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Optimal sensorimotor control in eye movement sequences

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1 Summary

Fast and accurate motor behavior requires the combination of noisy and delayed sensory information with knowledge of our own self-generated body motion. A growing body of experiments suggests that humans integrate sensory and motor information in a nearly optimal fashion when controlling their arm movements. However, it is still unclear whether the same principles apply to sequences of saccadic eye movements. In this study, we measured to what extent humans use their visual sensory feedback and the efferent copy of the motor command when performing two saccades in rapid succession, the first one to a visual target and the second one to a memorized target. Unbeknownst to the subject, we introduced an artificial motor error by randomly “jumping” the visual target during the first saccade. The correction of the second saccade (to the memorized target) as a function of the jump of the first saccade target allowed us to measure the relative contribution of the visual feedback and the efferent copy in updating the motor plan. To test whether humans adjusted the gain of their visual feedback as a function of its reliability as compared to the efferent copy, we manipulated the motor variance by changing the size of the first saccade. We found that the gain of the visual feedback co-varied with the motor variance, and was far below 100% even if the subject performed a corrective saccade, as predicted if humans acted as optimal controllers. This suggests that humans combine optimally their efferent copy and sensory feedback when performing sequences of eye movements.
2 Introduction

Arm movements have been shown to be neither purely driven by sensory feedback, nor purely “ballistic” i.e. unfolding as a function of a pre-programmed sequence of muscle contraction (Goodale et al., 1986; Desmurget and Grafton, 2000). Instead, a growing consensus is that the motor system uses an internal forward model of the limbs’s dynamics in order to compute an estimate of the current sensorimotor state (e.g. arm position and velocity). The discrepancy between the observed sensory feedback and the sensory feedback predicted by the model is used to correct the internal estimate, while an inverse model is used to compute the new motor command given the corrected internal estimate (Wolpert et al., 1995; Wolpert and Kawato, 1998; Todorov, 2004).

This internal estimate for the state of the motor plant is the result of a combination of two unreliable cues: the efferent copy of the motor command, and the sensory feedback. The forward model predicts the current sensorimotor state from the past state and the efferent copy, but is necessarily imperfect because movements are variables (Schmidt et al., 1979; van Beers et al., 2004). The sensory feedback (e.g. visual, proprioceptive) can also be used to directly estimate the sensori-motor state, but is unfortunately noisy and delayed. The combination of the forward prediction and the feedback estimate is optimal, i.e. the internal model is most precise, when the two sources of information are weighted according to their reliability. The optimal relative contributions of the sensory feedback and the forward prediction are described by “Kalman gains” computed recursively from the sensory and motor variance (Deneve et al., 2007). Kalman gains increase as a function of the motor noise and decreases as a function of the sensory noise (see method section).

While the relative contribution of the forward model and the sensory feedback is still a matter of debate, it is now widely accepted that they both contribute to the motor control of the upper limb (Prablanc and Martin, 1992; Connolly and Goodale, 1999; van Beers et al., 1999; Sabes, 2000; Ariff et al., 2002; Baddeley et al., 2003). Recent experiments suggest that humans use a kalman filter (Kalman and Bucy, 1961), i.e. they optimally weight the forward and feedback contributions, when performing arm movements, (Wolpert and Ghahramani, 2000; Saunders and Knill, 2004). However, it is still unclear whether the same principles apply to saccadic eye movements, a kind of movement containing variability even if the amount of noise is lower compared to other kinds of motion such as arm displacement. This lack is particularly surprising that the relative simplicity of these movements and
the central contribution of the vision for human behaviour led the authors to use this system as a major model for the sensorimotor mechanism studies (Pierrot-Deseilligny et al., 2003). Robinson (1975) introduced the idea that saccade generations were not ballistics but can be controlled by loop based on an efferent copy of the initial saccadic command. After this initial model, numerous studies provided arguments that saccadic system can be driven by an efferent copy and/or by sensory feedback such as visual feedback (for a review see Girard and Berthoz, 2005). However the capacity of the saccadic system to combine efferent copy and sensory feedback and the way in which these different elements are used by saccadic system to update the motor command remain unclear. In fact on average saccadic eye movement execution is fast (50-80ms) (Robinson, 1964) as compared to sensory delays, and “saccadic suppression” prevents the visual sensory feedback from influencing the trajectory of the eye during the saccade (Bridgeman et al., 1975; Thiele et al., 2002). On the other hand, during sequences of fast saccadic eye movements, the sensory feedback (proprioceptive or visual) received during the fixation periods could be used to re-estimate the new eye position and compute the next eye movement, corresponding to a purely feedback-driven control. Alternatively, the system could rely entirely on internal loops (forward model), updating an internal estimate of the eye position after each saccade using the efferent motor command. Evidence exist for both type of controls (Ditterich et al., 1998; Gaveau et al., 2003) and internal loops for saccadic eye movements are implemented in subcortical structures (Gnadt et al., 2001) suggesting that these two processes might be combined for controlling sequences of saccades.

The goal of this study was to investigate whether forward and feedback estimates are optimally combined for controlling sequences of saccades. To do so, we asked human subjects to perform two eye movements in quick succession, and we introduced an artificial motor error by randomly moving the target of the first saccade during the movement. The extent to which the second saccade (directed towards a memorized target) was corrected by this visual feedback, allowed us to directly measure the “Kalman gain” (see methods). We varied the size of the first saccade and found that this “kalman gain” co-varied with the motor variance as predicted for an optimal controller.
3 Materials and methods

3.1 Experimental protocol

This study was constituted of two different experiments: the first one has to be considered as the main and the second was an experiment intended to validate and to refine our models.

