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Extent of compensation for variations in monkey saccadic eye movements

Received: 13 July 1999 / Accepted: 2 December 1999 / Published online: 23 February 2000
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Abstract We investigated and quantified the ability of the primate saccadic system to generate accurate eye movements in spite of naturally occurring variations in saccadic speed and trajectory. We show that the amplitude of a series of saccades directed to the *same* target is positively correlated to their peak speed, i.e., the faster the saccade, the bigger its amplitude. We demonstrate that this result cannot be simply accounted for by the main sequence, and that on average the saccadic system is able to compensate for only 61% of the variability in speed. Deviations from the average trajectory are also only partially compensated: the underlying mechanism, which tends to bring the eyes back toward the desired trajectory, underperforms for small movements and overperforms for large movements. We also demonstrate that the performance of this compensatory mechanism, and the metrics of saccades in general, do not depend on the presence of visual information during the movement. By showing that deviations from the desired behavior are corrected during the saccade, our results further support the hypothesis that the innervation signal that generates saccadic eye movements is not pre-programmed but rather is dynamically adjusted during the movement. However, the compensation for deviations from the desired behavior is only partial, and the underlying mechanisms have yet to be completely understood. Although none of the current models of the saccadic system can account for our results, some of them, if appropriately modified, probably could.

Key words Saccades · Accuracy · Curvature · Compensation · Monkey

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Introduction

Common sense argues that saccadic eye movements have one property that differentiates them from most movements: during saccades neither the speed nor the trajectory of the eyes is under voluntary control. The only voluntary decisions that one can make are where and, to a certain extent, when to make a saccade. The reason for this behavior is very simple: during saccadic eye movements vision is seriously impaired (Carpenter 1988). This has two implications: first, to minimize the intervals of poor vision one has to minimize the duration (i.e., to maximize the speed) of saccades. Second, because during the movement we cannot see, it makes no difference which trajectory the eyes follow: all that matters is their orientation when they stabilize. Consequently, the only strategy that makes sense (from an evolutionary standpoint) is to redirect, and thereafter stabilize, the eyes as quickly as possible. Under these conditions it makes perfect sense that, once the target for a saccade has been identified, a saccadic generator should simply produce the fastest movement possible under the current conditions, excluding any voluntary control.

In the last 30 years many researchers have worked to understand how the saccadic generator produces the critical element of the innervation required to make a saccade, the burst or pulse. Over 20 years ago it was proposed that the pulse is not pre-programmed, but rather is dynamically generated by a feedback controller (Robinson 1975). Visual information was excluded as a source of information about the residual motor error, because saccades are fast and delays in the visual pathways are long. Instead, it was proposed that an internal estimate of the dynamic motor error is computed by using the efference copy of the motor command to estimate either the position of the eyes in the orbit (Robinson 1975; Zee et al. 1976) or the displacement of the eyes since the beginning of the movement (Jürgens et al. 1981). One of the implications of such a scheme is that variations in the speed or direction of saccadic eye movements should have a negligible effect on their accuracy, because alterations in the move-

ment kinematics would be compensated by the feedback loop mechanism. In the last 20 years a wealth of behavioral, physiological and anatomical experiments have focused on the properties of the saccadic system, often taking inspiration from the above mentioned models. Even though perturbation studies based on electrical stimulation have shown that some kind of feedback mechanism is likely to be at work (e.g., Becker et al. 1981; Keller et al. 1996), little is known about how well the saccadic system is actually able to compensate for deviations from the desired behavior.

In this study we investigated the ability of monkeys to make accurate saccadic eye movements despite variability in their speed and trajectory. It should be noted that, while the vast majority of the physiological data available come from experiments in monkeys, compensation has never been investigated in these animals. Only three studies, all on human subjects, have investigated the relationship between the speed and the accuracy of saccades. The conclusion of one study (Jürgens et al. 1981) was that, for saccades directed to the same visual target, changes in velocity have negligible effect on movement amplitude, even though a positive correlation between saccade duration and amplitude was found. The second study (Smit et al. 1987), where a different behavioral paradigm was used, found no correlation between amplitude and duration. However, it appears from their Fig. 5 that some correlation between amplitude and peak speed was present, even though it was not investigated. Finally, the third paper (Bains et al. 1992) found no correlation between amplitude and peak speed (i.e., they reported perfect compensation), but did not investigate the amplitude-duration relationship. Thus, it seems possible to conclude from these studies that the human saccadic system largely compensates for speed variations, even though it remains unclear how well it does so.

Similarly, compensation for deviations from the desired trajectory have only been investigated in three studies, all with human subjects (Becker and Jürgens 1990; Erkelens and Sloot 1995; Erkelens and Vogels 1995). Here again the results are not in perfect agreement: while the earliest study found evidence indicating partial compensation (e.g., if the eyes start to the left of the target they end up to the left of it, but less so), the more recent ones reported overcompensation (e.g., if the eyes start to the left of the target they end up to the right of it). Unfortunately, those studies evaluated the compensatory ability of the saccadic system relying on a measure that has some major drawbacks (see “Materials and methods”).

In this paper we provide data regarding the compensatory ability of the monkey saccadic system, and we try to reconcile the discrepancies between previous studies in humans. A necessary step to study deviations from the desired behavior is to define the desired behavior. Although there is no way to know what the monkey’s desired behavior was on a trial by trial basis, we think that the best estimate of it is represented by the average behavior. Thus, we estimated the desired amplitude and tra-

jectory of saccades to a given target as the average amplitude and trajectory of a series of saccades directed to that target (see “Materials and methods”). We then computed the extent to which the saccadic system compensates for deviations from this desired behavior. We find evidence in support of a dynamic generation of the saccadic innervation signal, because there is some compensation during the saccade for deviations from the desired behavior. However, we find that this compensation is only partial, and that there appear to be some differences between how the system compensates for variations in eye speed and for deviations that bring the eyes away from the desired trajectory.

Materials and methods

Behavioral procedures

Three male rhesus monkeys (*Macaca mulatta*) were trained to perform oculomotor tasks for a liquid reward. Eye positions were recorded using the magnetic search coil technique (Fuchs and Robinson 1966) with an implanted eye coil (Judge et al. 1980). The eye position signals were sampled at 1 kHz; eye velocity was computed using a central difference algorithm. All animal care and experimental procedures were approved by the Institute Animal Care and Use Committee and complied with Public Health Service Policy on the humane care and use of laboratory animals.

Monkeys made saccades between a fixation point and visual targets located at four different eccentricities (5°, 10°, 25° and 38°) and in different directions [8 for the three smallest eccentricities (every 45° starting from purely horizontal), and 3 for 38° saccades (45° up and to the right, straight up and 45° up and to the left)]. The fixation point was located in the center of the screen for the three smallest eccentricities, whereas it was offset for 38° saccades. The target locations were randomly interleaved, and the fixation point was always turned off at the same time the target came on. To test for the contribution of visual mechanisms, the target was either visible throughout the saccade (stable condition) or briefly (100 ms) presented (flashed condition). In all compensation experiments these two conditions were randomly interleaved. In an additional experiment we added a third condition, wherein the target was extinguished just after (within 5 ms) saccade start. Monkey 1 had some previous experience with the tasks used in this study, monkey 2 was highly trained, and monkey 3 had never been used in any experiment.

Data analysis

For each saccade we computed amplitude, peak speed (i.e., the maximum value of the magnitude of the velocity vector) and duration, using a speed criterion (20°/s) to identify saccade start and end. Note that using a different criterion would have a negligible effect on the amplitude measure but, because of the slow drifts that sometimes follow saccades, a different criterion could produce much different estimates of saccade duration. Accordingly, we consider amplitude and peak speed as the most reliable measures for this study, and we will use duration only to compare our study with previous ones.

