller signals by the dominating saccadic signal. They proposed, that a high level 'predictive' capacity or 'local feedback' to control the saccadic eye magnitude may not be necessary, although they did not intend to explain all nonlinearities of the saccade-VOR interaction through peripheral dynamics.

Existing detailed gaze feedback models of eye–head coordination neglected feed-forward commands from cortical or cortico–cerebellar subsystems. Thus, it was difficult to integrate predictive changes of eye–head interaction into their schemes. Although recent research concentrated on the cortical control of the saccadic system[58], the morphological structures encoding preview control signals and the associated pathways remained incompletely identified. Predictive head-fixed saccades in monkeys seem to depend on an intact function of the frontal eye field[59].

The dominant influence of the head motor system on time optimization of predictive saccades has been described previously. Zangemeister and Stark[13] reported that the head motor system responds more flexibly to different levels of target predictability than the saccadic system. Compared to visually guided saccades, that showed almost equal high level control delays of +120 msec for eye and head, head system high level delay dropped to −230 msec with anticipation, whereas high level eye delay decreased only to −115 msec. Our study showed variable latencies of eye and head as well as differential head contributions to gaze saccades as a function of prediction within similar ranges. These findings suggested, that previous control circuits are capable of sending independent control signals to the eye and head premotor circuits. Dissociated preview control commands seemed to be contradictory to the hypothesis of a common gaze control mechanism[27] and to the evidence of a tight coupling of the control signals of human eye and head motor systems, that were previously described with head fixed[32,33] as well as free head movements[3,6,49]. However, the visual stimuli used in these studies on humans were randomized in frequency, in amplitude, or in both. Therefore, the efficacy of preview control was likely to be very limited. A dissociation of eye and fixed saccades. This speed up of saccades was combined with reduced gaze saccade durations, so that accuracy remained almost the same. When head trajectory was perturbed the initial gaze saccades occasionally undershot. In these cases, re-acceleration of the released head was accompanied by a rapid eye movement, that drove the visual axis quite accurately towards the reappeared target. It remained uncertain, whether this secondary eye shift depended on central reprogramming or represented a vestibulary triggered quick phase, as presumed by Guitton and colleagues[9,21]. The results of head perturbation experiments were generally less suitable to assess the effects of target predictability, because the sudden perturbation, an unpredictable external factor, clearly interfered with the predictive eye–head control system. Prediction became less effective with head perturbations, even when highly predictable target sequences appeared. This led to more variable head and eye latency patterns as well as large standard deviations in the statistical assessment of the kinematics.

Effects of gaze amplitude

Many previous authors reported, that contribution of active head rotations to the coordinated gaze saccade is correlated to gaze amplitude[1,3,5,6,8–13,17,20,21,23,24,27].

In this study, relative earlier head onset with respect to the eye was obtained in larger gaze saccades, as well as increased head magnitude to eye magnitude ratios, increased head velocities during the saccade and evidence of an increased level of intrasaccadic VOR gain suppression. In small gaze saccades of 20° amplitude, no statistical change of head dynamics occurred with prediction.

Corresponding to our hypothesis, that predictive modification of eye–head interaction depends on the increase of the relative head contribution, anticipatory changes in response to higher levels of target predictability were more effective with large gaze shifts. Lead of the head trajectory in the predictable target paradigm was maximal in gaze saccades of 80° amplitude. The paradigm related differences of head velocity and peak gaze velocity during gaze saccades correlated with gaze amplitude. In the statistical assessment of intrasaccadic VOR gain, some subjects showed VOR suppression during gaze shifts of 40° amplitude. However, relevant differences of VOR suppression between the paradigms were only found in saccades exceeding 60° amplitudes. The relatively small head contribution during gaze saccades of 20° amplitude, that was obtained in all paradigms, resulted in almost indistinguishable gaze dynamics between head free and head fixed condition. Summarizing these observations, the relative head contribution and its effect on resulting gaze velocity depended at least on two factors: gaze saccade amplitude and prediction.

Parametric modulation of the intrasaccadic VOR

In our experiments on unperturbed gaze saccades, we used the comparison of head fixed saccades and eye–head gaze saccades to assess the intrasaccadic VOR gain. Laurutis and Robinson[20] discussed the problem, that eye shifts are limited by the oculomotor range and that eye velocities of centripetal saccades were faster than centrifugal, when they approached more peripheral positions in the orbit. We limited target movements to an amplitude range of +/−40° away from the central position. That was well within the subjects oculomotor range when head was fixed. We used the same range for all paradigms, so that mechanical limits of the eye did not explain different kinematics of the head fixed saccades. In the head free condition, eye saccades generally started centripetal saccades from more peripheral positions in the orbit, when highly randomized trials were applied. This was caused by relatively smaller amplitudes of the head movement. According to previous results[20], one might expect the fastest gaze saccades in the randomized paradigms, but our results demonstrated the opposite effect. Thus, mechanical limitation of the eye movements did not plausibly explain different levels of VOR gain suppression.

Pulaski *et al.*[48] found a progressive saturation of the human VOR gain, when concurrent head velocities during constant rotations exceeded 350°/sec. We found different head velocities during the saccade, depending on the given paradigms. That rose the question, whether the predictive modification of the VOR gain was caused by saturation phenomena. VOR gain data of two of our subjects (T.H., R.D.) may have been influenced by this effect. During predictive saccades of 80° amplitude, their mean head velocities at the time of peak gaze velocity were 414°/sec and 420°/sec, respectively. However, we also found significant modulation of the intrasaccadic VOR gain during much slower head trajectories like mean head velocities of 223°/sec in predictive and 187°/sec in visually guided saccades (P.M.). Additionally, we found clear evidence of VOR gain suppression during perturbed gaze saccades, although perturbation velocities rarely exceeded 170°/sec. Thus, VOR saturation effects were likely to be quite limited during gaze saccades with active head contribution.

Previous results concerning human VOR gain during gaze saccades, showed differences of the experimental protocol, such as variable levels of target randomization, that were associated with certain results of VOR assessment, that demonstrate the importance of prediction. Previous experiments[20] supported maximal prediction, because they advised their subjects to make self paced saccades between fixed target positions. Corresponding to our hypothesis, they obtained very accurate, fast gaze saccades with a highly reproducible intrasaccadic VOR suppression. In two subjects, a calculated VOR gain of 0.17 (+/−0.21) and 0.11 (+/−0.2) was obtained in gaze saccades of 40° amplitude, while using head perturbations. Guitton and Volle[9] found significant interindividual and intratask variability of the VOR gain during gaze saccades ranging from 30° to 160°. Here, target stimuli patterns always included randomized frequencies. Pelisson *et al.*[10] randomized the direction of target steps and their amplitudes varied between 20° and 40°. Their results were difficult to compare with the previously mentioned studies because they modified the accompanied head trajectory either by driving it passively or by verbal commands of the experimenter. However, maximal head velocities of three subjects in the 'natural head free-condition', which was comparable to our study, were only slightly faster than those of head fixed saccades. The role of the VOR during coordinated gaze

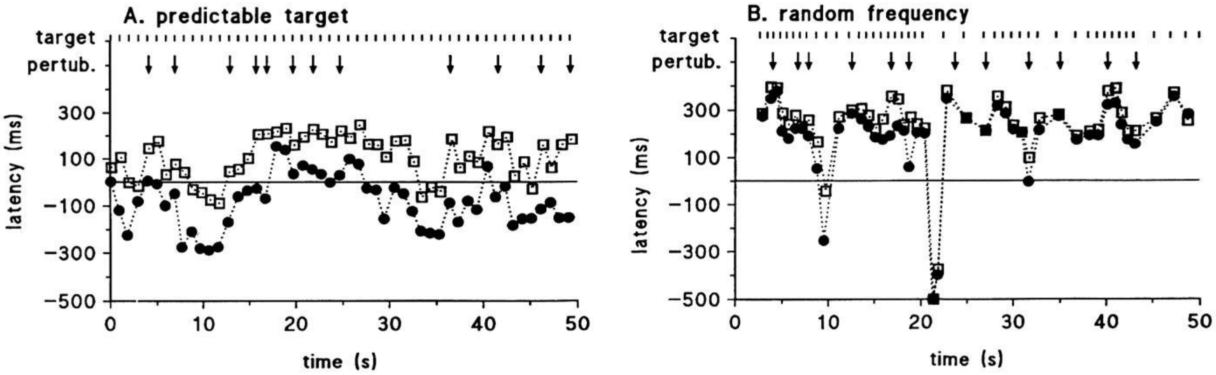

Figure 11: Head movement perturbation effects on eye (open squares) and head (solid circles) latencies during a sequence of 80 target steps (duration of 50 sec; subject S.H.). Target steps are marked by tickmarks in the uppermost row and the small arrows represent perturbation onsets. Compared to unperturbed gaze saccades (*Figure 3*), eye–head latency patterns became more irregular when perturbations were applied. Sudden perturbations were often followed by an immediate increase of eye and head latencies. Head trajectories still preceded the saccade, when the target steps remained highly predictable (**A**). In the random frequency paradigm, (**B**), some predictive saccades were obtained when the frequency suddenly increased after a number of short target step intervals, because some subjects tended to anticipate when subsequences of pseudo-predictive target steps appeared