In the first experiment eleven healthy human subjects (9 males, 2 females; 22-32 years old) with normal or corrected to normal vision participated. Subjects were placed 35 cm in front of a 17 inch, 800*600 pixels, CRT screen at 100Hz refresh rate, in a dimly lit room. Their head was maintained in a fixed position by a chin piece and by requiring the subjects to bite on their own dental print. Eye movements were recorded using an optometric system: EyelinkI system (SR Research, Mississauga, Ontario, Canada). Eye positions were continually recorded at 250 Hz.

The protocol on this main experiment was adapted from the usual double-step paradigm, and is schematically represented in figure 1. The subject were instructed (1) to gaze a white cross, 0.80° wide, the fixation point (FP), positioned in the center of the screen. (2) After a brief fixation period (300 ms), a green target (diameter 0.80°), was turned on at the right or on the left of the FP. (3) 490 ms later, a red target was flashed during 200 ms (diameter 0.80°) and the FP disappeared at the end of this flash. Subjects were instructed to consider this red flashed target as a “go signal”, and to perform two saccades in rapid successions, first (4) to the green target (target 1, T1), and then (6) to the memorized location of the red target (target 2, T2). However (5), for 2/3 of the trials, T1 “jumped” unpredictably from its initial position in the direction of the first saccade (positive/centrifugal jump) or in the opposite direction (negative/centripetal jump) as soon as the distance between the average eye position during the last 6 records at 250 Hz and the new eye position reached 0.75 degrees. The amplitude of this jump was 20% of the distance between FP and T1 (i.e., approximately 20% of the amplitude of the first saccade). In agreement with previous studies using intrasaccadic target displacements (Prablanc and Martin, 1992) we found that subjects never detected the target jump, i.e. they never reported seeing a change in position of T1 during the first saccade. We thus postulate that the target jump introduced an artificial motor error on the first saccade endpoint. In order to limit the occurrence of short corrective saccades, T1 was extinguished 90 ms after completion of the first saccade. This always occurred before the start of the memorized saccade to T2.
T1 appeared at one of three eccentricities (6° for small saccades, 12° for medium saccades, and 18° for large saccades), on the right or left of the fixation point, for a total of 6 possible T1 locations. T2 appeared in one of 4 possible location relative to T1 (9° above or below, and 9° left or right of T2). Finally, as stated above, T1 either stayed at the same location (1/3 of the trials), jumped to the right by 20% of the distance between FP and T1 (1/3 of the trials) or jumped to the left by 20% of the distance between FP and T1 (1/3 of the trials), for a total of 6x4x3=72 different conditions. The order of presentation for the different conditions was randomized separately for each subject. Each subject performed 4 blocks of 72 trials with a short break after the second block. If subject moved their eyes before the “go signal” or if the two saccades were not completed within 1710ms, the trial was aborted. A saccade was considered to be completed when the distance between the average eye position during the last 6 records and the new eye position was less than 0.6 degrees. Note that we allowed for the existence of a single small “corrective saccade” after the first saccade to T1 and before the saccade to T2.
Figure 1. Description of the task and experimental predictions. **A.** Time frame for a trial with positive target jump. **B and C.** Predictions of the last saccade direction, for a trial without corrective saccade - **B** - or with corrective saccade - **C** -, if the eye is completely controlled by sensory feedback (dotted and dashed arrows represents respectively direction of the last saccade for trials with negative and positive jump) or a forward model based on the efferent copy (solid black arrow for the two target jump direction).

A positive percentage of correction equal to 100% will correspond to the end points (corresponding to the final eye position after the last saccade) of dotted and dashed arrows for trials with negative and positive jump respectively. However if this percentage is not total (i.e 100%) but superior to 0%, the end point of the arrows will be between the end point of solid black arrow and the end points of dotted
or dashed arrows for trials with negative and positive target jump respectively. If the end point will be on the right or on the left of the real T2 position (solid black arrow) for respectively trials with negative or positive target jump in that case the percentage of correction will be negative (i.e inferior to 0%).

The second experiment involved eight subjects: four from the first one (3 men, 1 female, 25-30 years old) and four new subjects (3 men, 1 female, 24-32 years old). The conditions were exactly the same than in the experiment excepted for T1 characteristics. In 50% of the case T1 remained 90 ms on the screen at the end the first saccade (corresponding to a trial without target jump in experiment 1) but in 50% of the case T1 was extinguished during the first saccade at the same moment than the target jump in the first experiment. The only difference was the none reappearance of T1 after extinction. Each subject performed 6 blocks of 48 trials (6x4x2).

3.2 Data analyses

We separated the trials into two main categories: Trials where the saccades to T1 and to T2 occurred is immediate succession without corrective saccades (trials without corrective saccades), and those where a single corrective saccade occurred between T1 and T2 (trials with corrective saccade). Other types of trials (those that did not contain a specified sequence of saccade as describe below) were eliminated from the analyses. The first saccade to T1 had to bring the eye from a rectangular window of 2.5 x 2.5 degrees around the fixation point to a rectangular window around the location of T1 (before the jump) representing 40% of the first saccade amplitude in length and 3 degrees in width. A corrective saccade was detected when the second saccade brought the eye within a rectangular window of 5.7 x 2.3 degrees around the new position of T1 after the jump. A memorized saccade to T2 brought the eye within a 7.3 x 4.6 degree window around T2. A correct trial had to contain a saccade to T1 followed by a saccade to T2 (trial without corrective saccade), or a saccade to T1 followed by a single corrective saccade and a saccade to T2 (trial with corrective saccade).