Speed compensation measure

To quantify the ability of the saccadic system to compensate for variations in movement speed, we must first clearly define the behavior expected from a system that perfectly compensates and from one that does not compensate at all. Thus we decided to look at models of the saccadic system that on average produce accurate

saccades that fall on the main sequence (Bahill et al. 1975) and that have such compensatory behaviors.

An example of a model that displays perfect compensation is Robinson's model (Robinson 1975; Zee et al. 1976); when the magnitude of the pulse of innervation is perturbed, the speed of the eyes is altered, but the eyes still get accurately on target. In other words, the speed-amplitude relationship predicted by that model has a null slope. The other extreme of the spectrum is represented, for example, by a time-duration controller, like the one proposed by Clark and Stark (1975). In this case the variable controlled is the duration of the movement (or, more precisely, of the pulse of innervation); if this variable is a proper function of the desired amplitude, on average saccades will get on target. However, variations in speed will not be compensated for, and a doubling in speed (for a fixed desired amplitude) would cause a doubling in the amplitude of the movement produced (because the duration would remain constant). The slope of the speed-amplitude relationship would then be equal to the desired amplitude divided by the speed necessary to acquire that target (remember that, because there is no compensation, by definition only one speed will be appropriate to acquire the target).

Unfortunately, this last slope (which represents the no-compensation case) varies as one moves along the main sequence. This means that it is not possible to use the slopes of the speed-amplitude relationships extracted from the data to directly quantify the compensatory ability of the saccadic system. To address this problem we introduce the following measure, called percent compensation for speed:

$$C_S = 100 \left(1 - k \frac{\overline{PS}}{\overline{A}} \right)$$

where k is the slope of the relationship between peak speed and amplitude for a group of saccades, \overline{PS} is the average peak speed for those saccades, and \overline{A} is their average amplitude. This measure indicates where the slope extracted from the data lies relative to the null slope (i.e., perfect compensation) and the no-compensation slope (which is equal to $\overline{A}/\overline{PS}$). C_S is equal to 0 for no compensation, 100 for perfect compensation, and it is greater than 100 if the system overcompensates. Values between 0 and 100 indicate a partial compensation.

Trajectory compensation measures

It is much more difficult to define a measure that quantifies the compensation for deviations that bring the eyes away from the desired trajectory. Even defining the desired trajectory is a major problem. The most intuitive definition would be a saccade straight to the target; however, there are two problems with this approach. First, it is known that saccades often are characterized by an idiosyncratic curvature, i.e., they are curved, even on average (Bahill and Stark 1977; King et al. 1986; Viviani et al. 1977). Thus, assuming that the saccadic system attempts to produce straight saccades is unrealistic (because it does not do so, even on average). Second, it is impossible to rule out the possibility that some of the curvature observed is due to an imperfect calibration of the eye coil signals, or to the use of a two-dimensional recording system to record three-dimensional movements (which implies that we are looking at the projection of the movement on a plane). These effects could be important, because the deviations we observed were usually smaller than 1° . The most conservative solution to address both these problems is to define the desired trajectory as the average trajectory, and then to compute, for each saccade, the difference between the actual trajectory and this average trajectory.

To compute the average trajectory we used the following procedure. We first divided up the saccades into separate groups for each monkey, target location and behavioral paradigm. Then, within each group, we translated the origin of each saccade to the location of the fixation point (this translation was always very small, on average equal to 0.28° and smaller than 0.56° for 95% of the saccades), and we converted the trajectory from Cartesian to

polar coordinates. Then we sampled each trajectory at 50 equally spaced eccentricities r_k , measuring the angle $\varphi(r_k)$ for each value of r_k . Thus, we can express the i -th trajectory as:

$$T_i = [r, \varphi_i(r)]$$

where r is a vector containing all the r_k . Computing, for each r_k , the average $\overline{\varphi}(r_k)$ we obtained the average trajectory for each group of saccades, which we can express as:

$$\overline{T}_i = [r, \overline{\varphi}_i(r)]$$

Because not all the saccades in one group have the same amplitude, as r_k increases the number of saccades with at least that amplitude decreases. When only a few saccades are left (for large values of r_k), the average $\overline{\varphi}(r_k)$ becomes unreliable. Thus, we computed the average trajectory up to an eccentricity that was achieved by at least 25% of the saccades, and then truncated all the saccades to this value of eccentricity (note: this was done only for the trajectory study). To obtain the deviations of each trajectory from the average, we then computed, for each saccade, the differential trajectory:

$$T_i^{diff} = T_i - \overline{T}_i = [r, \varphi_i(r) - \overline{\varphi}_i(r)]$$

In Fig. 1A we show a family of saccadic trajectories from monkey 1 (thin lines); the average trajectory \overline{T} is also plotted (thick line), together with the truncation line (dashed line indicates where the saccades are truncated to compute \overline{T} and T_i^{diff} , because of some variability in the origin of saccades, this line does not exactly indicate the truncation points, but it is a very good approximation). Two things should be noted: first, the amount of truncation (i.e., the part of the trajectories that goes past the truncation line) is minimal, and significant only for a handful of saccades. Second, for saccades incurring significant truncation, the truncated portion can be directed either away or towards the target (i.e., the truncation does not hide any consistent pattern of compensation). This is true for the whole data set (based on our visual inspection). In Fig. 1B we show the trajectories T_i^{diff} obtained by subtracting the average trajectory from the individual trajectories (note that the abscissa and ordinate have different scales). Once this procedure has been applied we simply consider positions along and away from the desired (average) trajectory, rather than horizontal and vertical displacements. It is now easy to separate saccades into three groups: those that exhibited no compensation at all (e.g., dashed line in Fig. 1C), a partial compensation (e.g., dash-dotted line in Fig. 1C), or an excessive compensation (e.g., solid thick line in Fig. 1C).

To quantify the amount of compensation, we measured, for each saccade, the distance that the eyes have covered towards the desired trajectory after having deviated away from it. This was simply defined as the difference (c in Fig. 1D) between the maximum and the final deviation from the desired trajectory (m and f , respectively, in Fig. 1D). Note that the maximum deviation was always measured in the direction of the initial deviation of the eyes (otherwise several saccades characterized by overcompensation would be classified as having no compensation, see solid line in Fig. 1C). Finally, to get an indication of what fraction of the deviation was compensated for, we defined the percent compensation for trajectory:

$$C_r = 100 \cdot \frac{c}{m}$$

Similar to C_S , this measure is equal to 0 for no compensation, between 0 and 100 for partial compensation, and larger than 100 for excessive compensation.

