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Eye position signals in human saccadic processing

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Summary. *1.* We studied saccades to briefly flashed targets in 8 human subjects. The target flash occurred (i) during smooth pursuit ("ramp-flash"), (ii) just before a saccade to another target ("step-flash"), or (iii) during steady fixation ("flash only"). All lights were extinguished after the target flash so that smooth pursuit or saccadic eye movements occurred during the interval of complete darkness between the target flash and the saccade to it. We compared these saccades to those made without intervening eye movement (flash only), and quantified the extent to which the saccadic system compensated for the change in eye position that occurred during the dark interval. *2.* Saccades to control flashes were reasonably accurate (mean gain 0.87) and consistent. Compensation for the intervening eye movement in the ramp-flash and step-flash paradigms was highly variable from trial to trial. On average, subjects compensated for 27% of the intervening pursuit eye movement on ramp-flash trials and for 58% of intervening saccadic movement on step-flash trials. *3.* Multiple regression analysis showed that the variability did not depend on factors such as variations in underlying saccadic gain, response latency, timing of stimuli or size of the required response. We conclude that this variability is intrinsic to saccadic responses that require the use of an eye position signal. *4.*. These results show that an eye position signal is available to the saccadic system but that this signal has low fidelity. The high variability and low fidelity of the eye position signal suggest that the saccadic system does not normally operate in spatial coordinates, which require the use of an *accurate* eye position signal, but rather in retinal coordinates.

Key words: Saccades – Pursuit – Eye position – Craniotopic – Human

Introduction

Experimental evidence suggests that the saccadic system uses a combination of visual information and information about eye position in programming saccades. Hallett and Lightstone (1976a, b) showed that humans made reasonably accurate saccades to briefly flashed targets, even if the target was presented in mid-saccade. As the saccade to the flashed target started from a location different from that at which the target was seen, the visual information alone could not have determined the metrics of the saccade. The system must have reconstructed the target location by knowing the position of the eye at the time of the target flash. Similarly, Sparks and Mays and colleagues (Mays and Sparks 1980; Sparks and Mays 1983; Sparks et al. 1987) and Schiller and Sandell (1983) showed that monkeys could direct saccades in darkness to flashed targets even if electric stimulation moved the eyes after the flash and before the saccade. This supported a model of the saccadic system (Robinson 1975) in which target position was specified relative to the head by adding a signal encoding eye position to one encoding target position on the retina. These findings were taken to "demonstrate unequivocally that saccades are calculated not retinotopically. . . but craniotopically" (Carpenter 1988).

The general validity of this model was questioned by McKenzie and Lisberger (1986). In their study three monkeys were required to make saccades to targets that were flashed briefly during smooth pursuit. Two of the three monkeys made saccades that were related to the retinal position of the target rather than its position in space. They ignored the intervening pursuit movement. The authors concluded that the saccadic system receives information about eye position related only to saccadic movements. Schlag et al. (1990), however, showed that the saccadic system could account for pursuit movement if the animal was allowed to maintain smooth pursuit for a longer time. Saccadic performance was less accurate than usual. They suggested that the inaccuracy represented an underestimate of pursuit velocity.

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We studied the use of eye position information in the human saccadic system. We found that compensation for eye movements intervening between presentation of a target and a saccade to that target was poor and highly variable. This was true whether the intervening eye movement was pursuit or a saccade. Our findings suggest that under ordinary circumstances saccades are calculated not craniotopically but retinotopically. A brief report of these findings has appeared (Gellman and Fletcher 1990).

Material and methods

Subjects for these experiments were 5 men and 3 women. Three subjects were experienced and knew the goal of the experiment; the others were naive. Subjects sat in a completely dark room. Targets were projected onto a hemispheric screen at a distance of 1 m. Eye movements were recorded with the search-coil technique, using search coils made by Skalar and 6′ phase-angle field coils made by CNC Engineering. The coil was placed in the right eye after the cornea had been anaesthetized with 1–2 drops of Ophthaine®.

The experiment was controlled by a computer using the REX system (Hays et al. 1982). The computer controlled the motion of the target on the screen and sampled eye position and velocity at 250 Hz and target position at 125 Hz (position resolution after digitization: $<0.1°$). The target consisted of a red spot (about 0.2°; 2 log units above dark-adapted threshold) generated by projecting an ultrabright LED through appropriate optics. A pair of mirror galvanometers determined the position of the spot on the screen. To produce near-instantaneous steps that did not streak the image over the retina, two LED's and two sets of mirrors were used. A step was produced by simultaneously turning one LED off and the other on.

Experimental paradigms

Subjects were instructed to follow the target wherever it moved, and to look at the location of any flashed target even if it was no longer there. Three test conditions and one control condition were used. The goal of the test conditions was to dissociate the retinal location of the target from its spatial location so that we could determine toward which of these targets the saccade was directed. The target would flash when the eye was at one location and the saccade would be initiated after the eye had moved horizontally (in darkness) to a different location. In pilot studies it was difficult to determine whether a saccade was target-directed, or simply a non-specific response or a spontaneous saccade. This problem arose in part because it was difficult to know, a priori, whether the goal of the saccade was the retinal or spatial location of the target or somewhere in between. For this study we therefore added a vertical component to the displacement of the target flash (after McKenzie and Lisberger 1986). Because the eye moved only horizontally in the interval between the target flash and the saccade, the vertical displacement did not change. The vertical component of the saccade could thus be used to determine whether the saccade was intended to be directed at the target. All subjects participated in *ramp-flash* and *step-flash* paradigms that were presented in pseudo-random order. Three subjects participated in the *fixed reference* paradigm. Five subjects also were studied with the *flash only* (control) paradigm. In addition, occasional "dummy" trials, with no flash, were used to discourage predictive eye movements. Each experiment consisted of ≈400 trials.