Table 3: VOR gaze assessment of the perturbed gaze saccades given in *Figure 10*

Panel	ΔH′	ΔG′	VOR
A	−84.67	−56.11	0.34
B	−158.66	−46.82	0.70
C	−101.91	−61.24	0.40
D	−157.18	−67.86	0.57
E	−192.31	−179.80	0.07

For each saccade (A–E), the mean gaze and head velocity was compared to a corresponding unperturbed saccade. Mean velocities were calculated for the duration of the perturbation (max. interval = 200 msec). H shows drop in head velocity and G refers to synchronous decrease in the gaze velocity. An estimation of the VOR gain during the saccades is given in the column (VOR = 1 − deltG′/deltH′).

saccades depended on the control of several interactive factors.

Contribution of the concomitant head movement

In head fixed condition, predictive saccades were significantly slower than visually-guided ones. This result was in line with previous reports[42,44,45]. Based on experiments using gap paradigms, Fischer and Ramsberger[46,47] limited the minimal latency of visually guided saccades in humans to about 100 msec. We used this limit of 100 msec to separate predictive saccades from visually guided. Van Ginsbergen and Smit[45] found shorter dynamic transition times and precluded that a peripheral visual stimulus could speed up an already preprogrammed saccade. In all these studies, predictive saccades with head fixed, that clearly anticipated the target reappearance (gaze latency <0.0 msec), were significantly slower than visually guided saccades. This was in agreement with our experiment. However, contradictory findings occurred in head free condition. Here, peak velocities generally reached maximal values in predictive gaze saccades with respect to visually guided gaze shifts when gaze amplitude exceeded about 40°. It could be concluded, that the time optimization of coordinated gaze saccades was not only caused by predictive changes of saccadic commands, as proposed by the classical linear summation hypothesis[3]. Instead, it mainly depended on the increased contribution of the additional head movement, as previously reported[9–13,17,20,22].

The effective contribution of head movement on the resulting gaze saccade was determined by three aspects: (1) the relative onset time of the head trajectory, (2) its dynamic characteristics and (3) the simultaneous gain of the VOR. In this study we made several attempts to quantify these factors in order to assess the influence of varied target predictability levels.

Predictive changes of eye–head interaction

The head generally precedes the saccadic eye movement in response to a sequence of highly predictable visual stimuli. This predictive type of eye–head latency pattern was first studied by Bizzi *et al.*[2] in monkeys and Zangemeister and Stark[11–13,17] in man. Due to its earlier onset and forced acceleration, the head movement reached higher velocities during predictive saccades. No such effects were found in the highly unpredictable paradigms, that used randomized sequences of target positions. Here, large target steps were often followed by multiple step like saccades combined with small head movement contribution. Suppression of the intrasaccadic VOR increased with the efficacy of prediction, at least in large gaze saccades. Predictive modification of the VOR suppression was quantified in gaze saccades of 80° amplitude and supported by descriptive results in head perturbation experiments. Unfortunately, statistical calculation of the VOR gain in highly randomized tasks failed, because of problems with the method. Single, large gaze saccades in the random amplitude and the all random paradigm tended to be as fast as corresponding saccades with head restrained. Thus, we found no evidence of a time optimization of gaze saccades in the most unpredictable condition.

In unperturbed saccades of the predictable target paradigm, increased head contribution resulted in faster peak gaze velocities with respect to corresponding head

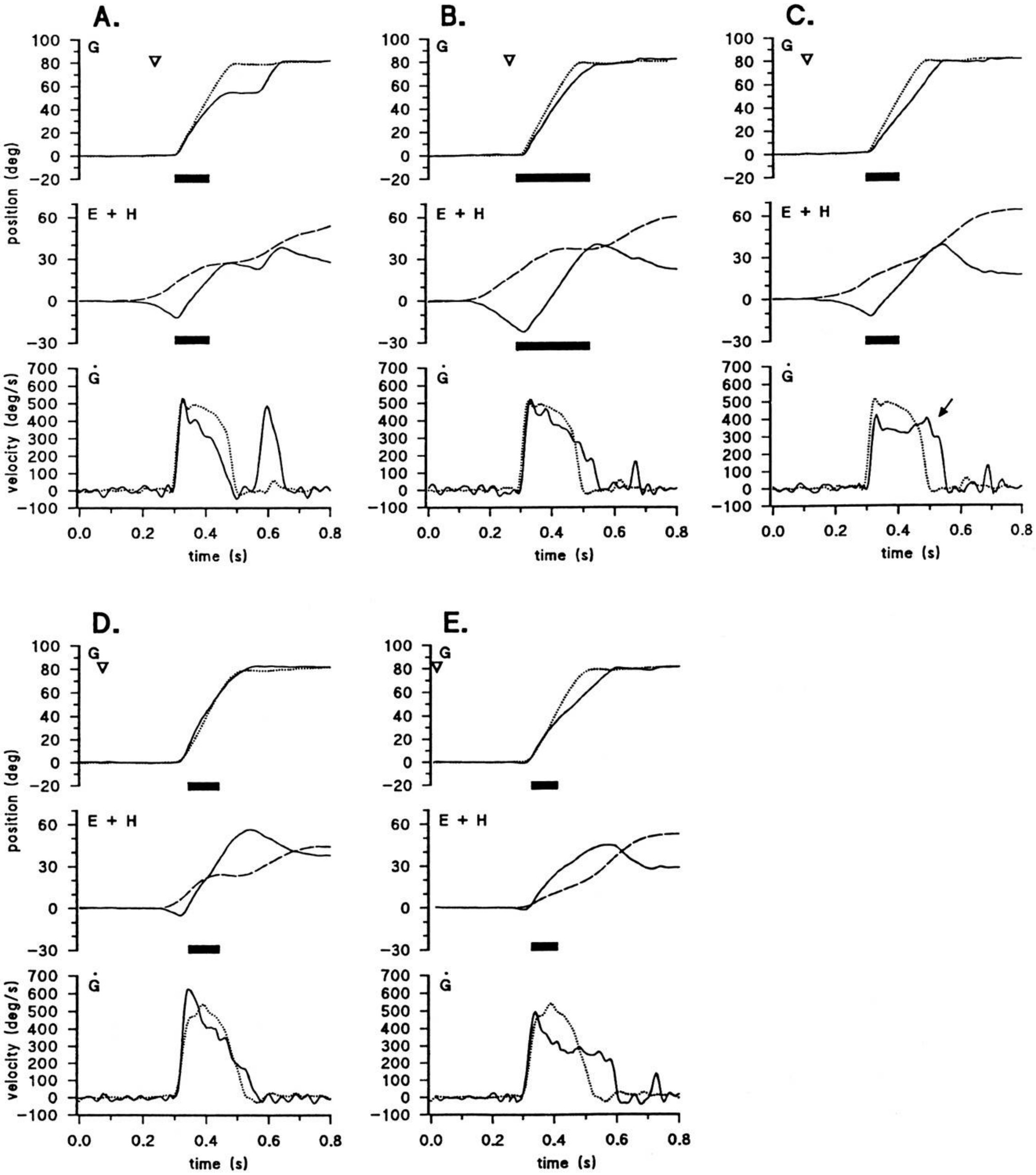

Figure 10: Typical gaze saccades during head perturbations in the predictable target paradigm (**A–C**) and the random frequency paradigm (**D,E**). The reappearance of the 80° target step is marked by a triangle. Thick bars represent the duration of perturbations. Upper panels show gaze position, middle panels the eye (solid) and head (dashed) position and lower panels present the corresponding gaze velocity profiles. Dotted traces represent an average of unperturbed gaze saccades ($n = 10$)

In the perturbed gaze saccades of the random frequency paradigm, an increased variability of the estimated intrasaccadic VOR gain occurred in all subjects. In a minority of all saccades, the initial drop of gaze velocity was compensated by a compensatory eye movement, so that the resulting gaze duration was approximately equal to corresponding unperturbed saccades (*Figure 10D*). In these cases, the intrasaccadic VOR gain was obviously comparatively high. However, most saccades also showed a significant drop of gaze velocity, that was caused by the slowing through head perturbation (*Figure 10E*).