To allow a comparison with previous studies we also computed the amount of compensation as the slope of the relationship between the overall direction (β in Fig. 2, dependent variable) and the initial direction (α in Fig. 2, independent variable); note that these directions are always relative to the target direction. Because the definition of initial direction in previous studies varied, we simply defined it as the direction relative to the target at 1° of eccentricity from saccade start. A slope of 1 has been used in the past to indicate a lack of compensation, a ratio between 1 and 0 for partial compensation, and a negative ratio for overcompensa-

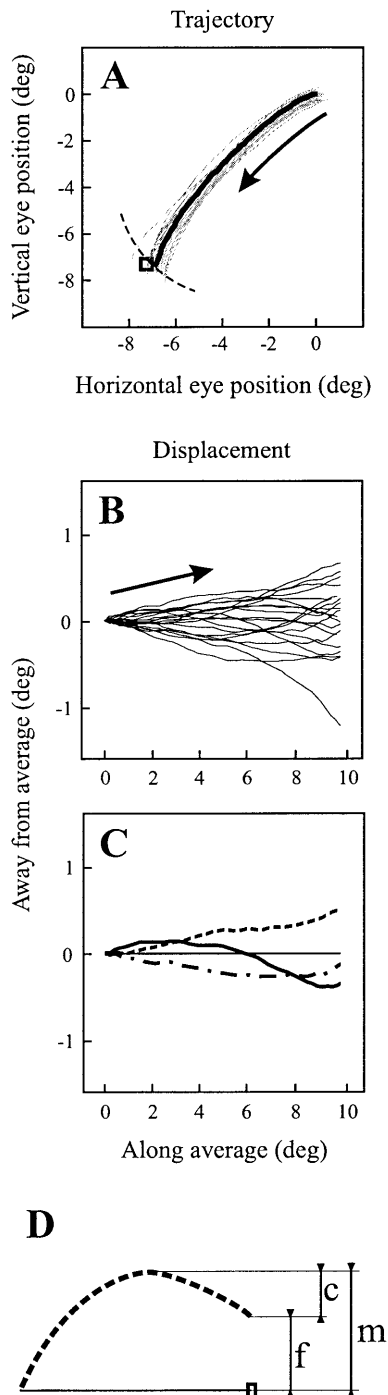


Fig. 1A–D Measuring trajectory compensation. **A** Saccades do not necessarily go straight to the target (*square*), even on average. The average trajectory for this data set is indicated with a *thick line*; the *dashed line* indicates the point where saccades were truncated to compute the average. The *arrow* indicates the direction of movement of the eyes. **B** The deviation from the average trajectory is computed by subtracting (see “Materials and methods”) the average trajectory from each individual trajectory. **C** Examples of different compensatory behaviors taken from **B**. Deviations can be partially compensated (*dot-dashed line*), overcompensated (*solid thick line*) or not compensated at all (*dashed line*). **D** m represents the maximum deviation from the desired trajectory in the direction of the initial deviation, f represents the deviation from the desired trajectory at the end of the movement, c is the difference between m and f , and represents the amount of compensation (i.e., how much the eyes turned back toward the target). Data from monkey 1

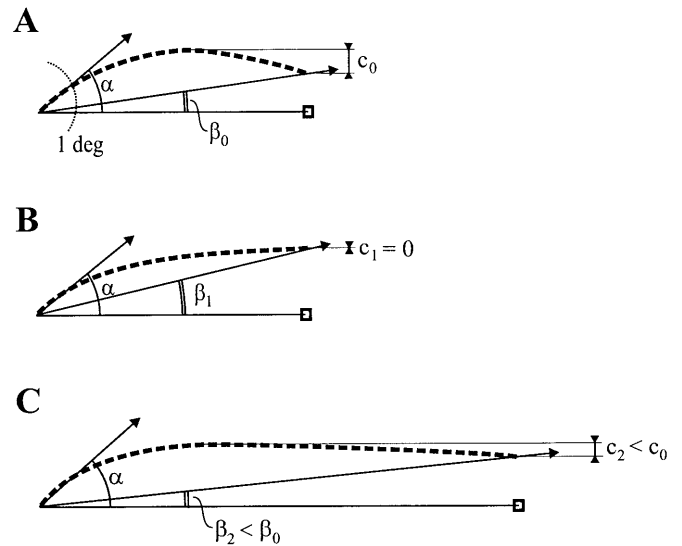


Fig. 2A–C Measures of compensation used in previous studies. **A** The initial direction α of a saccade is the angle between the line that goes through the origin of the saccade and the position when the eyes have covered 1° , and the line that goes through the origin of the saccade and the target. The overall direction β is defined similarly, but using the position of the eyes at the end of the saccade. The measure c that we use to compute the compensation (see Fig. 1) is also shown. **B** $\beta < \alpha$ does not imply that the eyes curve back towards the target (i.e., compensation). **C** $\beta_2 < \beta_0$ does not imply a larger compensation, which would require $c_2 > c_0$

tion (Erkelens and Sloot 1995). Becker and Jürgens (1990) used instead the slope of the relationship between $(\beta - \alpha)$ (dependent variable) and α (independent variable), which is essentially equivalent. Here we did not use this measure as our main tool because we think that it has some important limitations. First, we consider a redirection toward the target necessary to talk about compensation, and the simple fact that β is smaller than α (i.e., their ratio, and thus the slope of their relationship, is smaller than 1) does not necessarily imply that the eyes are redirected toward the target, as shown in Fig. 2B. For example, the saccade in Fig. 2B could be produced whenever a transient disturbance directs the eyes away from the desired trajectory at the beginning of the movement and then disappears. Without any compensation mechanism, the eyes would first deviate and then proceed parallel to their original trajectory: under these conditions, β would be smaller than α even though no compensation took place. Another problem with using the initial and overall angle is that, given a certain α , a smaller β (and thus a smaller slope for the relationship between α and β) supposedly indicates a better compensation. However, this holds only when movements of the same amplitude are considered. So, for example, β is smaller for the large movement in Fig. 2C than it is for the small movement in Fig. 2A but it would be very questionable to say that the movement in Fig. 2C is characterized by a better compensation. Thus, we feel that α and β cannot be used to make a direct comparison between saccades of different amplitude, which is one of the goals of this study. Consequently, we will present our data using the c_T percent compensation measure described previously, and we will use the slope of the relationship between α and β only to compare our data with previous studies.

The data analysis was performed using Matlab programs (The Mathworks, Natick, MA); all statistical tests were performed using the SPSS package (SPSS, Chicago, IL).

Results

Compensation for variations in speed

We studied, for each monkey, for each target location and each behavioral paradigm how the amplitude of saccades depends upon their peak speed. In Fig. 3 we plotted amplitude vs peak speed for saccades made to targets located at different eccentricities in one direction (see legend for details). For each monkey, and each direction and behavioral paradigm (stable or flashed target) we computed the main sequence (dashed line) by fitting (in the least squares sense) the data with the function:

$$PeakSpeed = A \cdot \left(1 - e^{-\frac{Amplitude-B}{G}}\right)$$

where A , B and G are free parameters. We also used a linear regression analysis to compute the slope and correlation coefficient of the amplitude-peak speed relationship for each group of saccades directed to the same target (this was done separately for saccades to stable and flashed targets); examples of such regression lines are plotted in Fig. 3 (solid lines).

If variations in saccade speed (from now on it is often implied that we are looking at peak speed) were fully compensated, the slope of the amplitude-peak speed regression lines would be zero. Clearly, in all three monkeys and for almost every target eccentricity, changes in peak speed affected the amplitude of saccades. More precisely, we found that the slope was significantly different from zero ($P < 0.05$) in 78% (126 out of 162 – 3 monkeys, 3 amplitudes for 5 directions, 4 amplitudes for 3 directions, 2 behavioral paradigms) of the cases, with fairly strong correlation coefficients (average = 0.61; 90% confidence interval = 0.12–0.90) that decreased slightly with target eccentricity, especially in the third monkey. When the slope was negative, it was never significantly different from zero, indicating that there was never overcompensation. For the three monkeys, the average slopes of the regression lines were 0.0070, 0.0104 and 0.0073 s, respectively. The overall average was 0.0082 s (90% confidence interval = 0.001–0.015 s). Thus, on average, a change of 100°/s in speed was associated with an amplitude change of almost 1°.

Before going on to quantify the extent of compensation, it is important to show that the dependency between amplitude and speed cannot be accounted for by a simple main sequence relationship (i.e., saccades to a given target could be different in size because they are so programmed, and the changes in peak speed would then be a consequence of that). To do so we first computed the main sequence for each direction (see above); then, for each saccade we computed the difference Δs between the speed of the saccade and the speed predicted by the main sequence for saccades of that amplitude. If our data were the result of noise superimposed on the main sequence, any correlation between the speed difference Δs and amplitude should only be due to chance.