Ramp-flash. The target appeared 15° or 30° to the left or right. After ≈500 ms it started moving at a constant speed of 15 or 30°/s (randomly chosen) toward the center of the screen for a variable duration of 800–1200 ms before being extinguished. When the moving target disappeared another target flashed for 20 ms at unpredictable vertical and horizontal offsets (4, 8 or 12° above or below, and 0, 1, 3, 4, 5, 7, 8, 10, 11 or 14° to the left or right) from the direction of gaze. (For 3 subjects the vertical offset was always limited to ±4°.) Pursuit eye movements usually continued, in darkness, between the presentation of the flash and the initiation of a saccade to it.

Step-flash. The target appeared at the center of the screen. After ≈500 ms it stepped 2, 4 or 7° to the left or right where it remained for 160–200 ms (see below). (These amplitudes were chosen to be comparable to the amplitudes of intervening pursuit movements in the ramp-flash paradigm.) Another target then flashed for 20 ms at the same unpredictable horizontal and vertical offsets as in the ramp-flash paradigm. The goal was for the flash to be over before the saccade to the first target location started so that a saccadic movement to the first target would intervene (in darkness) between presentation of the flashed target and a saccade to it. To achieve this in the face of differences in saccadic latencies between subjects, we adjusted the 160–200 ms interval during the experiment as required. For example, if a subject typically made her/his first saccade at a latency of 180 ms, the delay between the step and the flash was reduced to 120–160 ms, so that the flash would be over before the saccade started.

Fixed reference experiment. This paradigm was identical to the ramp-flash and step-flash paradigms except that 4 LED's, located at 20° right, left, up and down from the center, remained illuminated throughout the experiment. The purpose of this experiment was to determine whether the spatial information provided by fixed visual references improved the accuracy of saccades.

Flash only. The target appeared in the center of the screen. After ≈500 ms it disappeared and another target was flashed for 20 ms at one of the offsets described above. This condition was interleaved with the test conditions for two of our subjects and presented as a separate experiment for three others. This control condition allowed us to determine the accuracy of saccades to flashed targets without intervening eye movement.

Data analysis

Data was analyzed off-line with an interactive graphics program. The program determined the time of saccade onset, and measured its vertical and horizontal components, its starting position, and the eye position at the time of the onset of the flash. Trials were discarded if a saccade started before the end of the flash. To exclude from consideration factors that might affect saccadic accuracy other than intervening eye movement, we discarded trials in which the vertical component of the saccade was inaccurate by the greater of 1.5° or 30% of the step. To ensure that the intervening movement in the *ramp-flash* paradigm was purely pursuit, we excluded trials in which there was a catch-up saccade between the flash and the saccade toward it (i.e., the saccade with a vertical component). We analyzed only those trials in which the amplitude of the intervening pursuit was at least 1° so that our evaluation of saccadic compensation would not be affected by relatively small differences in saccadic amplitude or by small errors in measuring saccade amplitude. For the *step-flash* paradigm, trials were excluded if the first saccade occurred >120 ms after the flash to ensure that the first saccade was not significantly influenced by the flash (Becker and Jürgens 1979).

Once valid trials had been identified, we determined to what extent the saccade to the flashed target had compensated for the intervening saccadic or pursuit movement. Since the intervening eye movement was in the horizontal plane, only the horizontal component of the saccade was used in this computation. The schematic example in Fig. 1 shows the measures that were used in our analysis. In the upper part of the figure the target flashed at the location identified by the rectangle while the eye was at the location shown by the circle. The eye then moved in complete darkness further to the right (*eye movement*), and a saccade with a horizontal component of

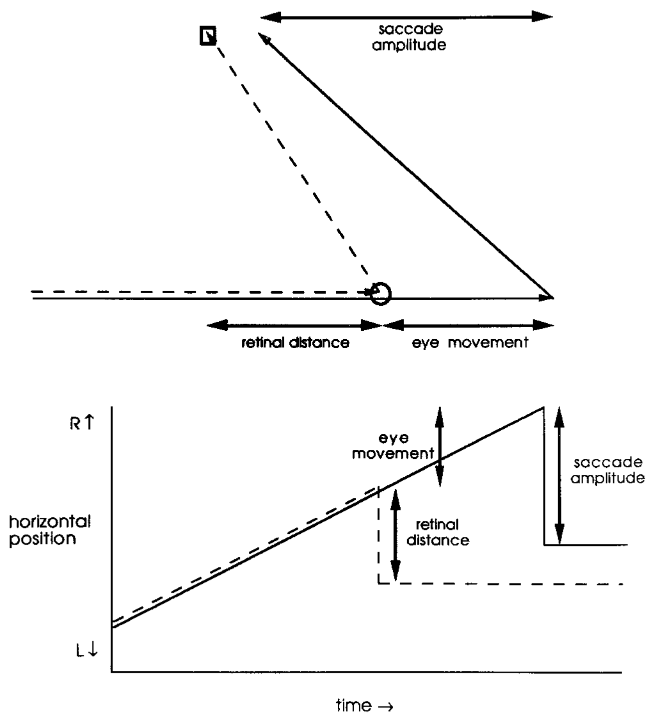

Fig. 1. Schematic representation of a trial, showing measures used for quantification of the response. The upper part shows an X–Y plot and the lower part shows the horizontal positions plotted as a function of time. In this and subsequent figures *solid lines* show eye position and *broken lines* show target position. The target moved to the right; when the eye was at the location shown by the *small circle* the target stepped up and to the left, to the position indicated by the *small rectangle*, and then disappeared. The eye continued moving to the right ("eye movement") in darkness, after which the saccade was initiated. The horizontal distance to the target, and hence the horizontal amplitude of a spatially accurate saccade, is the sum of *retinal distance* and *eye movement*

saccade amplitude was initiated from there. The horizontal component of a saccade based purely on the retinal signal would be the same as the retinal distance: the horizontal distance from the circle to the square. A spatially accurate saccade, in contrast, would have a horizontal component given by:

$$\textit{saccade amplitude} = \textit{retinal distance} + \textit{eye movement}.$$

If a recorded saccade had a smaller amplitude, as in the schematic example, we attributed this to an underestimate of *eye movement*. The estimated eye movement, *eye movement*$_{est}$, is *saccade amplitude–retinal distance*. We defined *compensation* for intervening eye movement as the ratio *eye movement*$_{est}$/*eye movement*. A saccade that is spatially accurate, i.e., one that compensates completely for the intervening eye movement, would have *compensation* = 1. A saccade that is purely "retinal" would have *compensation* = 0. This definition of compensation assumes unity saccadic gain: i.e., if *eye movement* = 0, then *saccade amplitude* = *retinal distance*. It is, however, possible that the amplitude of the saccade would be $G \cdot$ *retinal distance*, where G is the saccadic gain. Both possibilities are considered in Results.