Our main goal was to measure the influence of the target jump of T1 on the memorized saccade to T2 (Fig. 1-B and C for trials without and with corrective saccade respectively). We defined the “final
percentage of correction” as the deviation introduced by the target jump in the final eye position around T2, divided by the size of the target jump. The final eye position around T2 is the eye position at the end of the main saccade to T2 or at the end of subsequent corrective saccade, when executed.

Thus, for positive target jump this percentage of correction is defined as

\[
100 \times \left( \frac{e - \langle e \rangle_{\text{no-jump}}}{0.2 \ T1} \right)_{\text{jump-pos}}
\]

Where \( e \) is the horizontal position of the final eye position around T2, \( \langle e \rangle_{\text{jump-pos}} \) represents an average over all trials with positive jumps, \( \langle e \rangle_{\text{no-jump}} \) represents an average over trials with no target jump, and \( T1 \) is short-cut notation for the horizontal position of target 1 before the jump minus the position of the fixation point. e.g., a small rightward saccade corresponds to \( T1=6^o \), a medium leftward saccade \( T1=-12^o \).

Similarly, for negative jumps (i.e. \( T1 \) is displaced in the opposite direction to the first saccade) the final percentage of correction for small saccades is defined as:

\[
100 \times \left( \frac{\langle e \rangle_{\text{no-jump}} - e}{0.2 \ T1} \right)_{\text{jump-neg}}
\]

Where \( \langle e \rangle_{\text{jump-neg}} \) is the average over trials with no target jump. The global percentage of correction regardless of jump direction is defined as:

\[
100 \times \left( \frac{\langle e \rangle_{\text{jump-pos}} - \langle e \rangle_{\text{jump-neg}}}{0.4 \ T1} \right)
\]
We only report the results in terms of horizontal positions since the target jump occurred on the horizontal axis. Similar analyses performed on vertical position did not show any significant effects of the target jump.

In addition, we also computed the percentage of correction after the first saccade to T1, the percentage of correction after the corrective saccade (if there is one), and the percentage of correction of the eye displacement (“saccade vector”) during the saccade to T2. This is done by replacing “e” in the previous equations by the corresponding positions or displacements. For example, the percentage of correction after the corrective saccade is given by

\[
100 \times \frac{ \langle e(2) \rangle_{\text{jump-pos, corr-sacc}} - \langle e(2) \rangle_{\text{jump-neg, corr-sacc}} }{0.4 \ T1}
\]

Where \( \langle e(2) \rangle_{\text{jump-neg, corr-sacc}} \) is the position of the eye following the corrective saccade, averaged over all trials with corrective saccade and negative jumps. Similarly, the percentage of correction of the saccade vector (eye displacement) to T2, for trials without corrective saccade is given by:

\[
100 \times \frac{ \langle e(3) - e(2) \rangle_{\text{jump-pos, no-corr}} - \langle e(3) - e(2) \rangle_{\text{jump-neg, no-corr}} }{0.4 \ T1}
\]

Where \( e(3) - e(2) \) is the horizontal eye displacement for the memorized saccade to T2, and \( \langle \cdot \rangle_{\text{jump-pos, corr-sacc}} \) indicates an average over trials with positive jump and without corrective saccade.

### 3.3 Predictions of the Kalman filter model

If the saccadic system completely trusted its visual feedback, i.e. if it completely assigned the discrepancy between T1 and the eye position after the first saccade to a motor error, it should adjust the final eye position around T2 in the same direction and with approximately the same amplitude than the target jump (Fig. 1-B and C, dotted and dashed arrows). This would correspond to a percentage of correction of 100%. If, on the other hand, the saccadic system ignored the visual feedback and relied
entirely on the efferent copy to update the saccadic movement vector to T2, the jump should have no influence on the final eye position around T2 (Fig. 1-B and C; solid black arrow). This would correspond to a percentage of correction of 0%. If the subject combined both signals, the correction of the second saccade to T2 should fall between these two extremes, i.e. the percentage of correction should be intermediate between 0 and 100%.

The optimal percentage of correction, i.e. the percentage of correction minimizing the final eye position error, reflects the reliability of the visual sensory feedback relative to that of the forward prediction. We illustrate this prediction by a simplified model of the double saccade paradigm.

Let us consider a one dimensional model of the eye plant were the eye position $e(t)$ is “instantaneously” updated by the saccadic vector $\Delta(t)$, so that

$$e(t+1) = e(t) + \Delta(t) + \varepsilon_n(t).$$

$\Delta(t)$ corresponds to the “motor command” sent to the eye plant, $\varepsilon_n(t)$ represents the “motor noise”, or “execution noise”, which corresponds to noise in the eye plant. It is assumed to be Gaussian distributed with zero mean and variance $V_n$.

For an eye movement planned towards target T, the motor command sent to the eye plant is $\Delta(t) = T + \varepsilon_l(t)$, where $\varepsilon_l(t)$ is a Gaussian sensory noise with zero mean and variance $V_l$. $\varepsilon_l(t)$ corresponds to the localization error of target T. Errors in localization of the target largely contribute to the variability of saccadic eye movements and often exceed the motor noise (van Beers, 2007). However, contrary to motor noise, these errors can be predicted from the efferent motor commands. In our notations, the total variability of the saccade movement, $V_m = V_l + V_n$, is the result of the combination of target localization errors and noise in the eye plant.
The motor system could use the efferent copy of the motor command $\Delta(t)$ and its previous eye position internal estimate $\hat{e}(t)$ to compute a forward prediction for the new eye position,

$$\hat{e}'(t+1) = \hat{e}(t) + \Delta(t).$$

Unfortunately, this estimate does not take into account the motor noise $\varepsilon_n(t)$ and thus will accumulate errors after each saccade.