This was tested by using the bootstrap technique (Efron 1982; Efron and Tibshirani 1991) in the following

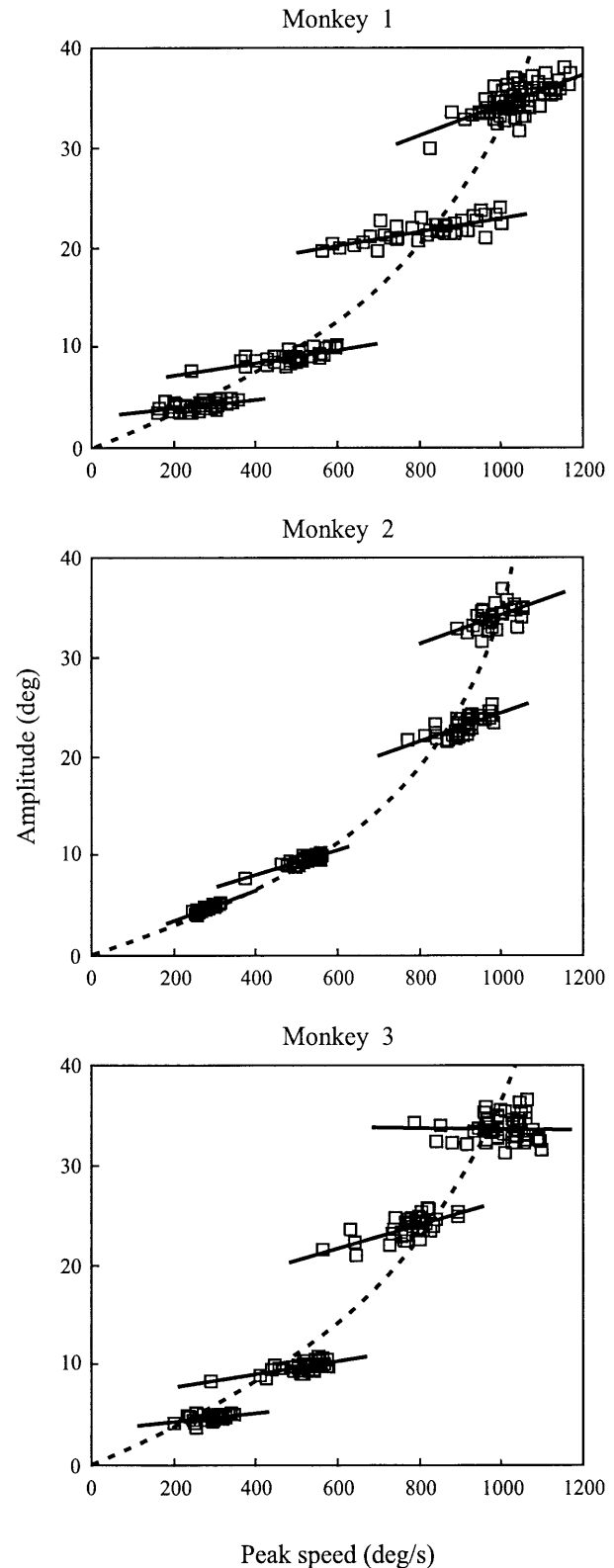


Fig. 3 Dependency of saccade amplitude on peak speed. Each cluster of points represents saccades to a different target (stable condition); within most clusters there is a clear positive correlation between amplitude and speed. The dashed lines indicate the so-called *main sequence* (see text). Each panel contains data from a different monkey and for a single direction (45° up and to the right for monkey 1, 45° up and to the left for monkey 2, and straight up for monkey 3)

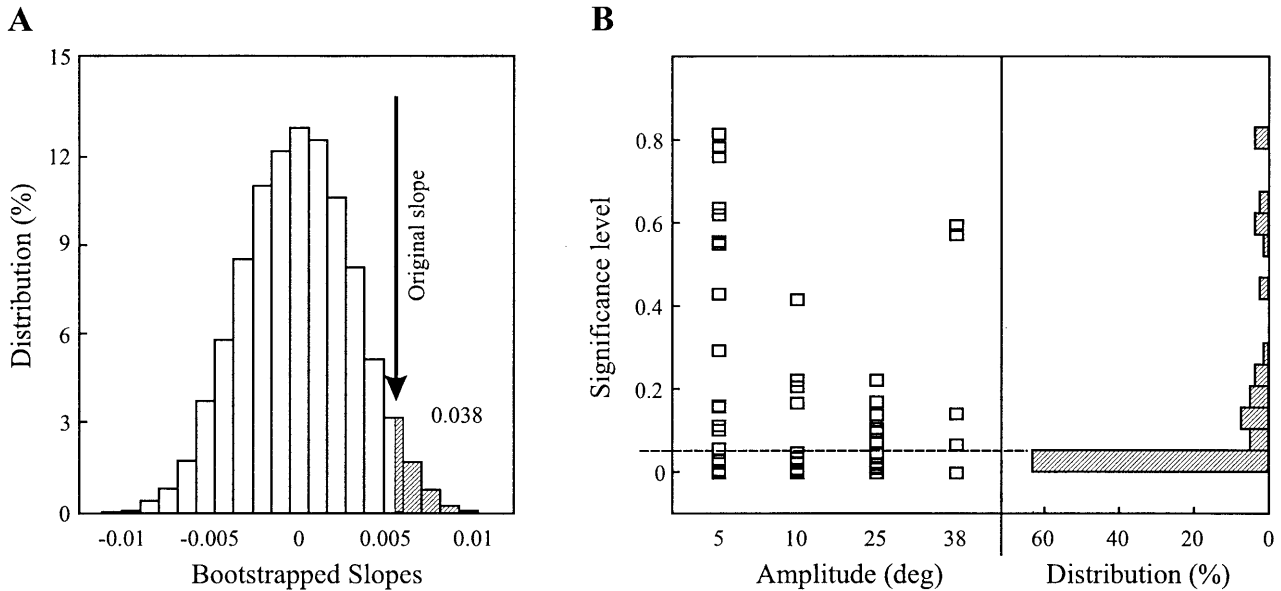


Fig. 4A,B Main sequence cannot account for speed-amplitude relationship of saccades to the same target. **A** Example of the distribution of slopes obtained by correlating the difference between the actual speed and the speed predicted by the main sequence with the amplitude of saccades after having randomly paired these measures for all the saccades to a given target (see text). The likelihood of obtaining a slope larger than or equal to the original one (i.e., that obtained with the original speed/amplitude pairings) is very small (3.8%, called significance level). **B** Summary of all the significance levels (one for each monkey and target location). Note that there are some high values for small saccades, in agreement with data shown in Fig. 3 (strong overlap between data and main sequence for some small saccades). Nonetheless, this analysis rules out the possibility that the speed-amplitude slopes are simply a consequence of a noisy main sequence

