

Extraretinal signal metrics in multiple-saccade sequences

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Executing sequences of memory-guided movements requires combining sensory information with information about previously made movements. In the oculomotor system, extraretinal information must be combined with stored visual information about target location. The use of extraretinal signals in oculomotor planning can be probed in the double-step task. Using this task and a multiple-step version, the present study examined whether an extraretinal signal was used on every trial, whether its metrics represented desired or actual eye displacement, and whether it was best characterized as a direct estimate of orbital eye position or a vector representation of eye displacement. The results show that accurate information, including saccadic adaptation, about the first saccade is used to plan the second saccade. Furthermore, with multiple saccades, endpoint variability increases with the number of saccades. Controls ruled out that this was due to the perceptual or memory requirements of storing several target locations. Instead, each memory-guided movement depends on an internal copy of an executed movement, which may present a small discrepancy with the actual movement. Increasing the number of estimates increases the variability because this small discrepancy accumulates over several saccades. Such accumulation is compatible with a corollary discharge signal carrying metric information about saccade vectors.

Keywords: extraretinal signal metrics, multiple-saccade sequence, memory-guided movement

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Introduction

When we move, a signal is sent to the cortical motor areas that ultimately control motor neurons. This causal motor signal is different from the signal that informs other brain areas that a movement has been made. Such information about self-movement does not cause movement but relays the change in body position to the rest of the brain. Sensory processing, in particular, needs information about self-movement. In the tactile system, for example, it is important to distinguish between tactile inputs due to self from those due to something else. The psychophysical correlate of this distinction is elevated thresholds to somatic stimuli during active movement, which requires information about self-movement. In the visual system, every eye movement changes the retinal location of visual objects, yet the visual world does not appear to jump with every saccade. Rather, we have the impression of a stable visual world. It has been proposed that this visual stability results from the combination of visual information with information about eye movements (Sperry, 1950; von Helmholtz, 1910/1925; von Holst & Mittelstaedt, 1950). Recently, the neurophysiological correlates of this eye movement information have been studied extensively (Sommer & Wurtz, 2008).

Information about self-movement is important for sensory processing, but it also plays a crucial role in motor planning. Indeed, accurate movements can be made

in the absence of immediately available sensory information, as in the case of memory-guided saccades. Single memory-guided saccades require a relatively simple sensory-to-motor transformation. However, if there are intervening eye movements between target presentation and saccade execution, accurate saccades to the target are widely assumed to require updating the stored location with information about the intervening saccades. Human and monkey observers can indeed make accurate saccades to briefly flashed visual targets after intervening eye movements (Becker & Jurgens, 1979; Mays & Sparks, 1980).¹

The use of self-movement information for movement planning has been studied with the double-step task, in which two peripheral targets are flashed in succession. Subjects then perform a sequence of two saccades to the remembered locations of the targets (Hallett & Lightstone, 1976). The first saccade requires a straightforward sensory-to-motor transformation, but correct performance of the second saccade requires a combination of sensory information about the second target with information about the first eye movement. The present study investigated the use of this information in the double-step task. Three issues were addressed in four experimental sessions. First, is an accurate eye movement signal used on every trial? This was investigated by examining the trial-by-trial relationship between first and second saccades in a double-step session in which participants had to make a sequence of two memory-guided saccades. Second, does

the eye movement signal reflect the desired eye displacement or the actual eye displacement? This question was addressed in the double-step session by adapting the first saccade and looking at the consequences on the second saccade. Third, what is the nature of the eye movement signal: corollary discharge vector versus direct eye position estimate? This was investigated by examining how saccade endpoint variability was influenced by the number of intervening movements in a multiple-step session. Participants had to make one to four memory-guided saccades, and the variability of saccades was examined as a function of the number of preceding saccades. The rationale was that if the extraretinal signal used to update stored spatial locations was a corollary discharge signal, then variability should increase with the number of updates. On the contrary, if the extraretinal signal was a direct estimate of orbital eye position, variability should not increase with the number of updates. To check that the increase in variability was due to the use of a corollary discharge signal and not to the need to hold target locations in memory when making multiple-saccade sequences, two control sessions were run. In the perceptual localization session, participants had to memorize the location of one to four targets and subsequently report one of them. In the memory-delay session, participants made single memory-guided saccades after variable delays. These control sessions made it possible to estimate the variability due to the memory and motor requirements of the multiple-saccade task and to subtract that from overall variability in the multiple-saccade session. The leftover variability should be due to updating the stored target location with one or more extraretinal signals.

Methods

Participants

Eight participants (aged 22–30; five women) from the Paris Descartes community took part in the experiment: seven in exchange for payment, plus the author. All had normal vision and, except for the author, were naïve with regard to the aim of the experiment. All gave their informed consent prior to starting the experiment, which was carried out according to the ethical standards of the Declaration of Helsinki (2004).