Results

General observations

No subjects reported afterimages. An afterimage would move with the eye, and a response based on the retinal location of the target might simply have reflected this. Subjects were not consciously aware of their performance, and none reported using any specific strategy for compensation. They sometimes failed, for unknown reasons, to look up or down toward the flash. An attempt to encourage accurate vertical saccadic components by providing an annoying tone on trials where the vertical was grossly inaccurate had no discernable effect. Inaccurate vertical components resulted in the rejection of 27% of all ramp-flash trials and 30% of step-flash trials. A further 41% of step-flash trials were rejected because the subjects ignored the step and responded only to the flash. There were no differences in performance between the naive and the informed subjects. There was no apparent improvement or deterioration in performance as the experiment progressed.

Flash only paradigm

The accuracy of saccades to a simple target flash without intervening eye movements was assessed with the flash only condition. The saccadic gain (ratio of horizontal saccade amplitude to horizontal target distance) was directly evaluated in 5 subjects (control gain, Table 1). We also used an indirect method (explained below) for estimating the gain of all subjects.

Ramp-flash paradigm

In the ramp-flash paradigm the mean intervening eye movement between the time of the flash and the start of the saccade was 3.3° (range: 1.1° to 7.9°). The most notable feature of the responses to the ramp-flash was their variability. Figure 2 illustrates the responses of one subject, recorded during one experimental session, to two different stimulus configurations. In the examples on the left the target stepped onwards, i.e., in the direction of the ramp motion, and beyond the point reached by pursuit motion. The amplitude of the saccade would therefore have to be *decreased* if the gaze is to be accurately directed at the location of the (now invisible) target. Such an

Table 1. Control and estimated gains. The first column shows gains in the control condition (flash only). The second and third columns show the gains computed from the ON-BACK asymmetry in the ramp-flash and step-flash conditions, respectively (see text). Subject NO did not make enough saccades in the ON condition to estimate her gain for the step-flash

Subject	Control gain [SD, N]	Ramp gain	Step gain
BLM	–	0.87	0.86
GIB	0.93 [0.22, 18]	0.86	0.82
LAG	–	0.89	0.83
LMA	0.88 [0.14, 21]	0.83	0.83
MCB	–	0.96	1.00
NO	0.78 [0.38, 67]	0.72	–
RSG	0.81 [0.25, 115]	1.00	0.93
WAF	0.97 [0.19, 144]	0.90	0.88

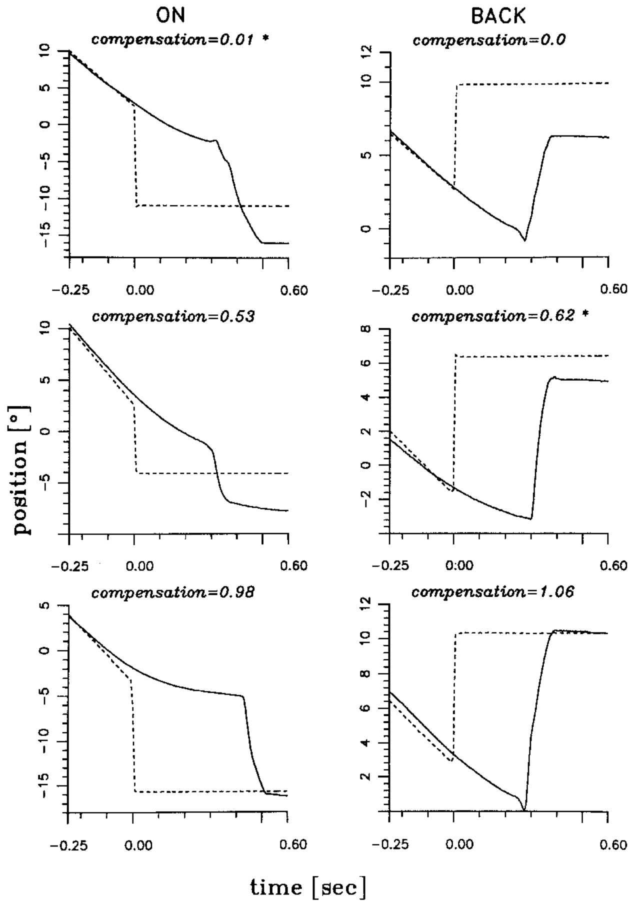

Fig. 2. Examples of responses to different ramp-flash stimulus configurations for one subject (RSG), recorded during one experimental session. Each panel shows the horizontal component of eye movement and target movement. The target remained illuminated for only 20 ms after the target step. The computed compensations are inset in each figure. In this figure and Fig. 5 an *asterisk* next to the compensation value indicates that we have inverted the horizontal component to simplify comparison. The *bottom row* shows saccades that were directed at the spatial location of the target, compensating for intervening pursuit movement. In the *top row* saccades were directed at the retinal location of the target; i.e., there was little or no compensation for the intervening pursuit movement, and in the *centre row* saccades were intermediate between the retinal and spatial locations. In the *left column* the target stepped onwards, in the direction of the ramp motion; in the *right column* it stepped backwards, opposite to the direction of ramp motion