Alternatively, it could rely on its proprioceptive and visual sensory feedbacks. We will not consider the contribution of the proprioceptive feedback since this protocol does not allow it to be distinguished from correction performed by the forward model, sometime referred as “internal loops”(Ditterich et al., 1998). If the target is still present after the end of the saccade, the visual feedback is provided by the difference in retinal target location after the saccade

$$s(t+1) = T' - e(t+1),$$

Where $T'$ is the target location after the saccade; In normal situations, $T' = T$, but in our experiments we introduced jumps in target location during the saccade and thus $T' = T + \text{jump}$. As a result, we have two different unreliable cues for estimating the new eye position: the forward estimate $\hat{e}'(t+1)$ and the feedback estimate, based on the difference between the target location before the saccade and the target location after the saccade: $\hat{e}'(t+1) = T + \varepsilon_i(t) - s(t+1)$. Here we assume that the same noisy target location estimate $T + \varepsilon_i(t)$ is used for planning the saccade and for computing the retinal displacement of the target after the saccade.

The optimal way of combining these signals is a weighed sum, with each cue weighted by the inverse of its variance (Ernst and Banks, 2002). Thus, the combined estimate of eye position is given by:
Where $V_i$ is the variance of the previous eye position estimate, $\hat{e}(t)$. $k_s$, the Kalman gain, represents the relative contribution of the forward model (or “efferent copy”) and the visual feedback. It is given by:

$$k_s = \frac{V_n}{V_n + V_i}$$

$k_s$ is zero when the sensory noise dominates the motor noise ($V_s \ll V_n$), and 1 when the motor noise dominates ($V_s \gg V_n$).

For our particular task, $e(0)$ is the position of the eye at fixation (set, by convention, at zero), $e(1)$ is the position of the eye after the first saccade, $e(2)$ is the position after the corrective saccade, and $e(3)$ is the position of the eye after the saccade to T2. $\Delta(1)$, $\Delta(2)$ and $\Delta(3)$ are the motor commands corresponding to the first saccade, corrective saccade and memorized saccade to T2. To simplify notations, we assumed that for trials without corrective saccades, $e(1) = e(2)$ and thus, $\Delta(2) = \Delta_n(2) = \Delta_n(1) = 0$. The visual feedback corresponds to the retinal position of T1 after the jump, i.e. $s(2) = T1 + \text{jump} - e(1)$.

The first saccade vector, $\Delta(1) = T1 + \Delta_i(1)$, brings the eye towards the first target. As a consequence, the first eye position is given by $e(1) = T1 + \Delta_i(1) + \Delta_n(1)$. From there we need to separate different kinds of trials.

Target extinction, no corrective saccade
In the absence of visual feedback (target extinction) the internal eye position estimate after the first saccade is simply equal to the forward estimate: \( \hat{e}(1) = T1 + e_i(1) \). The motor command for the next saccade is computed as the difference between the memorized location of the second target (corrupted by localization noise) and the current estimate of eye position:

\[
\Delta(3) = T2 + e_i(3) - \hat{e}(1) = T2 - T1 + e_i(3) - e_i(1)
\]

As a consequence, the final eye position is given by:

\[
e(3) = e(1) + \Delta(3) + e_n(3) = T2 + e_n(1) + e_i(3) + e_n(3)
\]

We use these trials to predict the Kalman gains for trials with visual feedback (i.e. with target jump). Kalman gains can be predicted directly from the covariation between the eye position after the first saccade and the final eye position. If fixation errors on the first saccade were entirely due to localization noise, they would be completely corrected in the second saccade, resulting in completely decorrelated eye positions and Kalman gains equal to zero. If, on the other hand, errors in the first saccades were entirely due to motor noise, they could not be corrected and would result in correlated eye positions and Kalman gains equal to one. More generally the Kalman gain can be measured as:

\[
k_s = \frac{V_n}{V_n + V_f} = \frac{\text{cov}(e(1), e(3))}{\text{var}(e(1))}
\]

Target jump, no corrective saccade

In the presence of visual feedback, the estimate for the eye position after the first saccade is given by the forward estimate corrected by the sensory feedback:

\[
\hat{e}(1) = T1 + e_i(1) + k_s \times (e_n(1) \times \text{jump}),
\]

where “jump” is the amplitude of the jump of target T1. Thus “jump” is \(0.2 \times T1\) for positive jumps, \(-0.2 \times T1\) for negative jumps and 0 when there is no jump.

When no corrective saccade occurs, \(\Delta(2) = 0\) the motor command for the second saccade is given by:

\[
\Delta(3) = T2 + e_i(3) - \hat{e}(1) = T2 - T1 + k_s \times \text{jump} - e_i(1) - k_s e_n(1) + e_i(3)
\]

And thus final eye position is
$$e(3) = e(1) + \Delta (3) + \varepsilon_n (3) = T2 + k_s \text{jump} + (1 - k_s) e_s (1) + \varepsilon_i (3) + \varepsilon_n (3)$$

In conclusion, the predicted percentage of correction for trials with target jump and without corrective saccade is $100k_s$.