Instruments and stimuli

The stimuli were 0.5°-diameter light gray (1.2 cd/m²) dots on a dark gray (0.15 cd/m²) background on a 22" Formac ProNitron 22800 screen, with a resolution of 800 ×

600 pixels and a refresh rate of 145 Hz. Participants were seated 57 cm from the screen and their head kept stable by chin and forehead rests. The fixation dot appeared in the center of the screen and 1–4 target dots were presented. The exact number of dots depended on session. There were four sessions. In the *double-step session*, two dots were selected from the positions illustrated in [Figure 1a](#). In the *multiple-saccade session*, 1–4 dots were selected randomly from the positions illustrated in [Figure 1b](#), with the restriction that no more than 2 dots could be on the same vertical or horizontal line. In the *perceptual localization session*, after target presentation (1–4 dots from positions in [Figure 1b](#)), a 1 × 1° open triangle appeared at screen center, which participants used as a mouse pointer. In the *memory-delay session*, only one dot was presented, chosen randomly from the positions in [Figure 1c](#).

Eye movement recording

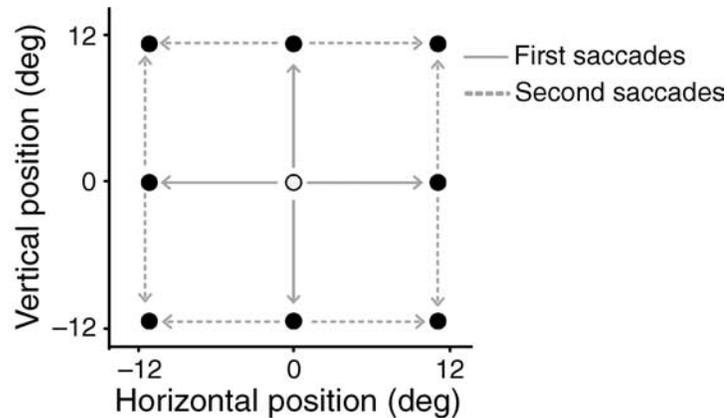
Eye movements were monitored with an Eyelink 1k (SR Research, Osgoode, Ontario, Canada) at 1000-Hz sampling rate. At the beginning of a session, the Eyelink was calibrated. Before each trial, central fixation was checked and compared to the calibration. If the distance between the fixation check and the calibration was greater than 1°, fixation was refused and a new calibration was initiated. Eye movement traces were subsequently analyzed offline. Instantaneous velocity and acceleration were computed for each data sample and compared to a threshold (30°/s and 8000°/s²). Saccade onset was defined as two consecutive above-threshold samples for both criteria. Saccade offset was defined as the beginning of the next 20-ms period of below-threshold samples.

In the multiple-saccade session, saccades smaller than 2° that brought the eyes closer to the same target as the previous saccade were considered to be “corrective” saccades and were eliminated. This was done so that such saccades were not counted as saccades that aimed for the following target, which would have artificially increased the noise of subsequent saccades. No other saccades were eliminated and the first to fourth saccades were used in the analyses.

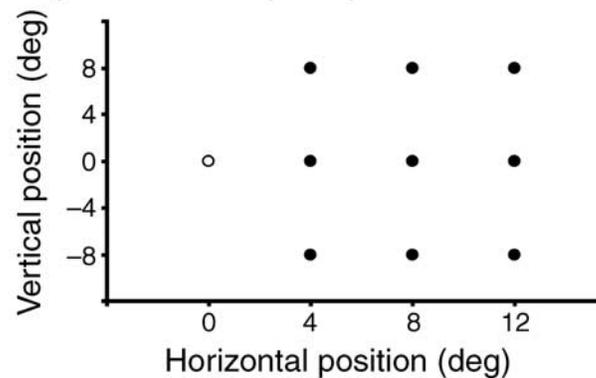
Tasks

All tasks were single saccades or variations on the classic double-step procedure, in which two targets are flashed successively and subjects are then required to make two saccades to the remembered locations (see [Figure 2](#) and below). In the double-step session, participants had to make two saccades to the remembered location of flashed targets. After baseline measurements, the metrics of the first saccade were modified by saccadic adaptation. Adaptation is the remarkable ability of the

a) Double-step session



b) Multiple-saccade & perceptual localization sessions



c) Memory-delay session

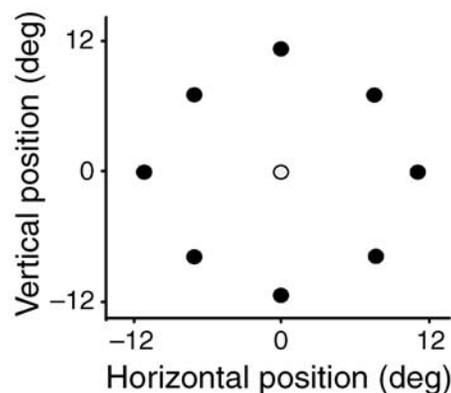


Figure 1. Spatial layout of possible target location in the four sessions: (a) the double-step session, (b) the multiple-step sessions (multiple-saccade and perceptual localization), and (c) the memory-delay session.