DISCUSSION

Our experiments demonstrated, that different levels of target predictability led to adaptive changes of eye–head interaction during horizontal gaze saccades. Successful prediction enabled human subjects to speed up the process of visual target refixation with high accuracy. This predictive time optimization of gaze

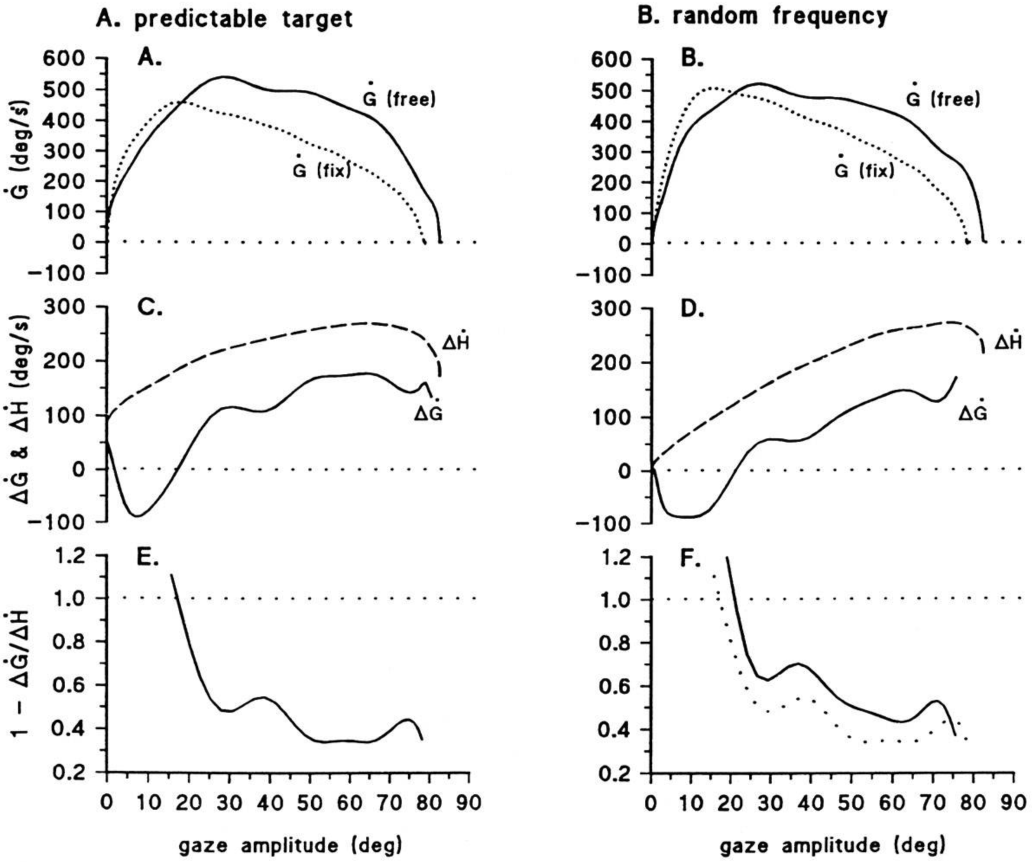

Figure 9: Gaze amplitude functions of 80° gaze shifts. **A,B**: gaze velocity profiles of head fixed saccades (dotted lines) and coordinated gaze saccades (solid lines) are plotted as a function of their synchronous amplitudes. Same averaged data of subj. A.L. were used as in *Figure 1*. **C,D**: show the calculated difference of gaze velocities (deltG') between head fixed and head free condition and the corresponding head velocity (deltH') in head free condition. In **E,F**, these data are transformed by the mathematical function 1-deltG'/deltH') which has been used by several previous authors[10,20] to assess the intrasaccadic VOR gain. Dotted line in F shows the corresponding result of the predictable target paradigm (E). The relative skewness of head fixed saccades resulted in negative values of deltG'-data (C,D) for the first 15° to 20° amplitude. However, deltG' increased with increasing head velocities (deltH'), i.e., the intrasaccadic VOR gain was reduced to some extent either in large predictive gaze saccades (predictable target) or visually guided gaze saccades (random frequency). The calculated VOR gain (E,F) demonstrated increased VOR gain suppression in the predictive task with respect to the random task, i.e., the efficacy of prediction modified the intrasaccadic VOR gain

change the gaze accuracy (*Figure 10C–E*). When active head movements were perturbed in the predictable target paradigm, a successful anticipation of the target became more difficult. The number of visually guided gaze saccades increased and the accuracy of predictive saccades slightly impaired. For example, in subject D.S. mean amplitude of corrective saccades decreased from 4.2% in unperturbed shifts to 12.7% in the perturbed ones. Statistically, these differences were not significant. The interval between eye and head movement onset in perturbed gaze saccades was more variable when compared to non-perturbation experiments (*Figure 1*).

During predictable target steps, the head trajectory preceeded the saccades even when perturbations were used. When perturbations occurred early during the leading head movement, the head–eye latency interval was often prolonged, so that saccade onset occurred more than 100 msec after the target reappearance (*Figure 10C*). The delayed saccade was accompanied by a secondary head movement after its release. Due to the variability of eye, head and perturbation latencies, it was difficult to estimate the influence of prediction on the exact interactive dynamics of the resulting gaze saccade (*Figure 10*). A quantification of the intrasaccadic VOR gain in perturbed gaze saccades did not show significant changes between the two paradigms, mainly because of the large standard deviations (*Table 3*). However, examination of clearly predictive gaze saccades (*Figure 10A, B*) generally demonstrated, that a head movement deceleration, due to the perturbation onset, was followed by a drop of gaze velocity. A notable VOR-related increase of eye velocity occurred in some predictive saccades (*Figure 10C*, marked by an arrow), but it was generally not fully compensatory. In the majority of predictive saccades, the efficacy of compensatory eye accelerations was very limited during the perturbation. Instead, a fast corrective saccade (or reflexive quick phase), following the released head, drove gaze accurately towards the new target position (*Figure 10A*). Thus, intrasaccadic VOR gain in response to head perturbations was highly suppressed when predictability was high.