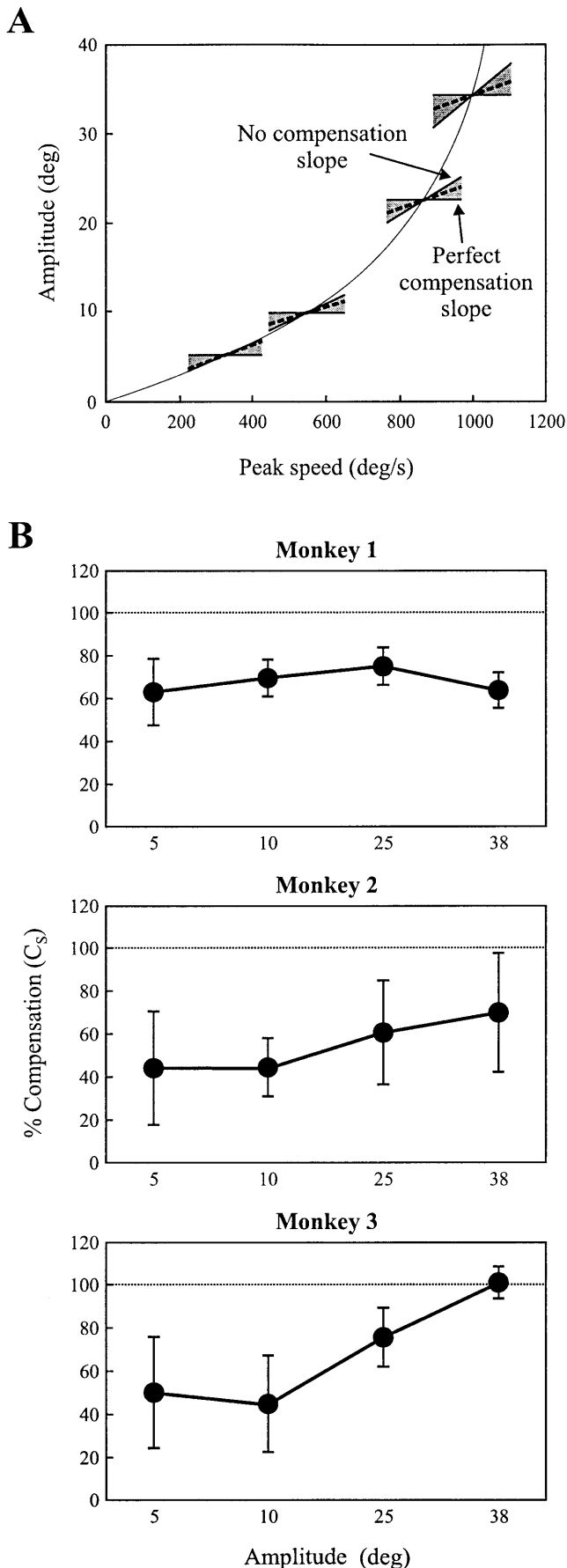
way: the Δs and amplitude values for saccades to each target were randomly paired (i.e., the Δs of each saccade was paired with the amplitude of one of the saccades to the same target, chosen at random), obtaining a new set of data points. Then, the slope of the relationship between Δs and amplitude for this bootstrapped data set was computed. This process was repeated 1000 times for each group of saccades to different targets, so that we obtained a distribution of slopes (an example of one such distribution is reported in Fig. 4A). This distribution can now be used to quantify the likelihood that a slope larger than or equal to that obtained with the original (i.e., not bootstrapped) data set is due to chance. This value essentially represents the probability that the relationship between amplitude and speed for saccades to that target arises because of a noisy main sequence. For the example shown in Fig. 4A this probability (approximately equal to the dashed area, although we counted the actual number of bootstrapped data sets having a larger slope) is equal to 3.8%, i.e., the significance level is equal to 0.038.

In Fig. 4B we report all the significance levels so obtained (one for each monkey and target location); note that for more than 60% of the cases the significance level is lower than 0.05. It is worth pointing out that even if

this were true in a very limited number of cases (theoretically just one) we could conclude that the relationship we observed between speed and amplitude is *not* due to a main sequence effect. The fact that this was true in so many cases makes the case even stronger, indicating that changes in peak speed indeed *cause* changes in amplitude (if the test had failed we would have concluded the opposite, i.e., that changes in desired amplitude cause changes in peak speed).

Now that we have ruled out the possibility that the amplitude dependence on speed can be imputed to a main sequence effect, we can go on to quantify how well the saccadic system compensates for variations in speed. As we pointed out in “Materials and methods” (“Speed compensation measure”), because the slope expected if there were no compensation is not a constant, the slopes can tell us only whether the system compensates or not, but they cannot be used to directly establish how good the compensation is. In Fig. 5A we have re-plotted (dashed lines) the slopes from the middle panel (monkey 2) in Fig. 3, together with the perfect compensation (null slope, one extreme of each bow tie) and no compensation (positive slope, other extreme of each bow tie) slopes. Note that the latter slope, whose computation has been explained in detail in “Materials and methods,” is different for the different groups of saccades (if extended it would always go through the origin of the axes). To quantify where each slope is relative to the perfect compensation slope and to the no compensation slopes, we computed, for each group of saccades, the percent compensation C_S (see “Materials and methods”). This parameter equals 100 when the compensation is perfect (horizontal slope) and 0 when there is no compensation (slope at the steep extreme of the bow tie); in other words it indicates the percentage of the variation in speed that is compensated for.

To test whether this parameter varied across monkeys and whether the behavioral paradigm (stable or flashed target) and target eccentricity were influential factors, we



performed a univariate ANOVA test. We found that it varied across monkeys and as a function of eccentricity; the interaction of these parameters also had a significant effect. On the other hand, the paradigm (stable vs flashed target) was not a significant factor. Because of these results we only pooled saccades across paradigms, and we report here separately the data for the three monkeys and for the various amplitudes (Fig. 5B). In the three monkeys the average percent compensation was 68%, 53% and 62%, respectively. The overall average was 61%. In monkeys 2 and 3, there was a clear tendency for the compensation to be larger for large amplitudes, but that was not the case for the first animal.

Finally, we looked at the correlation between the duration and the amplitude of movements to each target location (again independently for each monkey and paradigm). There was a significant correlation ($P < 0.05$) in only 24% of the cases, and amongst these the slope was positive in 40% of the cases, and negative in the remaining 60%. The overall average slope and correlation coefficient were $-7.7^\circ/\text{s}$ and -0.03 , respectively. Thus, amplitude was largely independent of duration, although it was strongly dependent upon peak speed.

Compensation for trajectory deviations

To test the ability of the saccadic system to compensate for deviations that bring the eyes away from the desired trajectory, we computed the percent compensation for each saccade (see “Materials and methods” and Fig. 1). Because this parameter is not normally distributed, we studied its overall distribution, and started off by testing whether it varied with target eccentricity as well as across monkeys and behavioral paradigms. This was done using two non-parametric measures: Kendall’s correlation coefficient and Spearman’s correlation coefficient. Both tests gave the same answer: the percent compensation was influenced only by the eccentricity of the target ($P < 0.001$); no significant differences were observed among the three monkeys and the paradigm was not influential. Thus, in Fig. 6 we plotted the distribution of the percent compensation for each target eccentricity, pooling the data across directions, paradigms, and monkeys. Note that both the median (dashed line) and the mean (solid line) compensation increase considerably with target eccentricity, indicating that larger saccades are indeed characterized by more compensation.