oculomotor system to adjust to systematic targeting errors. In the laboratory, adaptation is evoked by displacing the target by a small amount while the primary saccade is in mid-flight (McLaughlin, 1967). Because displacement detection is low during saccades (Bridgeman, Hendry, & Stark, 1975), subjects usually do not notice the displacement. Nevertheless, after 50–100 trials (Deubel, Wolf, & Hauske, 1986), the amplitude of the saccade adapts such that it becomes appropriate to the displaced target

position. With this intra-saccadic displacement procedure, systematic under- or overshoots of the original target can be evoked (for a review about adaptation, see Pélisson, Alahyane, Panouillères, & Tilikete, 2010). In the multiple-saccade session, participants had to make one to four saccades in a multiple-step procedure. In the perceptual localization session, they had to report the localization of one of the targets presented in the multiple-step procedure. In the memory-delay session, they made single

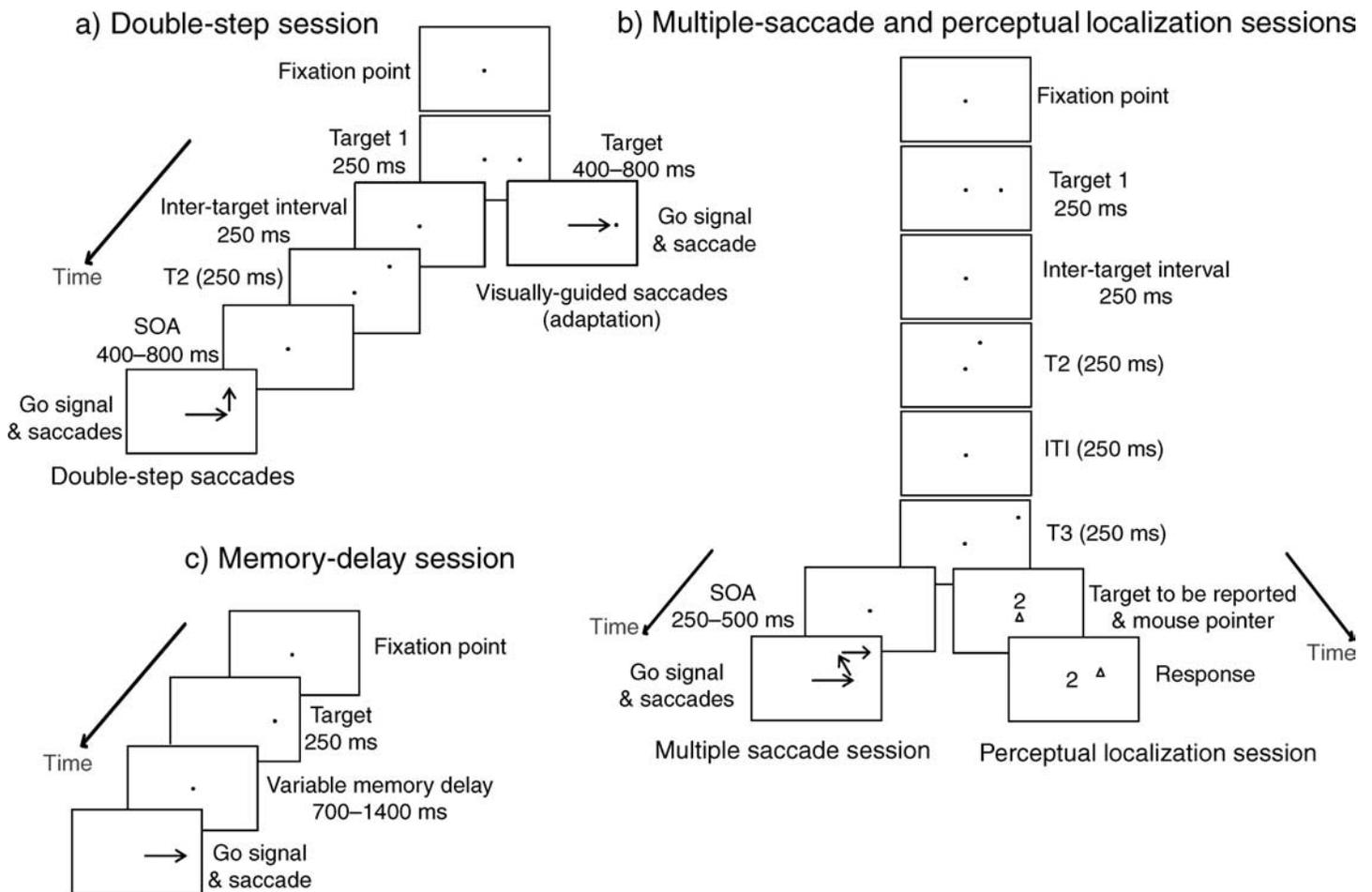


Figure 2. Temporal structure of the four sessions. (a) Double-step session: The fixation point appeared at screen center followed by T1. In the double-step trials, T1 was presented for 250 ms, followed by an inter-target interval of 250 ms, T2 for 250 ms, and an SOA of 400–800 ms until fixation dot offset. This instructed the participant to make two saccades. In the visually guided trials, T1 was present until fixation dot offset, after which participants made a saccade to T1. (b) Multiple-saccade, perceptual localization and memory-delay sessions. The fixation point appeared at screen center, followed by the first target for 250 ms. In the multiple-saccade and perceptual localization sessions, after a 250-ms inter-trial interval, the second target appeared for 250 ms, and so forth, up to 4 targets. After final target presentation and an SOA of 250–500 ms, the fixation dot turned off (multiple-saccade session), instructing the participant to make the memory-guided saccade sequence, or turned into a number (perceptual localization session) with a mouse pointer to report the perceived location. In the memory-delay session, after T1 presentation and a variable memory delay of 700–1400 ms, the fixation dot disappeared, instructing participants to make their saccade.

memory-guided saccades with variable memory delays. Specific procedures are detailed below.