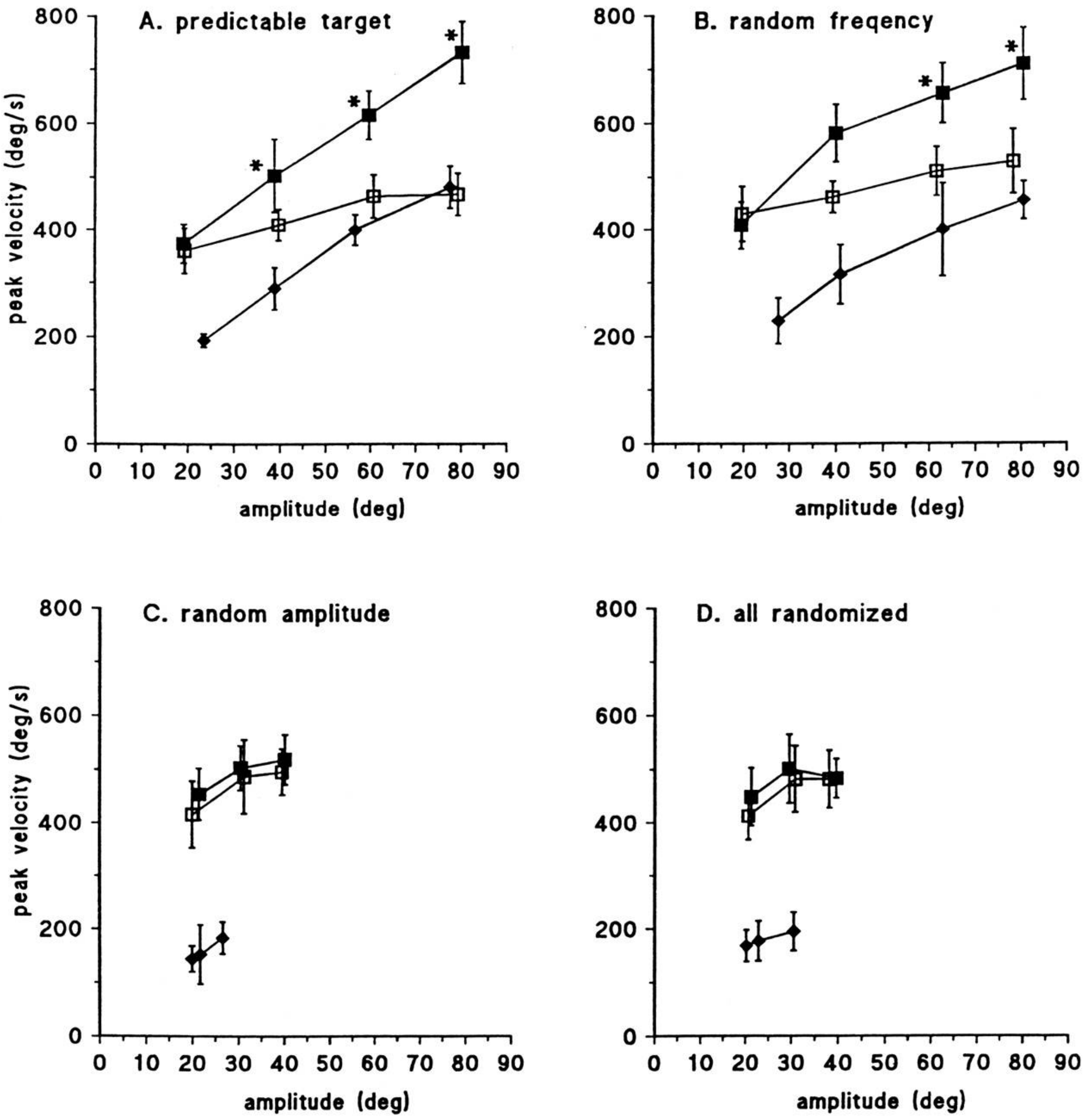

Figure 8: Peak velocities of gaze and head in a main sequence plot (subj. T.H.; $n=10$ per dot; mean +/−1 SD). Peak gaze velocities (solid squares) and the concomitant head velocity (solid diamonds) obtained in head free condition as well as peak velocities of head fixed saccades (open squares are plotted versus corresponding magnitudes. Highly significant differences of gaze velocities in similar amplitude bins ($p<0.001$) are marked by stars. Gaze saccade velocities were significantly increased in the paradigms, that permitted more prediction (**A–B**). With low predictability of the target step sequence, gaze velocities remained unchanged (**C,D**)

Table 2: Relative intrasaccadic VOR gain (IVOR) of 80° gaze saccades using a normalized maximum gain of 1.0

Subjects	IVOR in the predictable target-paradigm mean [1 SD]	IVOR in the random frequency-paradigm mean [1 SD]	Significance of Δ IVOR
A.L.	0.69 [0.22]	1.00 [0.28]	S
S.H.	0.29 [0.29]	1.00 [0.40]	S
P.M.	0.59 [0.14]	1.00 [0.31]	S
R.D.	0.71 [0.31]	1.00 [0.29]	NS
T.H.	0.69 [0.25]	1.00 [0.42]	NS
Average	0.59 [0.22]	1.00 [0.34]	

The IVOR gain was calculated using peak velocities of head free condition and averaged peak velocities of corresponding head fixed condition (IVOR gain = 1 − delt G′/delt H′). H′ is equal to head velocity at the moment of peak gaze saccade velocity. When the IVOR in the randomized task was normalized to unity for each subject, the corresponding mean IVOR gain in the predictable task was approximately 0.59, i.e., the VOR suppression amounted 40% with higher efficacy of prediction. Considering the intersubject variability, this reduction was significant in 3 out of 5 subjects ($p<0.01$).

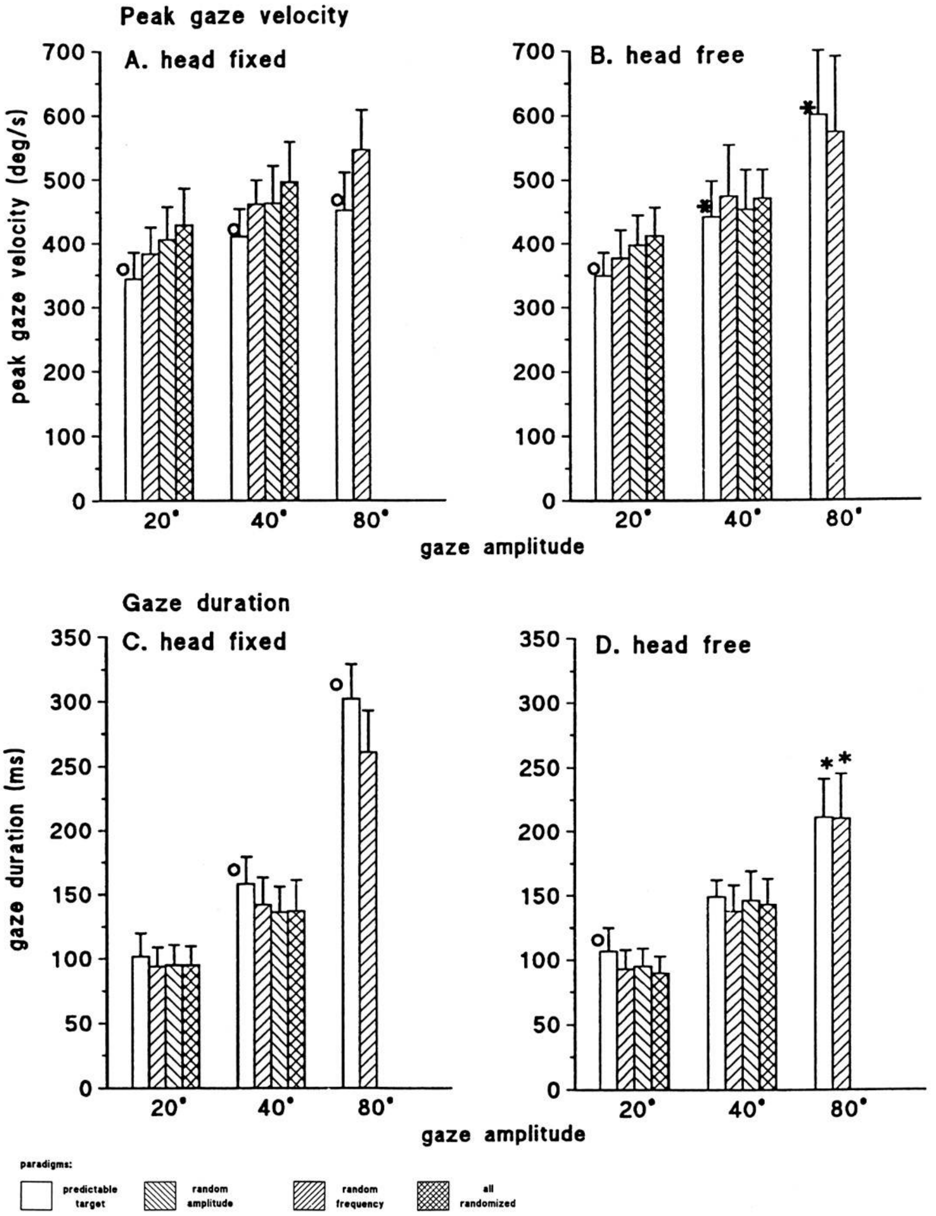

Figure 7: Peak gaze velocities and gaze durations (mean +/−1 SD). Pooled maximal velocities of head fixed saccades (**A**, $n = 436$) and coordinated gaze saccades (**B**, $n = 423$) are compared in the upper plots (5 subj.). In the head fixed condition, peak saccade velocities of predictable target trials were significantly slower than comparative velocities of randomized trials ($p < 0.005$; marked by circles). When the additional fast head movements were performed, almost equal velocities were found in small gaze saccades (compare 20° shifts in B). However, significantly increased peak velocities were obtained for larger predictive gaze saccades of 40° and 80° amplitude ($p < 0.005$; marked by stars). Gaze durations (4 subj.) of head fixed saccades (**C**, $n = 386$) increased in the predictable target paradigm corresponding to the velocity data in A (significant differences in amplitudes of 40° and 80°, $p < 0.005$; marked by circles). Duration of large gaze saccades (**D**, $n = 378$) decreased significantly with the additional head movements ($p < 0.005$, marked by stars), whereas no significant change of the durations was found in amplitudes of 20° and 40°