Fig. 5A,B Compensation for deviations in speed. **A** To evaluate the ability of the saccadic system to compensate for variations in speed we compute where the actual speed-amplitude relationship (dashed lines) lies in respect to the perfect compensation slope (horizontal line delimiting each bow tie) and to the no-compensation slope (tilted line delimiting each bow tie). Note that this latter slope is a function of amplitude. Data from Fig. 4, middle panel (monkey 2). **B** Mean and standard deviations of the percent compensation C_S for the three monkeys. The data are grouped based on amplitude, whereas they are pooled across directions and paradigms

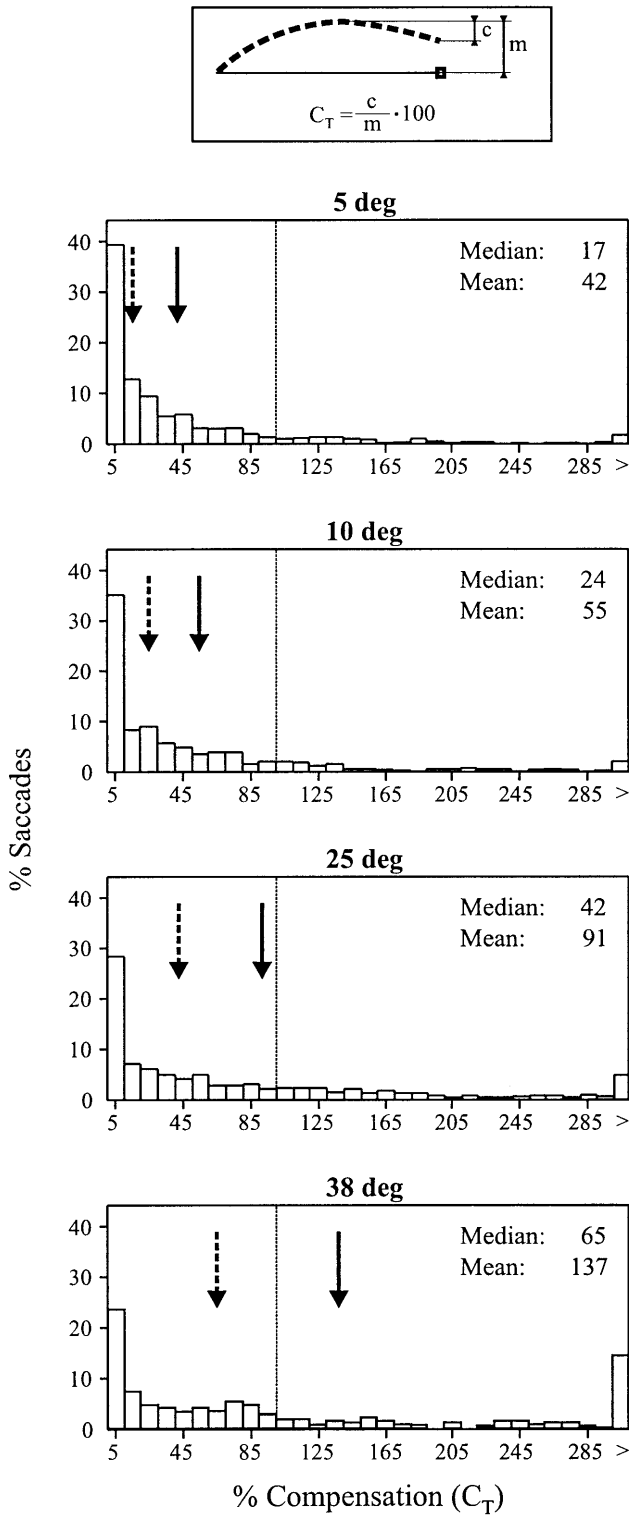


Fig. 6 Compensation for deviations away from the desired trajectory. Distribution of the percent compensation C_T (see top inset) as a function of target eccentricity. The arrows indicate the median (dashed) and mean (solid) value. A value of compensation larger than 100% (vertical dashed line) indicates that if, for example, a vertical saccade started to the left of the target, it ended up to the right of it, and vice versa. Data pooled from all monkeys, amplitudes, directions and paradigms

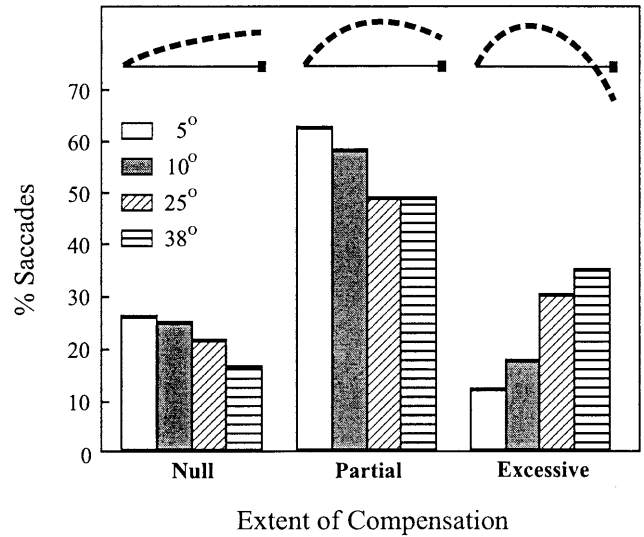


Fig. 7 Probability of null (0%), partial (between 0% and 100%) and excessive (>100%) compensation as a function of target eccentricity. Schematics representative of each extent of compensation are reported at the top of each group. As in Fig. 6, the whole data set is represented

Subsequently we grouped the saccades represented in Fig. 6 according to the extent of compensation, which could be either partial, excessive or null (see “Materials and methods” and Fig. 1D). We plotted (Fig. 7) the proportion of each group as a function of target eccentricity; schematics of saccades belonging to each group are plotted on top of each group of bars. Note that as saccade amplitude increases, more saccades exhibit an excess of compensation, while fewer show a partial or null compensation.

To determine whether the compensatory behavior observed was due to the presence of a compensation mechanism or simply to chance fluctuations in the innervation, we formulated the null hypothesis that if there were no compensation mechanism, the likelihood of compensation should be independent of the amount of deviation from the average trajectory. Alternatively, if a compensatory mechanism were at work, one would expect that compensation is more likely to occur when the deviation is large. To test this hypothesis, we computed the deviation from the average trajectory when the eyes had traveled 4° from the beginning of the saccade (a value chosen because it was smaller than the smallest target eccentricity used in our experiment). We then plotted the probability of compensation (i.e., the percentage of trials in which there was either partial or excessive compensation) as a function of this deviation, pooling all the data (Fig. 8A). Even though large deviations do not occur very often (Fig. 8B), the trend clearly indicates that larger deviations are more likely to be compensated, and thus strongly argues for the existence of a compensatory mechanism. We repeated this analysis separately for each target eccentricity, and obtained the same results. Finally, measuring the deviation earlier during the sac-

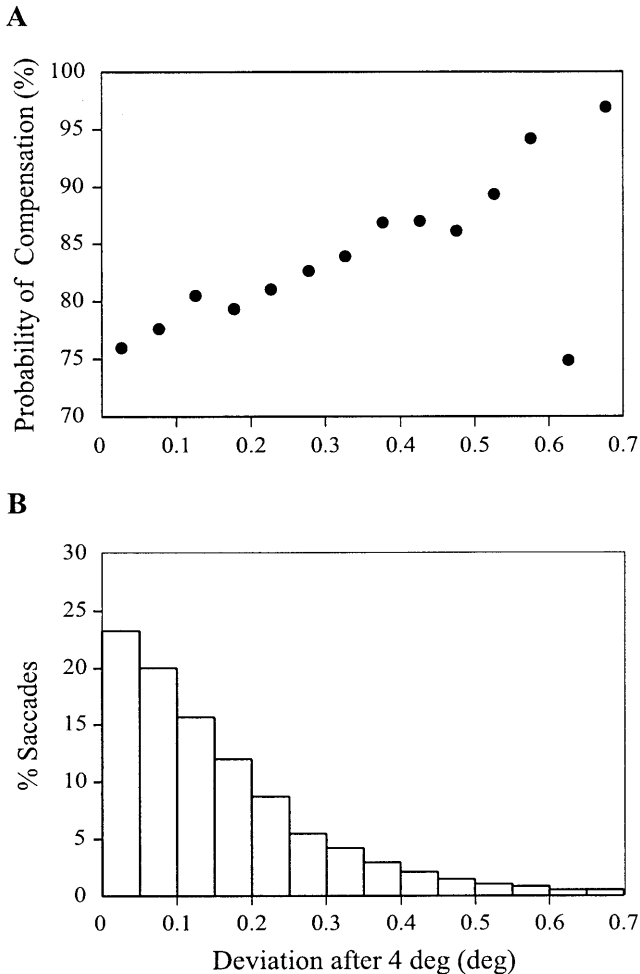


Fig. 8 Probability of compensation (**A**) and distribution of saccades (**B**) as a function of the deviation from the average trajectory at an eccentricity of 4° from saccade origin. Note that there are not many saccades for very large deviations, but the upward trend in **A** is already clear by 0.3° , up to where there is a considerable number of saccades in each bin. Thus, compensation is more likely if deviations are larger, as would be expected from a compensatory mechanism. Also, **B** reconciles Fig. 7 (where the overall probability of compensation, which is the sum of partial and excessive compensation, can be estimated at 80%) with **A**. The complete data set is represented

cade (e.g., 1° from saccade start) produced the same upward trend.