Procedure

Double-step session. Each participant ran one session. Two types of trials were tested (Figure 2a). In the double-step trials, after Eyelink calibration, participants had to fixate the light gray dot at screen center and press a button, which initiated a fixation check. If the fixation check was successful, the trial began. The fixation dot remained present and 500 ms later, the first target appeared for 250 ms, followed by a 250-ms blank and

then the second target for 250 ms. After a random delay of 400–800 ms, the fixation dot disappeared, instructing the participant to make two memory-guided saccades to the remembered locations of the targets, in the order they had been presented. In the visually guided saccade trials, participants fixated the central dot and completed the fixation check; 500 ms later, a single target appeared 12° to the left, right, above, or below. After a random delay of 400–800 ms, the fixation dot turned off. This was the go signal to make the saccade. Note that the target remained present and that the saccade was therefore visually guided. In trials requiring left-, up-, and downward saccades, the target appeared at 12° eccentricity and stayed there throughout the entire trial. In trials requiring a rightward

saccade, the target initially appeared 12° to the right and during saccade execution stepped back to 8° , in order to evoke adaptation.

The double-step session had three successive phases: baseline, adaptation, and test. The baseline (80 trials) included only double-step (memory-guided) saccades. The adaptation phase (180 trials) included only visually guided saccades (120 rightward saccades, 20 of each other direction). The test phase included 80 double-step trials and 40 rightward visually guided trials. These trials were included to maintain adaptation throughout the test but were not included in the analyses below. Comparisons between baseline and test therefore address the effect of adaptation on memory-guided saccade sequences.

Multiple-saccade session. This session was run in counterbalanced order with the perceptual localization session. Each session started with a calibration of the Eyelink and each trial with a fixation check. After a random 500- to 1000-ms delay, a series of 1–4 gray targets was presented. Each target appeared for 250 ms with 250-ms blanks between targets. After final target presentation and a random delay of 250–500 ms, the fixation dot disappeared. This was the go signal for the participant to execute a sequence of memory-guided saccades in the order the targets had been presented (Figure 2b). Participants were encouraged to make one saccade per target. There were 216 trials, 54 for each number of targets.

Perceptual localization session. The procedure was identical to the multiple-saccade session up to final target presentation and a random delay of 250–500 ms. At this point, the fixation dot turned into a number from 1 to 4, indicating which target participants were to report. An open triangle also appeared, which participants were to use as a mouse pointer and click on the remembered location of the target. There were 180 trials.

Memory-delay session. Six of eight participants ran this session. After the fixation check and a 250- to 500-ms delay, a target appeared at one of eight possible locations (see Figure 1c) for 250 ms. It then disappeared and the fixation dot stayed on for one of three durations: short (700 ± 109 ms), medium (1052 ± 92 ms), or long (1406 ± 98 ms). These delays were intended to mimic the average duration of one, two, or three saccades in the multiple-saccade session. Participants had to maintain the target location in memory for the duration of the delay, until fixation dot offset instructed them to make the memory-guided saccade. There were 240 trials.

In all sessions, eye movements were monitored. Participants were to maintain fixation throughout target presentation. In the double-step, multiple-saccade, and memory-delay sessions, the fixation requirement was lifted with the go signal to make a saccade. In the perceptual localization session, the fixation requirement was maintained throughout the response period. Broken fixation trials were aborted and put at the end of the trial queue.

Results

Double-step session

Participants performed sequences of memory-guided saccades and single visually guided saccades (see Figures 1a and 2a). Trials were collapsed over the vertical meridian because there were no significant differences between upward and downward saccade endpoints. From here on, all second saccades will be referred to as upward. For each participant, latency and endpoints were averaged for a given sequence (left–up, right–up, up–left, up–right) and a given phase (baseline, test). Saccade latency in sequences of 2 saccades was analyzed with a 4×2 ANOVA including factors Saccade Sequence and Phase. First saccade latency was affected by Phase ($F(1,7) = 33.8$, $p < 0.001^2$), with slightly faster test saccades than baseline saccades (244 ± 21 ms versus 279 ± 17 ms, average $\pm SEM$). This was probably due to practice with the double-step task. There was no effect of Sequence and no interaction ($ps > 0.36$). There were no main effects and no interaction on second saccade latency ($ps > 0.29$), which was on average 294 ± 36 ms.