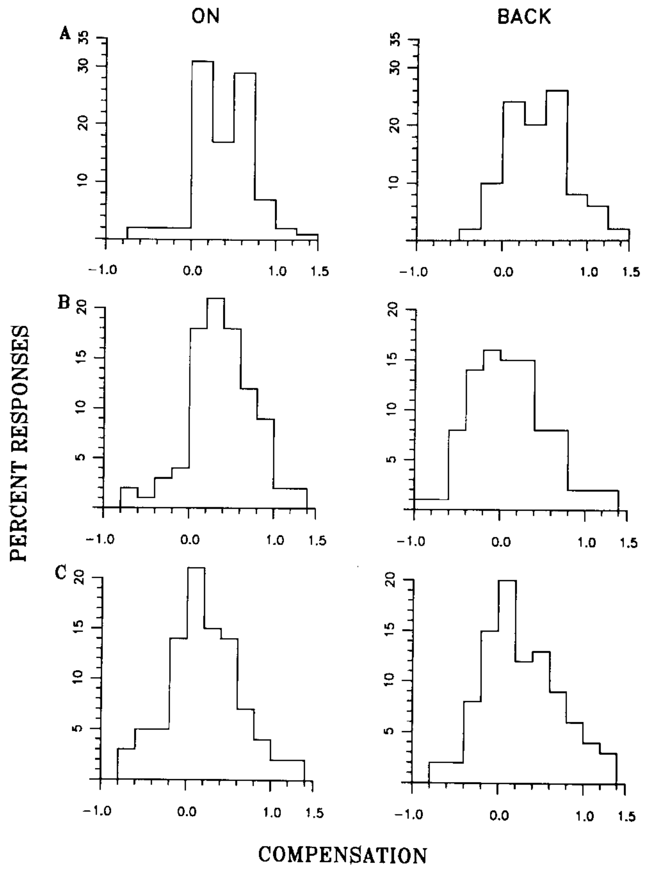

Fig. 3A–C. The distribution of compensations for trials with the ONward configuration (*left column*) compared with the BACKward configuration (*right column*) on the ramp-flash paradigm. **A** Histograms for the same subject as in Fig. 2 (RSG); **B** Histograms combining the responses of all the subjects. Note the asymmetry between ON and BACK. **C** When saccades are adjusted by the estimated gain (see text), this asymmetry is markedly lessened

example is shown on the bottom left, where the subject accurately compensated (compensation = 0.98) for 3.3° of pursuit motion intervening between the flash and the saccade. In the example shown on the top left, in contrast, the amplitude of the saccade ($\approx 14°$) was nearly equal to the distance of the target from the fovea (14°) at the time of the step. The subject did not compensate for the 5° of pursuit (compensation = 0.01). The central panel shows a more typical example, where the subject partially compensated (compensation = 0.53) for intervening pursuit movement (3.2°).

The right column of Fig. 2 shows examples for a configuration in which the target stepped backward, i.e., opposite to the direction of the ramp. In contrast to the onward steps, the saccade amplitude would have to be *increased* relative to the amplitude of the step to compensate for the intervening pursuit movement. Similar to the results of trials with onward steps, the extent of the compensation varied from 0 to about 1. The same was true for a stimulus configuration in which the target image stepped to a location directly above or below the fovea (not shown): i.e., the horizontal "retinal error" at the time of the flash was 0°.

To illustrate the variability suggested by the above examples, we show the distribution of compensations for all ramp-flash trials for 1 subject in Fig. 3A and for all the subjects combined in Fig. 3B, C. The figures show that compensation varied continuously, rather than discretely, from <0 to >1. For the 8 subjects studied, the mean compensation (mean of all trials) was 0.29 (*SD* 0.5, $N = 595$; range of individual values 0.08–0.39). Individual variability from trial to trial was high. The unadjusted mean values for all subjects are shown by the *hatched bars* in Fig. 4A. We also computed the compensation in polar coordinates by measuring the angular direction of the

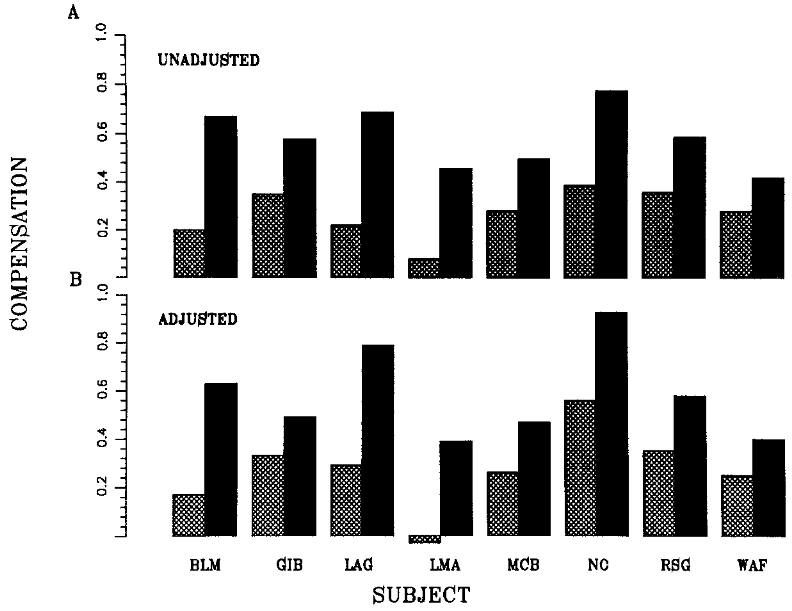

Fig. 4A, B. Mean compensations for all subjects for both the ramp-flash (*check pattern*) and the step-flash (*solid*) paradigms. **A** Values computed assuming saccadic gain = 1; **B** Values recomputed to reflect the estimated gains (Table 1)

Table 2. Ramp-flash on/back asymmetry. The first two columns show the mean values of compensation in the ramp-flash trials for ON and BACK conditions as computed with gain = 1. The third column shows the mean compensation computed when saccades were scaled by the estimated gain (Table 1)

Subject	ON compensation	BACK compensation	Adjusted compensation
BLM	0.41	−0.08	0.17
GIB	0.62	0.18	0.33
LAG	0.44	0.04	0.29
LMA	0.36	−0.28	−0.03
MCB	0.31	0.23	0.26
NO	0.62	0.21	0.58
RSG	0.34	0.42	0.35
WAF	0.50	0.14	0.25

saccade and comparing it to the angular directions of the retinal and spatial stimuli. The results were comparable: the mean compensation was 0.26.