differences between large numbers[20] prevented the statistical assessment of possible differences between the paradigms. In all subjects, a decrease of intrasaccadic VOR gain was found in predictive saccades in comparison to visually guided saccades in the random frequency paradigm. The decrease amounted approximately 40% of the VOR gain in the random frequency paradigm. In two subjects, the VOR gain in the latter paradigm was also less than unity (subj. T.H. = 0.52 [+/−0.13] and R.D. = 0.73 [+/−0.22]). The VOR gain differences in these subjects were not significant, although the intrasaccadic VOR of the predictive saccades was markedly suppressed (*Table 2*).

Results of the head perturbation experiments

Both paradigms in the perturbation experiments used constant target positions. The head perturbations during visually guided saccades did not markedly

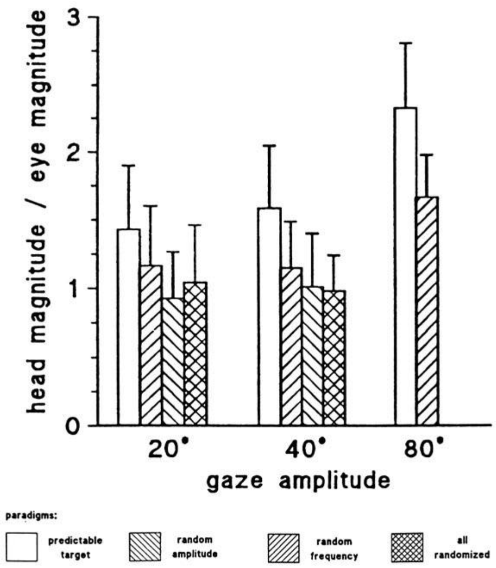

Figure 5: Ratio of head magnitude to eye magnitude as a function of gaze saccade amplitude and prediction (head free condition; pooled data of 5 subj.; $n=425$; mean +/−1 SD). The resulting head–eye magnitude gain was significantly increased in the predictable target paradigm in comparison to each of the randomized paradigms ($p<0.01$). Of course, large gaze amplitudes also precluded a larger proportion of head movement

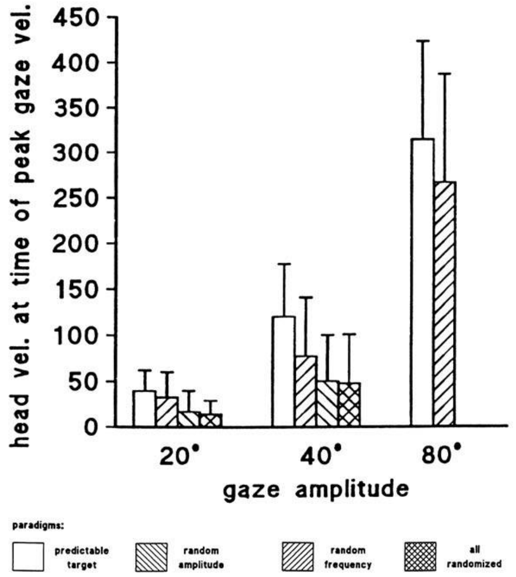

Figure 6: Head velocity during the saccadic eye movement. The head velocity was examined at the time of peak gaze velocity (head free-condition; 4 subj.; $n=378$; mean +/−1 SD). The velocity of the head movement during gaze saccades was highly correlated to the overall gaze displacement. Target predictability increased the head velocity, which became evident when saccades of similar amplitudes were compared

not increase significantly with respect to equally sized saccades with head restrained (*Figure 7A, B*). In predictable target trials, gaze displacements exceeding about 35° had increased peak velocities, when head movements were forced. The saccades of 60° or larger amplitude showed a corresponding significant decrease of gaze duration (*Figure 7C, D*). A significant increase of peak velocity in the random frequency paradigm occurred only in 2 out of 5 subjects. In subj. T.H. (*Figure 8*) significance was found in gaze shifts exceeding 30°, but in subj. R.D. velocity increase was limited to 80° gaze amplitudes. However, the pooled gaze duration was significantly reduced in gaze saccades of 80° amplitude during random frequency trials (*Figure 7D*), although this effect was more pronounced in the predictable target paradigm. In the paradigms using randomized sequences of target amplitudes, changes of peak velocities or duration were found neither in the statistical assessment of amplitudes up to 40° amplitude nor in single observations of larger gaze saccades.

The close relationship between maximal velocity, duration and corresponding amplitude, described as main sequence[43], remained stable. However, head contribution resulted in increased maximal gaze velocities (*Figure 8*) and shorter gaze durations with higher levels of target predictability.

Intrasaccadic VOR

Gaze velocity and duration data showed a strong evidence for a suppressed intrasaccadic VOR gain during predictive gaze saccades exceeding 30–40° amplitude. A more moderate reduction of gaze duration in large gaze saccades, that were triggered by the random frequency targets, and the corresponding significant increase of peak velocity in some subjects suggested, that the extent of intrasaccadic VOR gain suppression could be gradually modified by some predictive eye–head control mechanism. However, increased gaze velocities in more predictable target sequences were accompanied by increased head velocities during the saccade. Thus, the speed-up of coordinated gaze saccades with respect to the head fixed condition may be variable, due to the combined effects of increased head velocities and different levels of VOR suppression during gaze saccades.

In *Figure 9* the interaction between both effects has been depicted. Velocity profiles of eye saccades became increasingly asymmetric with large amplitudes, as peak velocity remained around the maximum values for 10° to 15° amplitude (see *Figure 9A, B*). This fact may be explained by the pulse width control of large amplitude eye saccades. Velocity profiles of coordinated gaze shifts were more symmetric, due to the additional head movement and its different mechanical properties. Gaze velocity profiles of 80° amplitude changed in both paradigms, when forced head movements were added. Concomitant head velocities were initially faster in predictive saccades. Additionally, the calculated VOR gain was suppressed to more extent. Whether this difference of VOR gain suppression was significant, was not detectable with this graphic method. We made the attempt to quantify the intrasaccadic VOR gain of different paradigms by comparing the difference of peak velocities of gaze and head between head free condition and head fixed condition (1-deltG′/deltH′). Results were obtained for saccades of 80° amplitude (*Table 2*), whereas in smaller saccades, relatively small

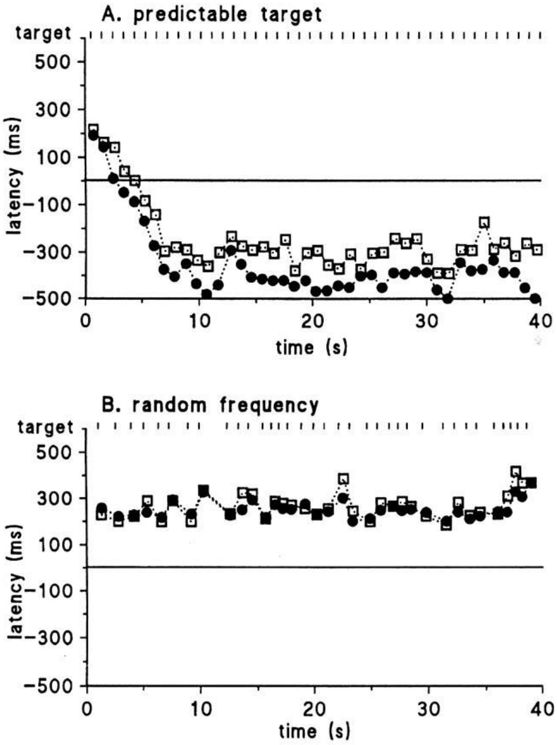

Figure 3: Eye and head latencies during a target step sequence of 80° amplitude (duration of 40 sec; subj. A.L.; head free condition). Tickmarks in the upper line represent the time of target reappearance. Latencies of saccadic eye movements (open squares) and concomitant head trajectories (solid circles) changed between the given predictable target (**A**) and random frequency paradigm (**B**). Due to previous experience, the subject started to anticipate the predictable target steps after a few seconds and showed a quite regular pattern