The baseline phase of the double-step session tested whether an extraretinal signal was used on a trial-by-trial basis in the double-step task. Alternatively, accurate performance in the double-step task could be achieved without any information about eye movements by memorizing spatial locations or pre-planning vectors (e.g., “first 10° right, then 8° up”). In this case, errors of the first saccade (undershoots or overshoots) should be propagated onto the second saccade, and there should be a positive correlation between first and second saccade errors. However, if there is no (or little) correlation between first and second saccade errors, this suggests that information about the first saccade (i.e., an extraretinal signal) was used by the second saccade to correct for first saccade errors. In the baseline phase, none of the participants showed a correlation between first and second saccade errors (individual correlation coefficients not significantly different from 0, $ps > 0.17$). If an extraretinal signal carrying information about the first saccade is used to plan the second saccade such that it can correct for first saccade errors, there should be a negative correlation between first saccade error (H_1 , defined as the distance between the endpoint and the target of the first saccade) and second saccade horizontal component (H_2):

$$H_2 = a * H_1 + b. \quad (1)$$

If the first saccade undershoots its target, then the second saccade should have a proportional but opposite horizontal component. Examining the horizontal component of the second saccade takes both direction and

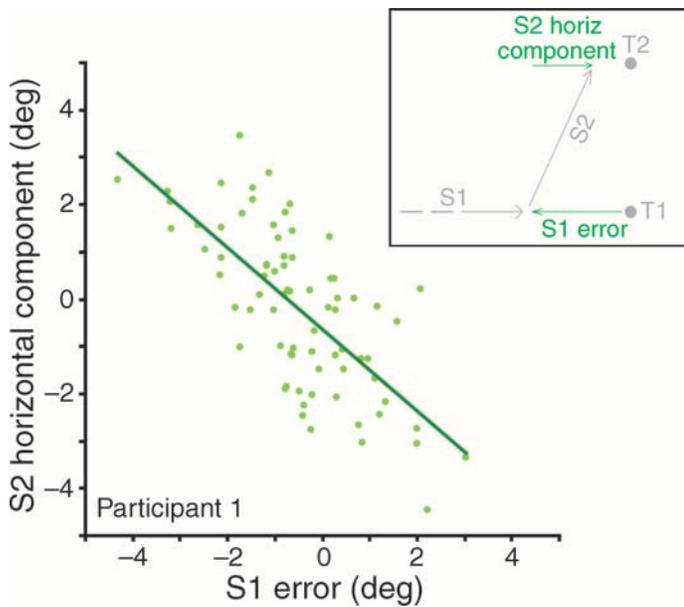


Figure 3. Correlation between first saccade error and second saccade horizontal component in an individual participant, in baseline trials. The regression for this participant is: $y = -0.86x - 0.63$, $r = -0.70$. The inset illustrates the negative correlation hypothesis.

amplitude compensations into account. Figure 3 illustrates the negative correlation hypothesis for rightward first saccades and upward second saccades. The slope of the linear regression is an index of how much the second saccade compensates for the first saccade. A perfect compensation would lead to a slope of 1. All eight participants showed a significant negative correlation between first saccade error and second saccade horizontal component (range of correlation coefficients: -0.34 to -0.88 ; all $ps < 0.01$). Figure 3 shows the results for a representative participant. Correlations were always analyzed individually, but over all participants, the average of

the individual correlation coefficients was -0.65 ± 0.07 (significantly different from 0, $t(7) = -9.7$, $p < 0.0001$) and the average of the individual slopes of the linear regression was -0.74 ± 0.09 ($t(7) = -8.1$, $p < 0.0001$): on average, the second saccade compensated for 74% of first saccade errors.³

The double-step session also examined whether the extraretinal signal represented the desired eye movement (i.e., target eccentricity) or whether it carried lower level metric information by adapting the first saccade and looking at the consequences on the second saccade. This would indicate the relative level at which it is generated: upstream or downstream of the level of saccadic adaptation.

Saccade endpoints are illustrated in Figure 4. The horizontal (h-) and vertical (v-) components were tested for statistical significance with two 2×4 ANOVAs, with factors Saccade (First versus Second) and Sequence (left-up, right-up, up-left, up-right). For the v-component, the Saccade by Sequence interaction was not significant ($F < 1$), confirming that there was no vertical change in saccades between baseline and test. The effect of adaptation can be seen on the h-component of rightward first saccades: the test endpoint is more foveal than the baseline endpoint. Indeed, for these saccades, there was a $2.9 \pm 0.4^\circ$ difference between the endpoint h-component in baseline and test phases ($12.4 \pm 0.5^\circ$ to $9.5 \pm 0.5^\circ$). Expressed in terms of amount of adaptation ($100 \times [\text{baseline} - \text{test}]/\text{baseline}$), it was a $24 \pm 4\%$ adaptation. The interaction between Saccade and Sequence was significant for the h-component ($F(3,21) = 5.8$, $p < 0.008$), revealing that the only significant difference between first and second saccades was for the right-up sequence ($t(7) = 5.5$, $p < 0.001$; all other $ps > 0.16$). The $1.0 \pm 0.9^\circ$ difference between baseline and test second saccades in this sequence was statistically significant and different from that observed on the first saccade. This suggests that the second saccade compensated for some, but not all, of the adaptation of the first saccade.