Our analysis has thus far assumed unity saccadic gain (see Methods). It is, however, well known that the gain of saccades to visible targets is typically < 1. An accurate estimate of gain is essential for an accurate determination of compensation. For example, in Fig. 2 (right column, middle), if the subject's saccadic gain were 0.85 rather than 1.0, the calculated value for compensation would be 1.0 instead of 0.62. Because of the importance of the value of gain to our calculation of compensation we used three methods for its estimation. The first was simply to use the gain from the control flash condition. The second was to use the gain of the vertical component for each trial. These two methods, however, make unproven assumptions: the gain in the control might be different from that during tracking, and the vertical and horizontal gains may not co-vary. The third method was suggested by the asymmetry of the compensation that was calculated for the ONward and BACKward trials (Table 2) when gain was assumed to be 1. When a value of < 1 was used the asymmetry decreased. By a method of successive approximations,[1] we could arrive at a gain (see Table 1) at which compensation was the same for ONward and BACKward saccades.[2] The values of gain obtained by all three methods were comparable. Figure 4B (and the right column of Table 2) shows the values of compensation adjusted for each subject's gain. All subjects except LMA compensated for some of the intervening pursuit movement. The overall mean compensation was unchanged (mean: 0.29 ± 0.5, $N = 585$).

In trials where an onward step of the target was smaller than the intervening smooth pursuit the "spatial" and

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[1] To find the gain (i.e., the quantity by which to scale each saccade) for which the asymmetry of compensation disappeared, we used the following method: assuming an arbitrary value of < 1 for mean gain, we recomputed the ON and BACK compensations after scaling each saccade by the assigned gain. If the asymmetry of mean ONward and BACKward trials persisted, we reduced the estimated gain; if the asymmetry reversed direction (BACK > ON), we increased the estimated gain. We repeated this procedure until ON and BACK compensations were equal

[2] It is possible that the gain is 1 and that the ON/BACK asymmetry is real. Such an asymmetry could be explained by the difference in hemispheric interactions required by the ONward conditions *vs* the BACKward conditions. For example, in the BACKward case the target flash is represented in the hemisphere that is generating the pursuit; in the ONward case the target is represented in the hemisphere opposite to that generating the pursuit. We ignore this possibility because the estimates of gain are reasonable and account sufficiently for the observations

"retinal" directions were opposite. These occurred 92 times for all the subjects taken together. On 70 of the 92 trials saccades were in the wrong horizontal direction, i.e., toward the "retinal" target. This contrasts sharply with responses to the analogous step-flash condition, described in the next section.

Step-flash paradigm

In the step-flash paradigm the mean intervening eye movement between the time of the flash and the start of the saccade was 4.2° (range: 1.1° to 9.5°). Figure 5 shows examples of responses of one subject to two stimulus configurations during one experimental session. In the example of onward steps (Fig. 5, left) the amplitudes of the first step (7°) and the first (intervening) saccade (5.5–5.8°) are similar in all three trials. The compensation, however, varies from almost zero (top) to 1 (bottom). In the right column of the figure we show trials in which the flash occurred in the hemifield opposite to that of the first step. Again, the variation in response was similar. Saccades were directed at the retinal target (top), the spatial target (bottom) or between the two (center). Among all subjects there were a total of 101 trials where the retinal and spatial directions were opposite (not shown). On 69 trials the direction of the saccade was toward the spatial location of the target. Thus, the *direction* of the saccades was correct on 68% of step-flash trials compared to 24% of analogous ramp-flash trials.

Figure 6 shows the distribution of compensations for the ON and the BACK cases, for one subject (A) and for the group (B, C). The wide distribution of compensations for step-flash experiments was comparable to that for the ramp-flashes (Fig. 3). The overall mean compensation (mean of all valid trials) was 0.53 (± 0.47, *SD*, $N=423$) for the step-flash (*vs* 0.29 ± 0.5 for the ramp-flash). For all subjects except WAF the mean compensation for the step-flash trials was significantly larger ($p < 0.05$) than that for the ramp-flash (Fig. 4). We computed the gains by a method analogous to that described for the ramp-flash; when adjusted for the estimated gain the mean compensation was 0.52 (± 0.49, $N=423$) (Fig. 4B). Again, gain computed by other methods produced similar results. The mean compensation measured in polar coordinates was 0.56.