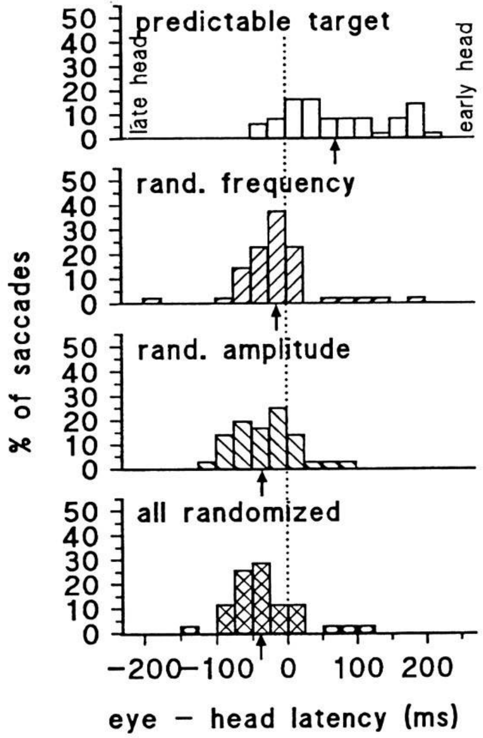

Figure 4 Eye latency minus head latency histograms of 40° saccades in head free condition (pooled data of 5 subj.; $n = 169$; 25 msec bins). Small arrows mark the statistical mean in each paradigm. Eye–head latencies increased with target predictability, i.e., early head movement onset was favoured in tasks, which permitted more prediction

randomized paradigms. However, the absolute peak eye velocity (PE'abs) of predictive gaze saccades was only slightly slower than peak eye velocities in the randomized trials. Therefore a relative peak eye velocity (PE'rel), defined here as the difference between the absolute peak eye velocity and the initial eye velocity[25], was equal or even higher in the predictable target paradigm with respect to the randomized trials. For example, in subject A.L., the predictive gaze saccades of 80° amplitude showed an E'ini of −95°/sec (+/−32) and a PE'abs of +366°/sec (+/−34), resulting in a PE'rel of +462°/sec (+/−39). The corresponding gaze saccades in the random frequency paradigm, led to an E'ini of −20.05°/sec (+/−10°/sec), a PE'abs of +420°/sec (+/−20) and a slower PE'rel of +440°/sec (+/−21).

One of the most interesting aspects of the present experiments was a hypothetical predictive modification of head contribution to the overall gaze displacement. Head amplitude was correlated to the resulting gaze amplitude, when saccades of the same paradigm were observed. Contrary to the instruction of the experimenter, head movement often fell short of the new target position, when gaze amplitude exceeded 40°. Comparison of equally sized gaze shifts demonstrated, that head magnitude decreased with higher levels of randomization (*Figure 1D, E*). To maintain gaze accuracy, concomitant saccade amplitudes increased. These findings were quantified by calculation of a head magnitude to eye magnitude ratio in *Figure 5*. The mean ratio in the predictable target paradigm increased from 1.42 in 20° shifts (due to slightly overshooting head movements) to 2.33 in 80° shifts and was significantly higher than corresponding data from randomized tasks.

An almost fully compensatory eye movement (CEM) occurred when the gaze position was in line with the new target. Due to this compensatory effect of the VOR, gaze velocity was independent from the synchronous head trajectory during this CEM phase. Changes of gaze velocity, that were caused by the additional head movement, depended on a reduction of VOR gain. Thus, they were limited to the saccadic phase of the gaze movement. We analysed the head velocity during saccadic eye movements by examination of head velocity at the time of peak gaze velocity (*Figure 6*). Resulting head velocities depended on the overall gaze displacement and again maximal values were obtained in the predictable target paradigm. This was obviously caused by the earlier start and increased peak velocities of the head with higher levels of target predictability. In small coordinated gaze shifts (amplitudes of 20° or less), the saccade was generally over before the head reached a larger velocity.

Corresponding to the concurrent slow head movements, peak gaze velocities of small gaze saccades did

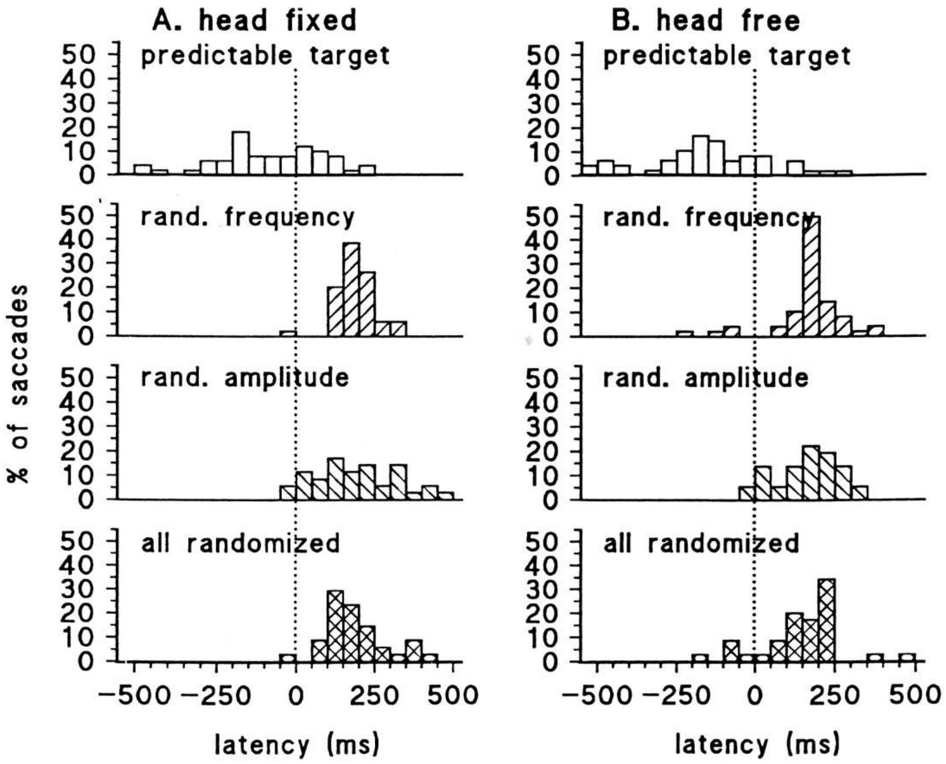

Figure 2: Gaze latency histograms of 40° shifts. Pooled data of 5 subj. were measured either in head fixed (**A**, *n* = 162) or head free condition (**B**, *n* = 169). Latencies were determined by movement onsets in the differentiated gaze position curve and grouped in 50 msec bins

They showed only a slight increase of very early responses (< −200 msec), when the predictable target steps were used. Very early head movements in the latter paradigm were at least partially compensated by a counter-rotatory eye movement (see velocity profiles in *Figure 1A, D*), so that onset time of the summed gaze movement was very close to onset of the saccadic component. As expected most of the gaze saccades in the predictable target paradigm anticipated the target step onset, whereas randomized target sequences led to mean gaze latencies of +150 msec to +200 msec (*Figures 2B* and 3). However, a considerable number of visually guided saccades occurred after the start of the earlier predictable target trials. These findings were caused by an adaptive interval, i.e., the time interval that was necessary to change from an initial visually guided mode to a predictive one. The adaptation interval decreased to a few seconds during the session, because the subjects benefitted from the experiences, which they made in previous predictable target trials (*Figure 3A*).