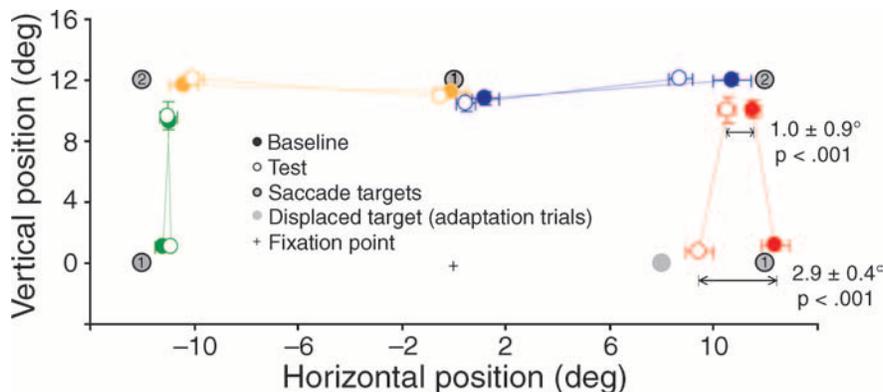


Figure 4. Average saccade endpoints in the double-step session. Error bars represent $\pm SEM$. Each saccade sequence is color coded: right-up in red, up-right in blue, left-up in green, up-left in orange. The numbers inside the gray saccade targets indicate whether the target was presented first or second.

For the right-up sequence, for which there was an effect of first saccade adaptation on the second saccade, the degree to which the second saccade compensated for the adaptation of the first saccade is given by: $1 - [(baseline\ second\ saccade - test\ second\ saccade)/(baseline\ first\ saccade - test\ first\ saccade)]$. On average, the second saccade compensated for 0.70 ± 0.30 of first saccade adaptation. This was significantly different from 0 ($t(7) = 5.2$, $p < 0.01$) and from 1 ($t(7) = 6.8$, $p < 0.01$).

Multiple-saccade, perceptual localization, and memory-delay sessions

One of the goals of the present study was to investigate the nature of the extraretinal signal used in the double-step task. It has been widely assumed to be information about relative eye displacements in the form of a corollary discharge signal that carries metric information (amplitude, direction) about the upcoming saccade vector (also called efference copy; Colby, Duhamel, & Goldberg, 1995; Goldberg & Bruce, 1990; Sommer & Wurtz, 2002). However, such information could also be provided by a direct estimate of eye position in the orbit. These two alternatives were distinguished in the multiple-saccade task. The corollary discharge hypothesis proposes that correct second saccade performance requires the system to perform some kind of vector subtraction between the stored retinal vector of the target and the corollary discharge. When several saccades intervene between target presentation and the saccade to that target, several corollary discharge signals must be combined. However, another option is a more direct estimate of eye position such as that provided by proprioception or the oculomotor neural integrator (van Grootel & van Opstal, 2009; Wang, Zhang, Cohen, & Goldberg, 2007). Both of these provide an estimate of orbital eye position and are not influenced by the number of preceding saccades. When only one intervening saccade occurs (as in the double-step task), the corollary discharge and direct estimate hypotheses are essentially the same; however, when two or more intervening saccades occur, it becomes possible to differentiate them. Indeed, each internal estimate of a motor command will be associated with some noise relative to the actual saccade. This noise is assumed to be independent for each saccade. If current eye position is estimated by adding several corollary discharge signals, then the more saccades, the greater the total amount of noise (van Grootel & van Opstal, 2009). Although the discrepancy between the executed eye movement and its internal estimate is small (Collins, Rolfs, Deubel, & Cavanagh, 2009), the variability of the internal estimate should increase with the number of saccades, and saccades of a given amplitude should be slightly noisier when they are the final saccade of a sequence of memory-guided saccades than when performed alone. Alternatively, if eye position is estimated by a direct estimate, only one

update occurs and the total number of intervening saccades should not influence the variability of the final saccade.

These hypotheses can be summarized as follows. The saccade to the n th target is a function of the perceptual representation of the n th target location, given by the following equation:

$$S_n = f(T_n) = P_n - E_n. \quad (2)$$

P_n is the retinal location of the target and E_n is the estimated eye position (at the time of saccade programming to target n). The corollary discharge hypothesis and the direct eye position hypothesis make different predictions as to the nature of E_n .

The corollary discharge hypothesis proposes that eye position at the time of saccade programming to target n is the sum of all saccade vectors made since target n presentation:

$$S_n = P_n - \sum_{k=1}^{n-1} S_k. \quad (3)$$

The direct eye position hypothesis proposes that eye position at the time of saccade programming to target n is given by an estimate of orbital eye position (O_n) from either proprioception or the neural integrator. Neither of these estimates is influenced by the number of preceding saccades:

$$S_n = P_n - O_n. \quad (4)$$

The saccade to target n will also be influenced by the precision of its perceptual localization (P_n), which in turn will depend on the need to hold the information in memory, with longer memory delays resulting in a degradation of the stored location. Maintaining target location in memory should lead to a noisier representation of target location. Saccades to target n will be influenced by these factors (perceptual location of the target, memory delays) and will also have some variability arising from the central planning and peripheral execution of the movement.