Target jump, with corrective saccade

When a corrective saccade occurs, it is a visually guided saccade aimed at target T1. It can be directly computed from the new retinal position of the target:

$$\Delta (2) = T1 + \text{jump} + \varepsilon_i (2) - e(1) = \text{jump} - \varepsilon_i (1) - \varepsilon_s (1) + \varepsilon_i (2)$$

As a consequence, the true eye position after the corrective saccade is

$$e(2) = e(1) + \Delta (2) + \varepsilon_n (2) = T1 + \text{jump} + \varepsilon_i (2) + \varepsilon_n (2)$$

The target is extinguished by the end of the corrective saccade, preventing subjects from receiving any additional visual feedback. However, the original location of the first target, $T1 + \varepsilon_i (1)$, provides indirect feedback about the eye position after the corrective saccade. In particular, if the first saccade was completely random, but the corrective saccade perfectly foveated the first target, the retinal displacement between T1 and T2 would be the subject “best guess” for the memorized saccade vector. In our framework, this would correspond to putting complete trust in the feedback and thus using $T1 + \varepsilon_i (1)$ as an internal estimate of eye location.

The forward estimate and the original target location can be combined as follow:

$$\hat{e} (2) = (1 - k_s) (\hat{e} (1) + \Delta (2)) + k_s (T1 + \varepsilon_i (1))$$

Where the new Kalman gain $k_s$ depends on the variance of the forward eye position estimate $\hat{\varepsilon} (2) = \hat{e} (1) + \Delta (2)$ and of the feedback estimate $\hat{e} (2) = T1 + \varepsilon_i (1)$. Here we assume that the small corrective saccade does not introduce additional motor noise, i.e. we neglect $\varepsilon_n (2)$ (see discussion).
The variance of the forward estimate is then \((1-k_\alpha)^2 V_n\), while the variance of the memorized target location is \(V_t\). The new Kalman gain is given by

\[
k'_\alpha = \frac{k_\alpha}{1 + k_\alpha^2 (1-k_\alpha)}
\]

The Kalman gain \(k_\alpha\) measured in this study range from 0 to 0.2. Within this range, \(k'_\alpha\) is less than 3% smaller than \(k_\alpha\). Thus, to simplify the equations, we considered \(k'_\alpha = k_\alpha\).

The resulting estimate for the eye position after the corrective saccade is:

\[
\hat{e}(2) = T1 + (1-k_\alpha)^2 \text{jump} + k_\epsilon (1) + (1-k_\alpha) \epsilon_i (2) - (1-k_\alpha)^2 \epsilon_n (1)
\]

Thus, the last saccade vector and final eye position are given by:

\[
\Delta(3) = T2 - T1 - \left(1-k_\alpha\right)^2 \text{jump} - k_\epsilon (1) - (1-k_\alpha) \epsilon_i (2) + (1-k_\alpha)^2 \epsilon_n (1) + \epsilon_i (3)
\]

\[
e(3) = T2 + \left(1-k_\alpha\right)^2 \text{jump} + k_\epsilon (\epsilon_i (2) - \epsilon_i (1)) + \epsilon_i (3) + \epsilon_n (3) + (1-k_\alpha)^2 \epsilon_n (1)
\]

In trials with target jump and with corrective saccade, the predicted percent correction is thus

\[
100 \times \left(1-\left(1-k_\alpha\right)^2\right).
\]
4 Results

To report the results we use the conventions in table 1. All positions are projected on the horizontal axis, and position zero corresponds to the fixation point. Positions to the right of the fixation point are positive, and positions to the left are negative.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tr>
<td>$e(0)$</td>
<td>Eye position at the start of the trial (fixation)</td>
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<tr>
<td>$T_1$</td>
<td>Position of the first (permanent) target before the jump.</td>
</tr>
<tr>
<td>Jump</td>
<td>Displacement of the first target during the first saccade</td>
</tr>
<tr>
<td>$T_1 + \text{jump}$</td>
<td>Position of $T_1$ after the jump.</td>
</tr>
<tr>
<td>$e(1)$</td>
<td>Eye position at the end of the first saccade to $T_1$</td>
</tr>
<tr>
<td>$T_2$</td>
<td>Position of the second (flashed) target</td>
</tr>
<tr>
<td>$e(2)$</td>
<td>Eye position at the end of the corrective saccade if there is one. Otherwise, $e(1) = e(2)$</td>
</tr>
<tr>
<td>$e(3)$</td>
<td>Eye position at the end of the saccade to the memorized target ($T_2$)</td>
</tr>
<tr>
<td>$\hat{e}(i)$</td>
<td>Internal (subjective) estimates of the corresponding eye position.</td>
</tr>
</tbody>
</table>

Table 1. Conventions for text symbols
Table 2. Means and standard deviations of reaction time (RT) and movement duration (MD) for the main saccades including jump and no-jump trials. S1 refers to the primary saccade around T1, CS to the presence or not of a corrective saccade in the trials after primary saccade and LS to the last saccade around T2.

<table>
<thead>
<tr>
<th>Trials with CS</th>
<th>Size S1 (deg)</th>
<th>RT S1 (ms)</th>
<th>MD S1 (ms)</th>
<th>RT CS (ms)</th>
<th>MD CS (ms)</th>
<th>RT LS (ms)</th>
<th>MD LS (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>307 ±109</td>
<td>44 ±6,7</td>
<td>138 ±70</td>
<td>33 ±6,4</td>
<td>199 ±103</td>
<td>66 ±16,9</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>304 ±115</td>
<td>58 ±7,5</td>
<td>129 ±58</td>
<td>36 ±6,4</td>
<td>193 ±106</td>
<td>67 ±17,7</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>318 ±110</td>
<td>70 ±9,4</td>
<td>121 ±54</td>
<td>38 ±6,9</td>
<td>206 ±110</td>
<td>64 ±16,7</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Trials without CS</th>
<th>Size S1 (deg)</th>
<th>RT S1 (ms)</th>
<th>MD S1 (ms)</th>
<th>RT LS (ms)</th>
<th>MD LS (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>317 ±114</td>
<td>46 ±5,8</td>
<td>275 ±130</td>
<td>66 ±18,2</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>323 ±106</td>
<td>60 ±12,9</td>
<td>265 ±117</td>
<td>66 ±20,3</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>333 ±111</td>
<td>73 ±17,4</td>
<td>253 ±109</td>
<td>63 ±19,5</td>
<td></td>
</tr>
</tbody>
</table>