Relationship between initial and overall direction

To compare our results with previous studies (see “Materials and methods”), we also computed the slope and the correlation coefficient of the relationship between the initial and the overall direction of saccades. This was done independently for each target location and behavioral paradigm (stable or flashed target). For each target eccentricity, on average there was a positive correlation between initial and overall direction, with a slope smaller than one, i.e., β is proportional to, but smaller than, α (see Fig. 2A).

In Fig. 9A–D we show the data for saccades to stable targets of different eccentricity in one direction for the third monkey. We found a fairly robust tendency: the larger the saccades, the smaller the slope of the relationship between initial and overall direction. The entire data set (three monkeys, all amplitudes, directions and paradigms) is summarized in Fig. 9E: the slope averaged 0.34 for 5° saccades, but only 0.05 for 38° saccades. In other words, this confirms our finding that trajectory deviations are only partially compensated, and that they tend to be compensated more during larger saccades. A similar trend can be seen in the correlation coefficient, which averaged 0.35 for 5° saccades and 0.23 for 38° saccades. Using a univariate ANOVA test, we verified that both the slope and the correlation coefficient depended only upon the target eccentricity ($P < 0.001$); there were no significant differences across monkeys or paradigms.

Contribution of visual mechanisms

In a recent study on human subjects, it was reported that the final position of the eyes is different for saccades directed to stable versus flashed targets (Klier and Crawford 1998). The authors suggested that one explanation for such differences might be that visual information is used during the saccade to guide the eyes toward the target. As we repeatedly pointed out, in our experiments we did not find any significant difference between the compensatory behavior of saccades directed to flashed as opposed to stable targets. However, when we compared, for each target location, the final eye position attained in the stable and flashed conditions we found some differences (Table 1). The mean vertical component was significantly different (t -test, $P < 0.05$) in 27 out of 81 cases (33%). In 26 out of the 27 cases, this difference was represented by an upward bias for saccades to flashed targets. The mean horizontal component was significantly different in 30 out of 81 cases (37%). In all three monkeys we observed the following general pattern for the horizontal component of saccades to flashed targets: upward saccades acquired a rightward component, downward saccades acquired a leftward component, and saccades in the other directions had a smaller horizontal component. As shown in Table 1, differences in scatter were very limited (F -test, $P < 0.05$).

To test whether these changes were due to visual information acquired *during* the saccade, we performed an additional experiment, in which we intermixed three paradigms: stable target, flashed target and extinguished target. In this last condition, the target was extinguished as soon as the saccade started. To produce a large number of trials for each target location and paradigm, we used only eight target locations (eight directions, 10° eccentricity). In this experiment, we found (see Table 2) essentially the same differences (i.e., same pattern, extent and similar frequency) between the stable and flashed target conditions as reported in Table 1. However, there were

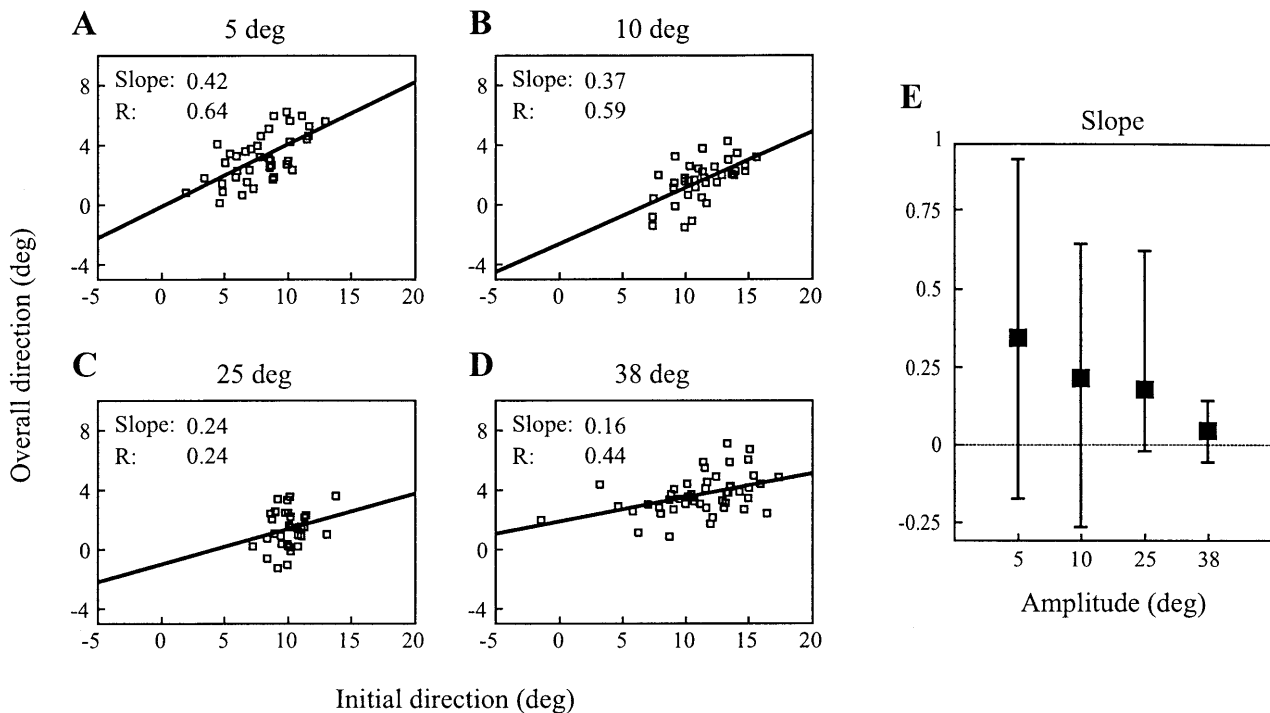


Table 1 Study of differences in final eye position between stable and flashed conditions. Percentage of statistically significant changes in mean (t -test, $P < 0.05$) and STD (F -test, $P < 0.05$) for horizontal and vertical components of final eye position obtained comparing saccades to stable and flashed targets. For each monkey we recorded the eye movements made to 27 different targets

Monkey	Horizontal component		Vertical component	
	Mean	STD	Mean	STD
1	63%	0%	33%	26%
2	44%	22%	52%	7%
3	4%	7%	15%	15%
AVG	37%	10%	33%	16%

Table 2 Effect of target presence on final eye position. Percentage of statistically significant changes in mean (t -test, $P < 0.05$) and STD (F -test, $P < 0.05$) for the horizontal and vertical components of the landing position of saccades. *Top* comparison between saccades to stable and flashed targets, *bottom* comparison between saccades to stable and extinguished targets. In this experiment the targets were located at 10° of eccentricity and in one of eight directions

Monkey	Differences horizontal component		Differences vertical component	
	Mean	STD	Mean	STD
Stable vs flashed				
1	25%	0%	38%	13%
2	63%	0%	50%	13%
3	13%	0%	50%	0%
AVG	33%	0%	46%	8%
Stable vs extinguished				
1	0%	13%	0%	0%
2	0%	0%	0%	0%
3	0%	13%	0%	0%
AVG	0%	8%	0%	0%

Fig. 9A–E Relationship between initial and overall direction. **A–D** Slope of the relationship for saccades directed to targets of different eccentricity in one direction (stable condition). Data from monkey 3. **E** Mean (squares) and 90% confidence interval (bars) of the slope as a function of target eccentricity averaged over all three monkeys

no significant differences between the stable target and the extinguished target conditions. Thus, the differences observed were *not* due to the processing of visual information *during* the saccade.