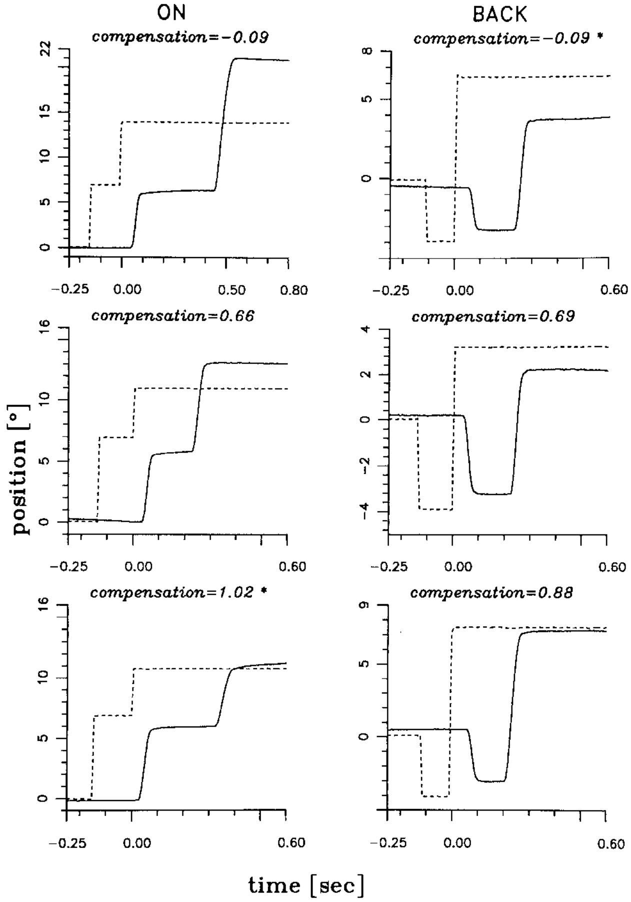

Fig. 5. Examples of responses to different step-flash stimulus configurations for 1 subject (LMA). Line styles, insets and organization are as in Fig. 2. In the examples on the *left* the target (flash) stepped onwards, in the same direction as the first step. On the *right* the flash occurred in the hemifield opposite to the first step

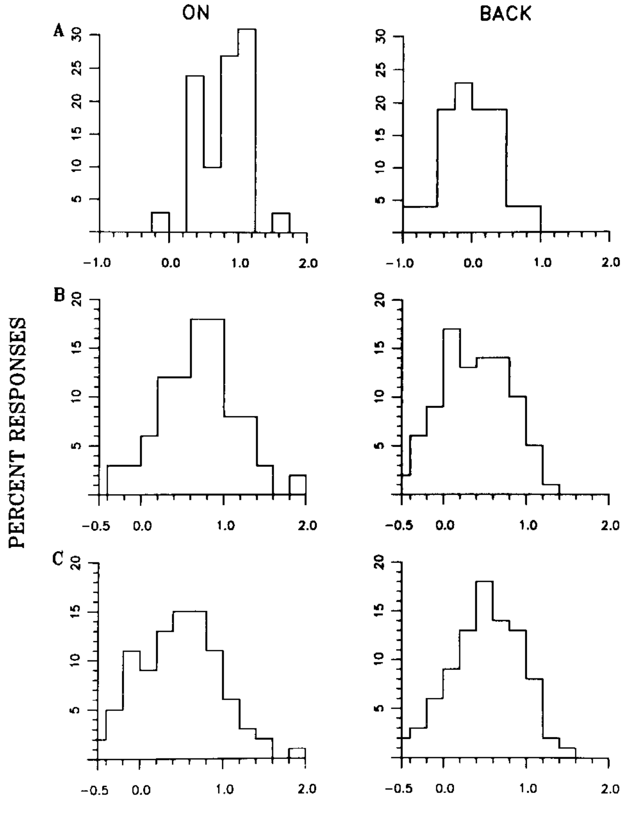

Fig. 6A–C. The distributions of compensations in the step-flash paradigm for the ONward (*left column*) and BACKward configurations (*right column*). **A** Histograms for the same subject as in Fig. 5 (LMA); **B** Histograms combining the responses of all the subjects. Note the asymmetry between ON and BACK. **C** When saccades are adjusted by the estimated gain (see text), this asymmetry is markedly lessened

Fixed reference experiment

In the fixed reference experiment all three subjects showed an increased compensation compared to an experiment with identical conditions without fixed references. For the step-flash the overall mean compensation was not significantly different (0.54, *vs* 0.56 for fixed reference). For the ramp-flash, in contrast, the difference was significant: 0.25 (± 0.53, $N=205$) *vs* 0.46 (± 0.47, $N=108$; $p<0.0005$).

Relationship of compensation to intervening eye movement

As noted above, trials were considered valid only if the vertical component was reasonably accurate. To ensure that the greater variability of the horizontal component, compared with that of the vertical, was not simply a reflection of the exclusion of trials with inaccurate vertical components, we compared the variability of the horizontal accuracy (both "retinal" and "spatial") to that of the vertical accuracy for *all* saccades made in the correct direction, regardless of vertical error. In the ramp-flash paradigm the mean coefficient of variance ($CV = SD/$mean) of gain for vertical components for each subject was less (mean: 0.32, range: 0.2–0.52) than that for horizontal components (mean: 0.55, range: 0.33–1.21). For the group of subjects the difference was significant ($p<0.05$). Similarly, for the step-flash paradigm the variability of the horizontal components was greater than that of the vertical components (mean CV of gain = 1.37 *vs* 0.47; $p<0.005$).

We have contended that the compensation is a parametric adjustment for intervening eye movement. One could argue that there is *no* use of an eye position signal at all; instead, the subjects simply compensate by an arbitrary amount in the appropriate direction. To test this, we determined whether saccade amplitude was related to the intervening eye movement by a stepwise multiple regression analysis (STEPWISE feature of the SPSS/PC + package). The assumption tested was that

$$\textit{saccade amplitude} = K + A \cdot \textit{retinal distance} + B \cdot \textit{intervening eye movement}.$$

If the amplitude of the intervening eye movement was not used, then the coefficient B would not be significantly different from 0. The statistical procedure does a linear regression on the first variable, then adds the second and determines whether this significantly improves the correlation (R^2). The procedure also estimates the values of the two coefficients, A and B. For the ramp-flash condition, retinal distance was significantly correlated for all subjects ($p<0.05$; $0.81<A<1$). Adding the intervening eye movement to the retinal distance significantly increased the value of R^2 for all subjects ($p<0.05$) except LMA ($-0.51<B<-0.13$; -0.01 for LMA). These results indicate that saccadic compensation was parametrically related to the intervening pursuit movement. A similar procedure for the step-flash condition revealed that addition of the intervening saccadic amplitude significantly ($p<0.05$) increased the value of R^2 for all subjects (range of equation coefficients: for retinal distance: 0.74 to 0.94; for intervening eye movement -0.41 to -0.88). We also tested the possibility that the saccade amplitude was determined by the *distance* between the two targets. The regression was significant ($0.65<R^2<0.92$), and the coefficient was between 0.67 and 0.83.