To assess the relative onset times of eye and head component during coordinated gaze saccades, we calculated the difference of eye and head latency (*Figure 4*). Prediction clearly changed the timing of the eye–head interaction during gaze saccades (compare also *Figure 3A* and 3B). All subjects demonstrated, that head movements generally preceeded the saccadic component in predictive gaze saccades. The interval between head and eye onset increased with larger gaze displacements (more than 40° amplitudes). Despite task related differences, a large intersubject variability of head latencies was found, especially with large gaze amplitudes. The averaged head latencies of 80° gaze shifts differed between −113 msec (+/−121) in subj. T.H. and −378 msec (+/−199) in subj. P.M.

In visually guided saccades of the randomized target paradigms, statistical means of the eye-minus-head latency data of 40° gaze shifts varied between −12 msec (+/−57) in the random frequency paradigm and −32 msec (+/−48) in the all randomized paradigm. The interindividual variability in randomized paradigms was relatively smaller. The well known delay of the head with respect to the eye increased with higher levels of target randomization. Zangemeister and Stark[13] found peripheral dynamic delays between neck EMG signal and resulting head movement of approximately 40 msec during gaze saccades towards randomized target, although a fast head movement was intended by the subject. Based on these observations, coupling of the neural trigger signals of eye and head movements can be assumed in the majority of visually guided saccades during randomized paradigms. However, head trajectories sometimes slightly preceeded the saccades in random frequency trials, when the gaze amplitudes exceeded 40° (*Figure 3B*).

Dynamics and durations

Due to early head movement onset in predictive gaze saccades, the eye made some reflexively triggered compensatory movement before the saccade occurred. Thus, the initial eye velocity (E′ini, i.e., the eye velocity at the onset time of the saccade) was generally negative in predictive saccades, but close to zero in the highly

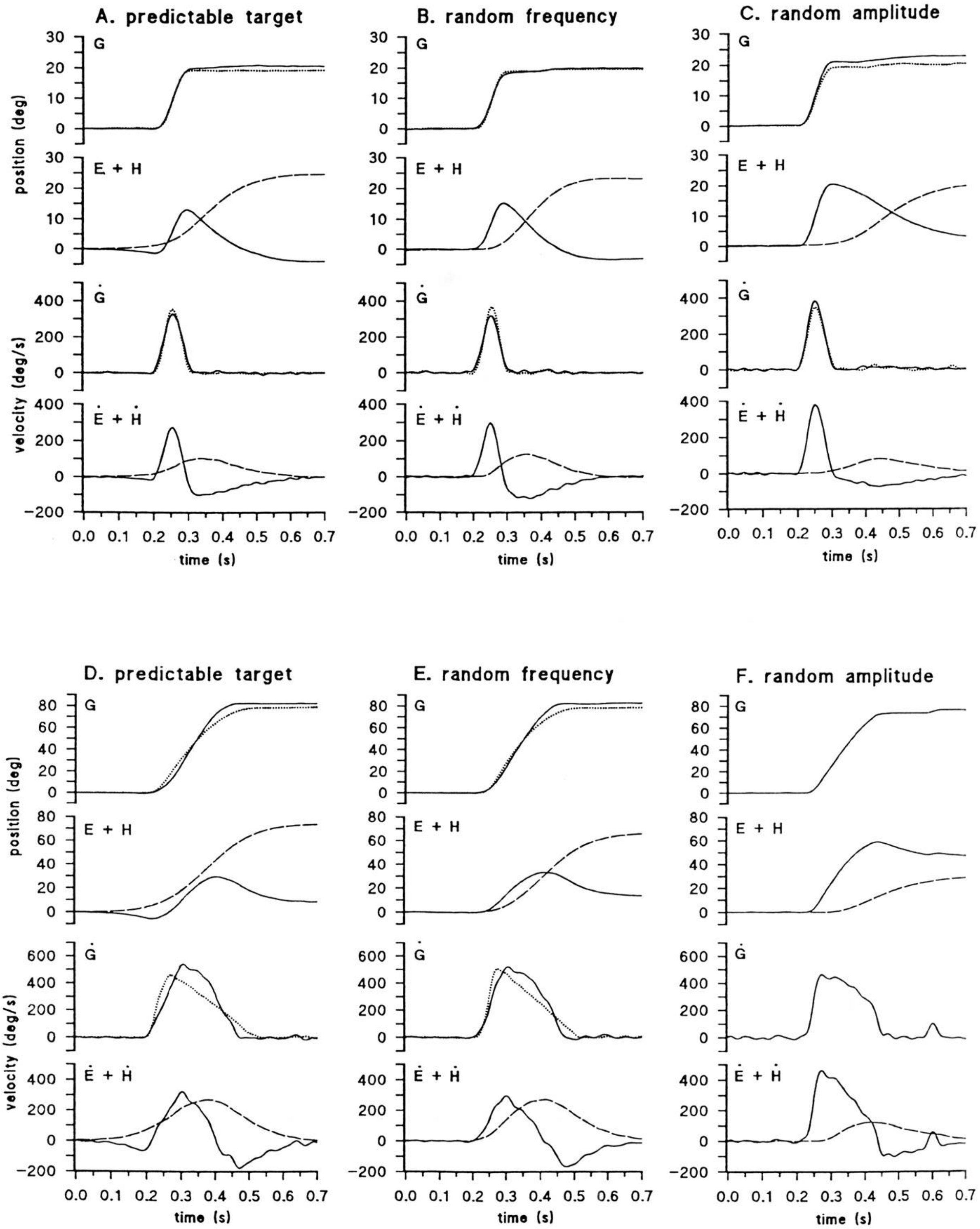

Figure 1: Amplitude and velocity vs. time-plots of small saccades, **A–C**, 20° amplitude and large saccades, **D–F**, 80° amplitude. The two upper panels of each plot show typical amplitude responses in the predictable target (A,D), random frequency (B,E) and random amplitude paradigm (C,F). The data, given in plot A–E, represent averages of 10 single saccades each (subj. A.L.), whereas F shows a typical single response (because large saccades in this paradigm occurred rarely). The uppermost panels show gaze amplitudes in head fixed condition (dotted) and head free condition (solid). Eye (solid) and head (dashed) amplitudes of the latter condition are given in the upper middle panels. The two lower panels show corresponding velocity profiles. They are slightly smoothed, due to the averaging procedure. The results of the 'all randomized paradigm' were not plotted, because they were almost undistinguishable from the random amplitude paradigm. Small post-saccadic peaks of the eye and head velocity traces were caused by single corrective saccades

to move their head as fast as possible towards the new target position during the refixation period. The subject received no verbal information about the ongoing paradigm.

In the head perturbation experiments, the predictable target paradigm and the random frequency paradigm were tested in head free condition, while target steps of 80 amplitude were presented. The intended head movement was suddenly slowed down in about 15%–20% of the saccades. Perturbations were manually performed by the experimenter using a simple mechanical apparatus with two cords, that were tangentially linked on both sides of the subject's helmet. To avoid slip (see next paragraph) of the helmet, the maximal perturbation was limited to about 200 deg/sec (resulting in maximal head decelerations of less than $-3300°/sec^2$). The helmet was fitted to the subject's head as tightly as tolerated.

Apparatus

Horizontal eye movements were measured by averaging the monocular horizontal DC electro-oculography (EOG) signals of both eyes. A polynomial regression curve from data of eight target positions was used to calibrate the EOG. The recording sessions started after at least 15 min in darkness and EOG calibration was repeated about every 15 min. The EOG measurement accuracy was around $\pm 1°$ for large amplitudes. The base line drift never exceeded 2° and was controlled after each trial. Head position was recorded by a low torque-high resolution potentiometer (linearity 0.13%), that was rigidly coupled to the rotational axis of the helmet. Additionally, a horizontal angular accelerometer (SCHAEVITZ) was used to exclude delays in the head latency and duration data, that were possibly caused by slip of the helmet. To confirm that slip would not artificially change latencies, measurements were undertaken that compared simultaneous recordings of latency of infrared sensor fixed to a bite bar with latency of the signal generated by the accelerometer that was fixed to the helmet. With the helmet tightly fixed there was no time lag of the accelerometer signal. Head movements were limited to free rotations in the horizontal plane.