The variability σ^2 of a saccade to target n can therefore be represented as follows, for the corollary discharge hypothesis:

$$\sigma_{S_n}^2 = \sigma_{P_n}^2 + n\sigma_M^2 + \sigma_{Mem}^2 + \sigma_{\sum S_k}^2. \quad (5)$$

Likewise, for the direct eye position estimate hypothesis:

$$\sigma_{S_n}^2 = \sigma_{P_n}^2 + n\sigma_M^2 + \sigma_{Mem}^2 + \sigma_{O_n}^2. \quad (6)$$

Estimating the different sources of variability was important because observing increased variability with the number of saccades in a multiple-saccade sequence may be due to perceptual and memory requirements alone. To determine whether an increase in variability is due to

the use of corollary discharge signals, it is necessary to subtract the other sources of variability.

Perceptual uncertainty (σ_{Pn}^2) was estimated in the perceptual localization session in which participants had to localize a single target. Perceptual error was defined as

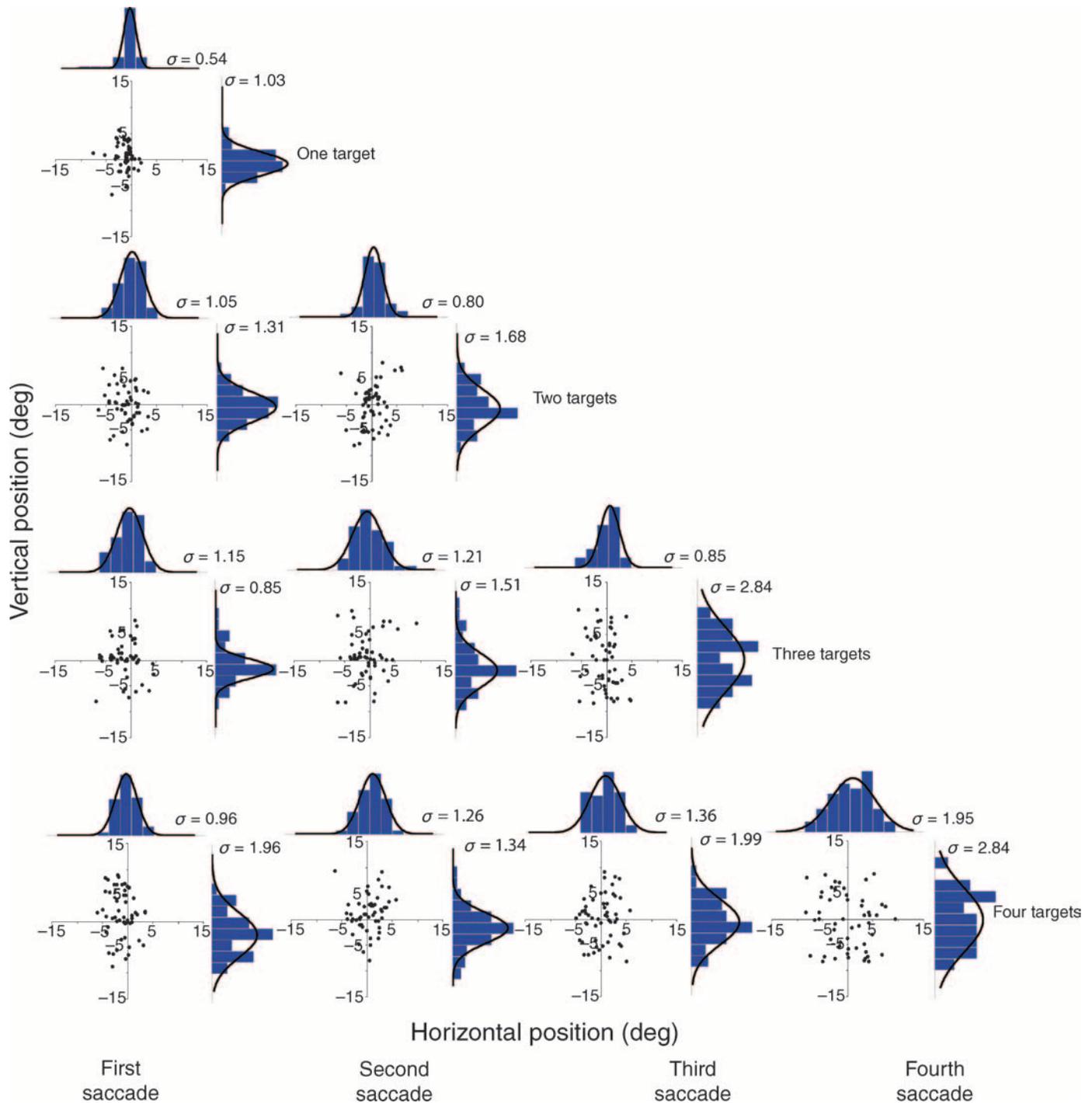


Figure 5. Scatter plots: saccade endpoints in the multiple-saccade session for one participant, according to the number of targets (1–4) and the number of the saccade in the sequence (first, second, third, or fourth saccade). Each point represents one saccade. Bar graphs represent normalized distributions for this participant, and the corresponding σ value represents the standard deviation of the fitted Gaussian.