4.1 Correction of the memorized saccade vector by fixation errors

In agreement with previous studies (Bock et al., 1995; Ditterich et al., 1998) we found that even in the absence of target jumps, the fixation error around T1 influences the saccade vector to the memorized location of T2. In other words, fixation errors are taken into account in order to correct the next saccade. Figure 2 shows an anti-correlation between the fixation error, defined as the position of the eye around T1 before the start of the saccade (i.e. \( e(2) - T1 \)), and the saccade vector to T2, defined as the eye displacement from the beginning to the end of the saccade (i.e. \( e(3) - e(2) \)). Each dot represents a trial without target jump, i.e. a trial when the target T1 stayed at the same location (jump=0). This anti-correlation \( (P < 0.001; r = -0.4; \text{Spearman rank correlation}) \) indicates that the two saccades do not unfold as a pre-programmed sequence of motor command; the memorized saccade is corrected by the previous fixation error around T1. We found similar results when we restricted the analyses to small saccade \( (P < 0.001, r = -0.39) \), medium saccade \( (P < 0.001, r = -0.32) \) or large saccades \( (P < 0.001, r = -0.43) \).
The fixation error signal used by the motor system in order to correct future saccade vectors could be the visual feedback from target T1, the proprioceptive feedback, or an internal prediction obtained by integrating the motor command sent to the eye plant (i.e. the forward model estimate). The goal of this study was to measure the contribution of the visual feedback to this correction, compared to the forward model and/or proprioceptive feedback. For this, we introduced unpredictable perturbations in the retinal location of the visual target during the first saccade. By varying the amplitude of this saccade, we also varied the motor noise, which we predicted would influence the Kalman gain.

![Figure 2. Horizontal vector eye displacement from T1 to T2 (subtract to the theoretical vector) as a function of the eye fixation error around T1. Each dot represents a trial without target jump (n = 929).](image)

**4.2 Effects of target jumps on the final eye position**

The final eye position around T2, $e(3)$, is significantly influenced by the direction of the target jump. As there were no significant differences in saccade accuracy between the four T2 endpoints, saccade
error and correction data were averaged for each subject across all T2 locations for a given T1 location. Figure 3 plots the global percentage of correction of the final eye position for small, medium and large saccades (Fig. 3, black columns). Data are represented as percentage correction of the target jump and show significant correction for medium and large saccades ($P < 0.001$; one-sample t-Test) but not for small saccades. One-way ANOVA analysis showed a significant effect of saccade size [$F(2,1639) = 7.27031; P < 0.001$] with significantly larger amount of correction for medium and large saccade than for small saccade ($P = 0.02$ and $P < 0.001$ respectively; test Post-Hoc HSD Tukey). Note that the target jump is itself a fixed percentage of the first saccade size. Thus, the same percentage of correction corresponds to a larger absolute correction of the final eye position following a larger first saccade.

When separating trials without and with corrective saccades (Fig. 3, grey and white columns) we found that the percent correction was significantly larger for trials with corrective saccades for both medium (25.4% v. 10.5%, $P = 0.038$; independent samples t-Test) and large saccades (29.3% v. 19.3%, $P = 0.046$).

An optimal controller should adjust the contribution of the visual feedback as a function of its reliability compared to that of the efferent copy. As explained previously, the percentage of correction is a direct measure of this contribution (see methods). As a result, an optimal controller model predicts that:

$$k_v = \frac{\text{percent correction}}{100} = \frac{V_m}{V_m + V_s}$$

where $V_s$ is the variance of the visual feedback, and $V_m$ is the variance of the forward prediction computed from the efferent copy. Under the reasonable assumptions that $V_m$ covaries with the variance in the first saccade endpoint ($\epsilon(1)$), and that the variance of the visual feedback is approximately constant, we expect the percent correction to co-vary with the motor variance.
Figure 3. Effects of T1 amplitude on final eye position around T2. Each column and error bar represents, respectively, the mean and standard error of three different groups of trials (all, without and with corrective saccade (CS)) for the three kind of saccade 1 (6° = small, 12° = medium, 18° = large). Percentage of correction for all the trials (black columns) improves with amplitude of the first saccade. Furthermore this correction is null for small trials. Dissociate trials (without CS/grey columns or with CS/white columns) present the same pattern of augmentation from small to large saccade 1. Moreover, for the same amplitude, the correction is stronger for trials with corrective saccade. Asterisks indicate significance between conditions (*\(P < 0.05\); ***\(P < 0.001\)).