The data were digitized on-line at a sampling frequency of 200 Hz (overall system bandwidth 0–70 Hz) and stored as data files on a 386-personal computer. A user-programmable software package (KEITHLEY) enabled inspection of the data during the session, so that trials could be repeated. Analysed saccades were visually selected by the experimenter and grouped into 10 bins. A total number of about 1300 saccades was evaluated. Gaze position (position of eye-in-space) was computed by adding the eye and head position signals. This summation represented not quite the true gaze, since the eyes rotate in the horizontal plane at different axes, that are closer to the target than the rotatory axis of the head. But to a first approximation, the resulting gaze trajectory should be proportional to the target change. Velocity data were obtained by digitally differentiating after low pass filtering at 45 Hz of eye and head position (zero phase lag). A 15 deg/sec-threshold determined the head movement onset to exclude slow head movements, that were not related to the gaze saccades. The statistical significance between means was calculated by using a two sample *t*-test and a Kolmogorov–Smirnov normality test. The level of significance was limited to $p < 0.01$.

RESULTS

General aspects

The following results refer to unperturbed coordinated gaze saccades, if not explicitly mentioned otherwise. Eye-head interaction during coordinated gaze saccades varied with respect to different experimental paradigms. Dynamic changes were not statistically significant in gaze shifts of 20° amplitude, but became more and more obvious in larger displacements. The accuracy of the initial saccade was remarkably high in all paradigms for gaze amplitudes of up to 40°. Beyond that amplitude range, undershooting primary saccades very often occurred in those paradigms, that used a random sequence of 13 different target positions. This effect led to a significant increase of corrective saccades exceeding 15% of the target displacement. Consequently, not enough large saccades ($>50°$) for statistical assessment were available in these paradigms. When only two alternating target positions appeared, the accuracy remained high for amplitudes up to 80°. The accuracy of saccades with head fixed and coordinated gaze saccades was very much the same in all paradigms, so that statistical comparison of both conditions was possible.

In small gaze saccades (*Figure 1A–C*), gaze amplitudes and corresponding gaze velocity profiles demonstrated approximately the same gaze shifts in all paradigms. However, amplitudes and latencies of eye and head changed with the ability to predict target movement. Relatively earlier head onset and increased head amplitudes in the predictable target paradigm were compensated by saccadic components, so that gaze traces in head fixed and head free condition remained unchanged.

In large gaze shifts (*Figure 1D–F*), the predictive modification of eye–head interaction became more substantial and was not fully compensated during the saccade. Head movement started earlier and increased in amplitude when the ongoing target step was predictable (*Figure 1D*). Eye movement amplitudes were limited to about 45° in this paradigm, whereas it reached almost 60° in the large saccades of the highly randomized trials (*Figure 1F*). However, saccades started from more eccentric positions in the orbit when targets were highly randomized. This was caused by relatively small head displacements during the previous gaze shift. Gain of the compensatory eye velocity was not altered by amplitude or prediction. It was close to unity, independent of gaze amplitude or prediction (*Figure 1*).

Latencies

Previous reports on latencies of head fixed saccades showed, that they were either triggered by the peripheral visual stimulus (visually guided) or predictability (predictive). The minimal latencies of fully visually guided saccades are around 100 to 120 msec in humans. Our gaze latency histograms (*Figure 2A*) of saccades with head fixed were in line with the previous studies (compare to Smit and Van Ginsbergen[42]). In the randomized paradigms, gaze latencies of coodinated gaze saccades (*Figure 2B*) did not differ significantly from corresponding saccades with head restrained (*Figure 3A*).

additional head velocity. Thus, gaze accuracy is maintained by subtracting head movement velocity (vestibular input signal) from simultaneous saccade velocity (saccadic controller signal). This so called 'linear summation hypothesis'[20] was supported by studies in cats[8,21], but most examined gaze amplitudes and head velocities in these studies were comparatively small. Other authors[22–24] found a suppressed or absent VOR during larger gaze saccades in cats (> 40°) and monkeys (> 25°). Of course, theoretically also peripheral dynamic interactions could account for this nonlinearity of the summation of a saccadic and a slower reflex triggered eye movement. Winters *et al.*[25] demonstrated this through computer simulations of a nonlinear eye movement model.

In humans, Zangemeister and Stark obtained increased gaze velocities with intended time optimal head movements[11–13], which inferred a reduction of the VOR gain during the gaze saccade[16,26]. Laurutis and Robinson[20] described similar increase of gaze velocity with additonal head movements and a highly reproducible disconnection of the intrasaccadic VOR, while human subjects performed self-paced movements between two known target positions (amplitudes between 40° and 200°). Guitton and Volle[27] reported a more gradual suppression of the VOR gain and a significant intersubject variability. In these studies accuracy of the initial saccade remained high, even when the head movement was passively perturbed. Pelisson *et al.*[10] demonstrated, that intrasaccadic VOR inhibition was correlated to gaze amplitude during active or passive head rotation, therefore VOR gain in humans may be suppressed, at least when gaze amplitudes exceed the natural human oculomotor range. Some uncertainty remains however, whether the intrasaccadic VOR is generally completely inhibited or gradually modified. In extension of previous models of the saccadic system, 'gaze feedback models' were developed, which used an internal copy of the actual gaze position to adjust the movements of eye and head[9,10,20,27]. In these models, the vestibular input was used to add the head position to the internal copy of actual gaze position, as proposed by Fuller *et al.*[22]

Other authors however reported evidence for a tight coupling of eye and head motor control signals. Tonic EMG activity of the dorsal neck muscles and position of eyes in orbit were concomitantly modulated in cats[28], and monkeys[29]. Phasic burst patterns appeared in the neck EMG that were linked to saccadic eye movements in rabbits[30], cats[31], and monkeys[2], when the head was fixed. Corresponding observations in the human neck-EMG patterns were reported by Andre-Deshayes *et al.*[32,33] using micro-electrode techniques in alert cats and monekys, reticulo-spinal neurons in the pontomedullary reticular formation[31,34,35] and neurons in the deeper layers of the superior colliculus[36,37] were found that send collaterals to oculomotor and head motor circuits, that showed synchronized gaze movement related activities. The role of possible gaze coding brainstem neurons and the tight coupling of eye and head motor systems in different species has been extensively reviewed[38–40].

Based on the assumption, that prediction is one of the crucial factors in coordination of gaze saccades, especially in humans, this study examined the effects of different levels of target predictability on latencies and kinematics of eye and head. We tried to find evidence for a modification of the intrasaccadic VOR gain. This would preserve a high accuracy when higher level control mechanisms change eye–head interaction in gaze saccades, as proposed by Zangemeister and Stark[11,13,26] and Ron and Berthoz[41].

METHODS

Experimental set up

The data of eight healthy volunteers (6 males, 2 females, 19–27 years of age) were represented in this study. Six of them were naive to neurophysiological experiments. Four subjects participated in the first series of experiments on unperturbed gaze saccades, three subjects in the second series using head movement perturbations and one participated in both series on two different days. Subjects were seated in a constantly darkened room. The target stimuli consisted of green LED lights (diameter of 0.29 that appeared on a white semicircular screen at a distance of 1.2 m from the head rotatory axis. Four experimental paradigms were designed to represent different levels of target predictability. Horizontal target step sequences within a range of 40° apart from the central position were used in all trials. Each sequence was triggered by a square-wave input signal and lasted between 40 sec and 60 sec. The paradigms were based on certain variations of target frequency, amplitude and direction as described in *Table 1*.

Constant amplitudes were examined, while the target jumped between two fixed positions, which were 20, 40, 60 or 80° apart. In the random amplitude trials, the ongoing target step followed a randomized sequence out of 13 different positions and in the random frequency trials, the target frequency varied pseudo-randomly between 0.25 Hz and 1.2 Hz. The subjects were repeatedly asked to refixate the target light as quickly and as accurately as possible during each trial to avoid the effects of drowsiness.

In the experiments on unperturbed gaze saccades, the subjects underwent all four paradigms while head movements were restrained (head fixed condition). In a second run, the head was free to move (head free condition) and the subjects were repeatedly advised

Table 1: A qualitative ranking of the paradigms shows the most predictable target pattern on top

Paradigm	Frequency of target shift onset	Amplitude of target shift	Direction of target shift
Predictable target	Constant (0.5 Hz)	Constant	Const. alternation
Random frequency	Randomized	Constant	Const. alternation
Random amplitude	Constant (0.5 Hz)	Randomized	Variable
All randomized	Randomized	Randomized	Variable

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