Discussion

By introducing some new measures, we have been able to quantify for the first time the ability of the monkey saccadic system to compensate for deviations from the desired (i.e., average) behavior.

Compensation for variations in speed

We found that on average only 61% of the variability in peak speed is compensated for, which is less than commonly assumed (e.g., see Becker 1989); we have also shown that these results cannot be accounted for by a main sequence relationship. Furthermore, in agreement with Smit and colleagues (1987) but in contrast with Jürgens and colleagues (1981), we found no correlation between amplitude and duration of saccades directed to any given target. We are not able to reconcile these differences, and can only speculate that the drugs (diazepam, used to slow down saccades) administered to the subjects in the study by Jürgens et al. (1981) could have

somehow affected not only the speed of the eye movements but also the functioning of the saccadic system. Alternatively, this difference could be species related.

Perfect compensation for speed variations has always been a firm requirement of every model of the saccadic system, and almost every model was designed with this goal in mind. Consequently, there is no model of the saccadic system that can, in its current form, predict our results. However, it is safe to say that two types of models cannot account for our results: those that posit a ballistic generation of the innervation signal (thus predicting no compensation) and those that embed a position feedback loop with unitary gain (thus predicting perfect compensation), irrespective of whether they include delays in the feedback pathway (which would introduce stability, and not accuracy, problems). On the other hand, models that use a predictor-corrector scheme to generate the innervation signal (e.g., Barto et al. 1999; Dean 1995; Houk et al. 1992; Lefèvre et al. 1998; Quaia et al. 1999) could probably be modified to fit our findings. It must also be noted that we cannot exclude the possibility that the eye plant plays some role in determining the amount of compensation; unfortunately a realistic dynamic model of the plant is still lacking.

Compensation for trajectory deviations

The second issue we addressed in our study was the ability of the saccadic system to compensate for deviations that bring the eyes away from the desired trajectory. In this case we also found considerable evidence in favor of a compensation mechanism, but it seems to underperform for small movements and to overperform for large movements. Furthermore, this mechanism appears to be very noisy (i.e., the distribution of C_T is highly scattered), whereas variations in speed are more reliably compensated. When we looked at the relationship between initial and overall direction, we found that it has a positive slope smaller than one. This finding is in qualitative agreement with the reports of Becker and Jürgens (1990) and Van Gisbergen and colleagues (1987) in humans, but it is at odds with the negative correlation (i.e., excess of compensation) reported by Erkelens and Sloot (1995), also in humans. We believe that our results can reconcile some of these differences, because Becker and Jürgens (1990) studied 20° saccades, whereas Erkelens and Sloot (1995) studied 38° saccades, and we have found that the amount of compensation increases with saccade amplitude. Even though overcompensation is not dominant for 38° saccades made by monkeys, it is possible that there is a larger tendency to overcompensate in some human subjects.

To the best of our knowledge, no current model can fully account for the pattern of trajectory compensation that we found. However, a model recently presented by our group had partially predicted these results (Lefèvre et al. 1998; Quaia et al. 1999) and might be a step in the right direction. In that model we proposed that the sac-

cadic innervation signal is the sum of two signals, one generated by the superior colliculus and the other by the cerebellum. Only the cerebellar contribution can be adjusted in flight. Under these constraints we have shown that the system cannot completely compensate for deviations from the desired trajectory. It must also be noted that at this point it is not possible to exclude an untimely reactivation of the omnipause neurons (OPN) as a possible cause for the limited compensation, even though the timing of the OPN reactivation with respect to saccade end (Everling et al. 1998; Paré and Guitton 1998) makes this possibility fairly unlikely.

Contribution of visual mechanisms

Our results rule out the use of visual information for saccade guidance in monkeys, which raises doubts about the recently suggested presence of such a mechanism in humans (Klier and Crawford 1998). The differences observed in the stable vs flashed conditions could be due to a degeneration of the encoding of target location during the interval between target extinction and movement onset. In fact, the differences we observed are very similar to those between saccades to visual and remembered (i.e., flashed) targets (Gnadt et al. 1991; White et al. 1994).

Saccade generation and internal feedback

Our experiments demonstrate that the monkey saccadic system partially compensates for deviations from the desired behavior, and it does so without using visual feedback. These results were consistent across all three monkeys, and thus the extent of training and idiosyncrasies among them were clearly not influential factors. Our findings further support the idea, suggested by several other studies (e.g., Becker et al. 1981; Keller et al. 1996), that the innervation signal that generates saccadic movements is not pre-programmed but is adjusted dynamically during the saccade. However, the compensatory mechanisms at work appear to be less than perfect. Thus, while we can reject the hypothesis that saccades are generated by an open-loop system, which would perform worse than the real saccadic system, we must also reject ideal closed-loop position feedback controllers, which would perform better.

One question that begs for an answer is whether the same mechanism is responsible for compensating for deviations that bring the eyes away from the desired trajectory and for deviations that affect only the speed of the movement. Unfortunately, because the distributions of the parameters used to describe the two phenomena are different, they cannot be directly compared. However, two observations indicate that there might be some difference: first, the dependency between C_S and amplitude is monkey dependent, whereas the dependency between C_T and amplitude is not significantly different across

monkeys. Second, whereas C_T indicates that trajectory deviations tend to be overcompensated as saccade amplitude increases, overcompensation is practically absent when speed variations are considered.

Even though we think that these results can provide some important insights, deviations that occur during normal behavior are often relatively small, while deviations that can push the system to the limit are relatively few (see Fig. 8B). Thus, it would be certainly valuable to look at how well the system compensates for external perturbations, which could be used to induce repeatedly large deviations. In the past changes in velocity, saccadic accuracy and increased curvature have been induced by means of lesions, especially in the superior colliculus (Aizawa and Wurtz 1998; Hikosaka and Wurtz 1985; Hikosaka and Wurtz 1986; Lee et al. 1988; Quaia et al. 1998; Sparks et al. 1990). However, because the lesions were placed at a relatively high level in the saccadic system, and because after a lesion it is difficult to know how much of the normal functionality of the system has been altered, we think that more precisely controllable methods would provide better information. For example, brief stimulation of the medium lead burst neuron region (which contains the saccadic burst generator) during saccades should be quite informative, allowing a quantification of the compensatory abilities of the system as a function of the duration, extent and timing of perturbations acting along or away from the desired trajectory.

Acknowledgements We thank Dr. Philippe Lefèvre and two anonymous reviewers for helpful comments; we also thank Dr. Stefano Ferraina for assistance during the experiments. C.Q. was partially supported by a grant (Sistemi naturali ed artificiali nei problemi cognitivi e dell'apprendimento) from Ministero dell'Università e della Ricerca Scientifica e Tecnologica to Paolo Inchingolo.

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