Relationship of compensation to other stimulus and response parameters

We considered the possibility that the variability in compensation from trial to trial (shown in Figs. 2 and 5) may have resulted from factors other than the intervening eye movement. To address this possibility, we plotted compensation values from individual trials against several stimulus and response parameters, including the specific stimulus configuration, the timing and amplitude of the responses and the attentional level of the subject (assessed indirectly by the gain of the vertical component of the saccade). Scatter plots showed that neither the extent of compensation nor its variability were related to either the horizontal or vertical step amplitude, to the distance between the step and the flash, to the vertical gain, or to the angular direction of the target. We used multiple regression techniques to determine whether compensation was significantly influenced by the variables listed in Table 3. The table shows that there were no consistent correlations: typically 1 or 2 subjects showed weak, albeit significant, correlations with one or two of the tested variables. One exception in the ramp-flash paradigm was the saccadic latency (see Discussion). For the combined data of all the subjects, the correlation of the tested variables taken together was 0.06 [$N=603$] for the ramp-flash and 0.07 [$N=431$] for the step-flash. Although these are significant correlations ($p<0.05$), it is clear that all these factors taken together explain little of the variance.

The influence of response latency is of particular interest in view of a recent brief report (Dassonville et al. 1990) that noted that the accuracy of saccades to targets that were briefly flashed around the time that another saccade occurred depended on the interval between the flash and the (first) saccade. The amplitude was found to be an exponential function of the elapsed time between the flash and the saccade. As Table 3 shows (*latency: flash-intervening saccade*), this was not a consistently related variable under our conditions.

During the experiments we tried to minimize fluctuations in attention by encouraging the subjects to attend to the targets. During analysis we discarded trials in which pursuit was poor or the subject failed to make a saccade to the step. We also excluded trials with inaccurate vertical components (gain <0.7 or >1.3). In addition, to ensure that attentional changes did not contaminate our results, we indirectly assayed attention by examining the accuracy (i.e., gain) of the vertical component for the five subjects for whom the vertical displacement of the target flash varied (see Methods). As inferred from the vertical accuracy,

Table 3. Multiple regression analysis of compensation. Variables which may have determined the extent of compensation are shown. The middle column shows the number of subjects for whom a significant ($p < 0.05$) correlation was found. The right column gives the coefficients of all variables that were significantly correlated on analysis of the pooled data. *Flash amplitude* and *step amplitude* refer to the retinal distance of the flash and the step respectively. The two *latency* measures for the step flash are the times from the flash to the first (intervening) saccade, and from the flash to the saccade directed at it. *Vertical gain* is the gain of the vertical component, and was used as an indirect measure of attention

Paradigm	Variable tested	N significant correlations		Combined coefficient
		Positive	Negative	
Ramp-flash	Flash amplitude	0	0	–
	Latency: flash-saccadic response	4	0	1.6
	Intervening movement	2	2	0.01
	Vertical gain	1	0	–
Step-flash	Step amplitude	1	1	0.02
	Flash amplitude	0	0	–
	Latency: flash-intervening saccade	1	0	3
	Latency: flash-saccadic response	1	0	–
	Vertical gain	0	0	–

attention was not a significant factor in determining the degree of compensation (Table 3).

Corrective saccades

Subjects occasionally made a second saccade toward the flashed target (mean: 29% of all trials). Determination of whether these were unrelated saccades or "corrective" saccades that should be included in the computation of compensation was inherently ambiguous. To determine whether such saccades had any influence on the outcome, we arbitrarily defined correctives as those saccades that improved (or did not worsen) the vertical accuracy of the first saccade to the flashed target. Including these saccades in the analysis improved the compensation by an average of 0.08 for the ramp-flash and by 0.02 for the step flash. When individual performance was compared with and without these "correctives", only one subject had a statistically significant ($p < 0.05$) improvement in compensation.

Discussion

Our results show that the saccadic system has a limited ability to localize targets in space by combining visual signals with information about eye position. This is true whether or not the position of the eye is reached by pursuit or saccadic eye movements, contrary to the finding of McKenzie and Lisberger (1986) in monkeys. However, the accuracy of saccades based on eye position signals is substantially less than normal saccadic accuracy. The poor performance of our subjects was not due to the brevity of the flash: performance was much better in the control-flash paradigm. It was also not due to a deficit in spatial memory: the elapsed time between the flash and the saccade on the ramp-flash and step-flash trials was comparable to normal saccadic latency (mean of <300 ms among subjects). Direction of attention away from the flashed target could not have been responsible either; if this were so, the vertical component of the saccade should have been equally inaccurate and variable, and it was not. The compensation was not all-or-none, rather it varied stochastically around a mean that was significantly less than unity (Figs. 3, 5).

Nature of the eye position signal used in saccades

Schiller and Stryker (1972) proposed a simple model of the saccadic system that reflected the known properties of the superior colliculus (SC). The location of the target was encoded in retinal coordinates by the retinotopic cells in the superficial layer of the SC. The location of activity in these cells determined the location of activity in the deep layer of the SC that, in turn, determined the amplitude and direction of the saccade. Visual information alone determined the metrics of the saccade. The demonstration by Hallett and Lightstone (1976a, b) that eye position information could also be used to determine target location (see Introduction) supported models of the saccadic system that combined retinal and eye position signals to reconstruct target position in spatial coordinates. The results of the studies by Sparks and Mays (1983) and Schiller and Sandell (1983) in which monkeys compensated for electrically evoked saccadic movement also were taken to support the "spatial" model (but see below).

Our analysis provides a quantitative estimate of the accuracy of the eye position signal available to the saccadic system. The results show that an eye position signal can be used in computing target location, but that this signal is inaccurate and variable. This seems to contradict the above studies, but those studies showed only that eye position signals were used when needed, not that they were *accurate*. For example, in the experiment by Schiller and Sandell (1983), compensatory saccades for intervening eye movements of about 18° typically brought the eye only within 4–8° of the target. Sparks and Mays (1983) and Sparks et al. (1987) noted that the saccadic accuracy in their study was poorer than usual. Data that might be interpreted as showing accurate use of an eye position signal is found in two studies (Skavenski and Steinman

1970; Hansen and Skavenski 1977) in which human subjects were required to fixate a target which was subsequently extinguished. In darkness, subjects were able to look away for about 5 s and then accurately return their gaze to the location of the previously fixated target. This finding does not, however, contradict our hypothesis that eye position signals are inaccurate: the accurate return saccade might simply signify the recall of a remembered motor command.