In agreement with Abrams et al. (Abrams et al., 1989) we found that the motor noise increased with the eye movement amplitude, from small to medium to large saccades. The percent of correction as a function of the prediction derived from the variance of the first saccade end-point is plotted in figure 4. The corresponding 6 point correlation has to be taken with caution, but is significant when we use a non parametric test (\(r = 0.81; P < 0.05\); Spearman rank correlation coefficient). Moreover we used two classical parametric tests in order to test independently the trials with or without corrective saccade. In this case the coefficient of correlation increase to \(r = 0.99 (P = 0.08)\) for trials with corrective saccade and \(r = 1 (P = 0.014)\) for trials without corrective saccade.
Figure 4. Regression line shows the percentage of correction around target 2 (T2) as a function of the percent of correction predicted by the model from the experiment with target extinction ($r = 0.81$; Spearman rank correlation). Colours black and white represent respectively, trials with and without corrective saccade. Each shape represents the amplitude of the first saccade: circles for small, triangles for medium and squares for large. Variance around T1 and percentage of eye correction around T2 increased with the amplitude of the first saccade (large $\geq$ medium $\geq$ small).

4.3 Origin of the final eye position correction.

The final eye position correction could originate from an on-line adjustment of the first saccade amplitude (i.e. $e(1)$), from a corrective saccade (i.e. $e(2) - e(1)$), or from a direct compensation on
the memorized saccade (i.e. $e(3) - e(2)$). To differentiate these 3 contributions, we computed the percentage of correction for each of these saccades.

### 4.3.1 Contribution of the first saccade

We found no sign of an on-line correction of the first saccade by the target jump during the saccade. The target jump influenced neither the saccade end-point nor its velocity profile, suggesting that the first saccade is entirely ballistic. Thus, the correction of the final eye position due to the target jump is implemented either by the corrective saccade, or by the memorized saccade, or a combination of both.

### 4.3.2 Contribution of the corrective saccade

Relative to no-jump trials, corrective saccades were less frequent when the target was jumped back (negative jump), and more frequent when it was jumped forward (positive jump). Corrective saccades were also more frequent for larger saccades (see table 3). In the absence of target jumps, corrective saccades were generated more often after a hypo-metric first saccade (not shown), in accord with previous reports (Prablanc et al., 1978; Viviani and Swensson, 1982; Becker, 1989, 1991).

<table>
<thead>
<tr>
<th>Condition</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMALL SACCade 1</td>
<td></td>
</tr>
<tr>
<td>Negative jump</td>
<td>2.9</td>
</tr>
<tr>
<td>No jump</td>
<td>5.4</td>
</tr>
<tr>
<td>Positive jump</td>
<td>12.9</td>
</tr>
<tr>
<td>MEDIUM SACCade 1</td>
<td></td>
</tr>
<tr>
<td>Negative jump</td>
<td>6.8</td>
</tr>
<tr>
<td>No jump</td>
<td>10</td>
</tr>
<tr>
<td>Positive jump</td>
<td>21.6</td>
</tr>
<tr>
<td>LARGE SACCade 1</td>
<td></td>
</tr>
<tr>
<td>Negative jump</td>
<td>4.7</td>
</tr>
<tr>
<td>No jump</td>
<td>14.8</td>
</tr>
<tr>
<td>Positive jump</td>
<td>20.9</td>
</tr>
</tbody>
</table>

Table 3. Percentage of trials by condition for trials with corrective saccade.
We measured the percentage of correction of $e(2)$ for trials with corrective saccade.

The results are reported in figure 5-A (hatched bars). The amount of correction introduced by the corrective saccade was between 70% and 80% for all saccade amplitudes, and thus compensated directly for most of the visual fixation error.

However, this result seemingly contradicts the results reported earlier. We found that even for trials with corrective saccades, the final eye position compensates for less than 1/3 of the target jump as if the eye position following the memorized saccade $e(3)$ “loses” part of the compensatory effect of corrective saccades (compare Fig. 5-A, hatched bars and Fig. 3, white columns). Even more strikingly, for small saccade, the corrective saccade compensate for 80% of target jump while the final correction is null. This is due to the fact that the effect of the corrective saccade is partly antagonized by the memorized saccade (see next section).
Figure 5. Eye movement characteristics during the task. **A.** Percentage of correction during corrective saccade (hatched columns) and eye displacement from T1 to T2 (grey columns) for trials with corrective saccade. Each column and error bar represents, respectively, the mean and standard error of the three different groups of trials according to the primary saccade amplitude. Note the opposite direction of the correction for corrective saccade and vector displacement to T2. There sum is the final eye correction plotted in figure 3 (white columns). **B and C,** representation of a trial containing positive target jump with T1 at 12°. Figure B represents a case without corrective saccade and figure C represents a trial with corrective saccade. Note for figure C that despite the corrective saccade driving the eye closed to the first target position after target jump (T1’’), corresponding to a correction of 80% of the target jump amplitude. The memorized saccade to T2 comes back to the real T2 position, i.e. the vector of the last saccade represents -55% of the target jump amplitude, resulting in a final eye correction of only 25% (80%-55%). Left and right vertical grey arrows indicate the theoretical final
eye position if the motor control was completely driven by the efferent copy ($k_e = 0$) or the visual feedback ($k_e = 1$)

4.3.3 Contribution of the memorized saccade

For trials without corrective saccades, the memorized saccade vector is completely responsible for the final eye position correction. For trials with corrective saccades, on the contrary, the correction introduced by the memorized saccade is negative, i.e. the saccadic vector ($e(3) - e(2)$) is adjusted in the direction opposite to the target jump (Fig. 5-A, grey columns). This is simply a question of geometry, as illustrated on figure 5-C: The corrective saccade almost completely compensates for the target jump (Fig. 5-A, hatched columns) while the final eye position is only corrected partially by the target jump (Fig. 3, white columns). Thus, the saccadic vector is necessarily corrected in the direction opposite to the final eye position, and in fact annihilates most of the effect of the corrective saccade (Fig. 5-A, grey columns). Since the correction introduced by the corrective saccades does not significantly depend on the first saccade amplitude (Fig. 5-A, hatched columns), while the correction of the final eye position ($e(3)$) increases with it (Fig. 3, white columns), it follows that the negative correction decreases with the size of the first saccade, as observed in figure 5-A.