Similarly, our finding that the eye position signal had low fidelity and low gain when saccadic movements intervened between the flash and the saccade seems at odds with the results of Hallett and Lightstone (1976a, b). Intuitively, one might expect better performance in our step-flash paradigm, where the flash was presented while the eyes were stationary, than in their paradigm where the target was presented in mid-saccade. This apparent contradiction may be resolved by noting that in their study: (1) the "gain" of the two subjects was low (0.67–0.89) and similar to the compensation of some of our subjects; and (2) as noted by Honda (1989) the flash was always initiated at a fixed time after the onset of a fixed amplitude saccade; the eyes would always have moved approximately the same distance when the flash occurred. Since the target was sometimes left on for >200 ms, subjects could have used such trials to learn how far the eye had moved. Alternatively, compensation by a constant amount, even if inaccurate, would result in reasonably accurate saccades.

Our results provide the first direct evidence against the routine use of an eye position signal by the saccadic system. Theoretical arguments had led previous investigators to a similar conclusion. Becker (1988) argued that a system that depends on eye position information is likely to be inaccurate for small saccades made at eccentric locations. For example, to program a saccade made from an eye position at 20° to a target at 20.5° would require addition of the signal encoding eye position (20°) to the signal encoding retinal error (0.5°), followed by subtraction of the eye position signal to arrive at the signal encoding the tiny saccade. This computation is redundant and likely to be more prone to error than the process of simply using the retinal signal to determine saccade size. McIlwain (1988) pointed out, based on an earlier argument by Albano and Wurtz (1982), that the gain in the eye position feedback loop may be less than unity; this would render reconstruction of the target position inaccurate. He suggested a model with a variable gain element in the eye position feedback loop.

Becker (1988) proposed a model of the saccadic system that, under normal circumstances, depends strictly on visual information. Our finding that compensation improved in the fixed reference experiment, where some visual information was available, is consistent with this idea. When conditions require, Becker's model allows the saccadic system to use eye position information to locate targets in spatial coordinates. Our data suggest one addition to this model: a variable gain element in the feedback loop containing the eye position signal. Our observation of trial-to-trial variability and inaccuracy of compensation suggests that this eye position feedback is noisy and that the gain of this loop varies stochastically around the mean compensation. Since saccades are usually accurate and less variable, it is unlikely that the saccadic system uses this signal under normal conditions.

Intervening pursuit compared with intervening saccades

McKenzie and Lisberger (1986) (see Introduction) concluded that, in monkeys, eye position information was not used in computing saccades when pursuit movements intervened between a flash and a saccade to it. However, one of their three monkeys did compensate for some of the intervening pursuit movement, like 7 of our 8 subjects. Our results show that compensation for pursuit is less than compensation for saccades, but that pursuit is not ignored. Schlag et al. (1990) also found that monkeys compensated for pursuit movements but that they underestimated the pursuit velocity.

Why is there a difference between performance on ramp-flash and step-flash trials? One possibility is that there is a fundamental dichotomy between pursuit and saccades, as proposed by McKenzie and Lisberger (1986). We suggest two alternative possibilities: (1) There may be a substantial delay in processing eye movement information. In the step-flash paradigm there are some 200 ms between the first and second saccades during which this information may be processed. In the ramp-flash paradigm, in contrast, the eye position changes until the moment of the saccade. Information about pursuit occurring during the final 100 ms or so before the saccade might not be available. The correlation between latency and compensation on the ramp-flash paradigm in four subjects is consistent with this idea. (2) In the step-flash paradigm the distance between the two targets provides *visual* information that may be used to compute the metrics of the second saccade. Assuming an accurate first saccade, the size of the second saccade is simply given by the distance between the two targets. Indeed, for all subjects linear regression of saccade amplitude on the distance between the two targets showed that this may have accounted for much of the response. In the ramp-flash paradigm, in contrast with the step-flash, there is normally no visual information available that would allow an accurate saccade. The improved compensation for the ramp-flash condition in the fixed reference experiment is consistent with the notion that visual information may explain the greater compensation in the step-flash paradigm. Another explanation was proposed by Becker (1988): if the target flash (in the ramp-flash experiment) is perceived as moving with the eye, the saccade determined by the retinal signal would be correct. Our subjects, however, perceived the flash as stationary and such an explanation does not explain similar inaccuracy after intervening saccadic movements.

Accuracy of eye position information used in other tasks

The accuracy of the eye position signal in the control of limb movements and visual perception has also been studied. Bock (1986) asked subjects to look in a chosen direction in the dark, and then to point their arm in the same direction. This pointing was, therefore, based purely on an eye position signal. He found that, while the gain (*arm position/eye position*) was close to unity, there was a great degree of variability. In contrast, Hansen and Skavenski (1977) found that a hammer blow could be directed with great accuracy $(<0.5^{\circ})$ using an eye position signal, even when the target was briefly illuminated during a saccade (Hansen and Skavenski 1985). For perceptual localization, Matin et al. (1969) showed inaccuracies in visual localization that persisted for up to 1 s after a saccade. Bridgeman et al. (1975) have shown that subjects often fail to detect displacement of the visual world during a saccade, suggesting that eye movement signals are unreliable. However, as noted by Jeannerod (1983) it may be incorrect to compare the results from studies of perception to those from studies of limb movements, since each of these functions involves different neural structures. Similarly, comparison between eye and limb movement may be inappropriate. Although some control systems may have access to an accurate eye position, our data suggests that an accurate signal is not available to the saccadic system.

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