This effect is predicted by the model: If the corrective saccade vector endpoint completely compensates for the target jump, i.e. if $\Delta(2) = \text{jump}$ (see methods), the third saccade that will bring the eye to the second target, $\Delta(3) = e(3) - e(2)$ should be:

$$\Delta(3) = T2 - \hat{e}(2) = T2 - \Delta(1) - \Delta(2) + k_e \text{jump} = T2 - T1 + (k_e - 1) \text{jump}$$

Since $(k_e - 1)$ is negative, the memorized saccade vector is corrected in the direction opposite to the jump, in contrast to the final eye position.
5 Discussion

In order to measure the relative contribution of the visual feedback and the efferent copy of the motor command in the control of sequences of eye movements, we introduced artificial visual fixation errors by moving the target during saccadic eye movements and measured its effect on a subsequent memorized saccade. We found that human subjects rely neither completely on the sensory feedback nor the efferent copy. Rather, their behaviour is compatible with that of a controller keeping an internal estimate of eye position, updating this estimate using the efferent copies after each eye movement, and correcting it with the noisy sensory feedback.

In addition, we found that the relative contribution of the visual feedback and the efferent copy is not fixed but varies with the amplitude of the eye movement, in the direction predicted by a Kalman filter model. As the amplitude of the eye movement increases, the variance of the eye movement and, presumably, of the efferent copy, also increases. As it becomes less reliable compared to the visual feedback, the confidence given to the visual feedback, and thus its contribution to the eye position estimate, should increase. This is indeed what was observed in this study.

Also in agreement with the rather consensual claim that saccades are ballistic movements, we found no evidence of an on-line correction of the saccadic eye movement due to the target jump. In the presence of a corrective saccade, we observed that the visual error is almost entirely compensated for, while part of this correction is annihilated by the next memorized saccade. Thus, we found an interesting dissociation between the partial update of the internal efferent copy and a more “automatic” corrective saccade system, driven (at least in part) by visual fixation errors.

Could the percentage of correction be directly and quantitatively predicted from the motor variance? One could naïvely assume that the variance of the forward prediction, \( V_m = V_n + V_s \), is equal to the measured motor variance. However, under this assumption, the effect of saccade size on the percentage of correction is stronger than the effect predicted from the model. Indeed, from small to medium and large saccades, the motor variance increases from 1.56 to 2.87 while the percentage of correction varies from 0 to 23%, an effect that is too strong to be accounted for by \( k_s = \frac{V_m}{V_m + V_s} \) if we...
assume that the sensory variance $V_s$ remain constant (or, at least do not decrease) with increasing saccade size. In particular, for small saccades, the percent correction is around zero, which would suggest that the variance of the forward prediction is so small that it is completely dominated by sensory noise.

In fact, the internal eye position estimate error $V_e$ is likely to be significantly smaller than the observed motor variance since the motor variance includes fluctuations in the motor command that could be predicted using internal corrective loops (or proprioceptive feedback). This is evidenced by the fact that during sequences of saccades in complete darkness, and thus in the absence of visual feedback, saccades vector are partially or totally corrected based on previous fixation errors (Bock et al., 1995; Ditterich et al., 1998). Moreover, the largest portion of end-point variance in saccades is due to target localization errors, not motor noise (van Beers, 2007). Drawing further quantitative comparison between motor behaviour and an optimal controller will require an independent measure of the contribution of this internal corrective loops to the internal eye position estimate, and in particular, which part of the motor variance cannot be predicted from the efferent copy of the motor command.

Numerous cortical areas are implied in the cortical network of saccadic movement such as frontal eye field (FEF), supplementary eye field, dorsolateral prefrontal cortex, parietal eye field, cerebellum and different sub-cortical regions as the superior colliculus and the brainstem reticular formation (Gaymard et al., 1998; Quaia et al., 1999; Munoz and Fecteau, 2002; Dorris et al., 2007). Previous studies suggest that the forward and inverse models used for sensory-motor control involve the cerebellum and parietal cortex (Zee et al., 1980; Wolpert et al., 1998; Imamizu et al., 2004; Bursztyn et al., 2006). Meanwhile, the anterior intraparietal sulcus is critical for dynamic error detection during goal-dependent reach-to-grasp arm movements (Tunik et al., 2005). A compelling signature of an internal model for eye position is the “visual remapping” observed in the lateral intraparietal area (LIP), whereby cells starts responding to memorized saccadic targets or salient stimuli far outside of their receptive field prior to an eye movement that would bring this position into their receptive field (Duhamel et al., 1992; Colby et al., 1995). Thus, an “internal representation” of future targets is updated by an efferent copy of the motor command sent to the eye plant. Corollary discharges (i.e. efferent motor commands) used in sequences of eye movements involves FEF (White and Snyder, 2007), an area strongly interconnected with LIP (Stanton et al., 1995). Thus the parietal cortex contains an internal model of target position, the question being whether this remapped target positions is also corrected by sensory feedback and modulated by the reliability of sensory and motor
signals, or is an “open loop” system corresponding to a forward prediction. Recording neural activities in parietal, premotor areas and cerebellum in animals performing double step saccades with target jumps could answer this question and untie different signals that were previously confounded, such as the internal estimate of eye position, the forward prediction, motor errors and planned corrective saccades.
6 References