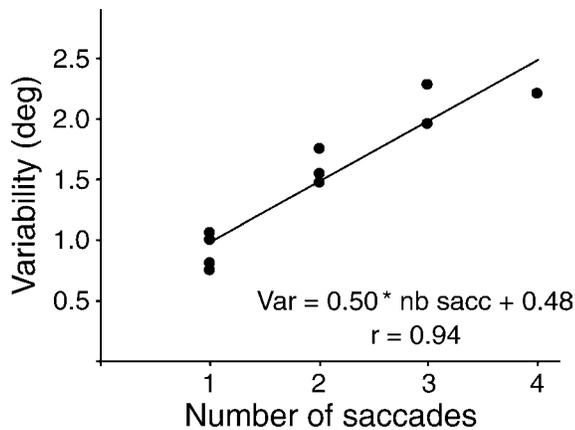


Figure 6. Correlation between the number of saccades and endpoint variability, measured by the standard deviation of Gaussian fits to the distribution of endpoint errors (as in bar graphs of Figure 5).

the distance between the physical target location and the perceived target location, and variability was defined as the variance of error for a given target. To give a single measure of variability, errors in the horizontal and vertical directions were averaged. Overall, when participants were asked to localize a briefly flashed target, they tended to report locations slightly more foveal than the physical target location. Average variability (σ_{Pn}^2) was $2.0 \pm 0.7^\circ$.

Holding a target location in memory may degrade the representation of that location, rendering saccades to it less precise. This added noise due to holding target location in memory (σ_{Mem}^2) was estimated by trials in the perceptual localization session in which participants had to hold the target in memory for one subsequent target (first of two targets, second of three, third of four), for two subsequent targets (first of three, second of four), and so forth. The difference between the variability measured in each of these conditions and perceptual uncertainty for a single target gives an estimate of target location decay in memory. The slight increase in variability with increased targets in memory was marginally significant (holding in memory for 1 subsequent target, $2.4 \pm 0.04^\circ$; for 2 subsequent targets, $2.8 \pm 0.03^\circ$; for 3, $4.8 \pm 0.09^\circ$; $F(2,14) = 5.2$, $p = 0.051$).

Memory for target location could also decay during the execution of intervening saccades, thus making saccades

late in a sequence appear more variable than early saccades. This contribution to σ_{Mem}^2 was estimated in the trials in which a single memory-guided saccade was triggered after a delay comparable to that incurred by executing saccades in the multiple-saccade task (after subtraction of perceptual uncertainty, σ_{Pn}^2). There was no increase in variability with increased time in memory (short delay, $2.7 \pm 0.08^\circ$; medium delay, $2.9 \pm 1.0^\circ$; long delay, $3.2 \pm 1.2^\circ$; $F < 1^4$).

Variability in the multiple-saccade task could also arise from motor noise. Indeed, every saccade is subject to motor noise, which can arise both at the level of central planning and at the level of peripheral execution. For the present purposes, both sources will be referred to as “motor noise,” estimated by the variance of first saccade endpoints, after subtracting perceptual and memory uncertainties as defined above. Variability due to motor noise (σ_M^2) was $3.8 \pm 0.7^\circ$.

In the multiple-saccade session, latency and amplitude were each analyzed with an ANOVA with Position of Saccade in Sequence (first, second, third, fourth) as a factor. On average, saccade latency was 330 ± 35 ms and did not depend on the position of the saccade in the sequence ($F(3,21) = 1.8$, $p > 0.18$). Average saccade amplitude was $9.6 \pm 0.4^\circ$ and was not affected by the position of the saccade in the sequence ($F(3,21) = 1.5$, $p > 0.23$).

Saccade endpoint error was defined as the distance between saccade endpoint and target position, and variability was defined as the variance of error for a given target. Errors in the horizontal and vertical directions were averaged. Figure 5 presents saccade endpoints in an individual participant, as well as the normalized distributions of error in the horizontal and vertical directions. Each distribution was fitted with a Gaussian, the standard deviation of which gives a measure of endpoint dispersion. Over all participants, there was a positive correlation between standard deviations and the number of saccades, with a correlation coefficient of 0.94 (Figure 6).

To determine whether this increase was due to combining several extraretinal signals, each variability estimate was corrected by subtracting the estimates of variability due to perceptual noise, memory, and motor requirements as outlined above. Table 1 presents the variability estimates.

	Second saccade	Third saccade	Fourth saccade
Two targets	9.9 ± 4.2 (<i>21.1 ± 3.8</i>)		
Three targets	10.2 ± 2.6 (<i>23.2 ± 2.6</i>)	22.9 ± 6.3 (<i>38.6 ± 5.6</i>)	
Four targets	7.6 ± 2.3 (<i>20.3 ± 2.2</i>)	9.3 ± 2.5 (<i>24.5 ± 2.7</i>)	21.3 ± 7.8 (<i>41.5 ± 7.4</i>)

Table 1. Variability of saccade endpoints (average \pm SEM) according to saccade number and number of targets (variance of saccade error, the distance between the physical location of the target and the saccade endpoint). Bold: corrected values, italics: uncorrected values.

Corrected variability increased with the number of preceding saccades. Separate ANOVAs were run on 2-, 3- and 4-saccade sequences with saccade number as a factor. For all sequences, the effect of saccade number was significant (2-saccade sequences: $F(1,7) = 6.7$, $p < 0.036$; 3-saccade sequences: $F(2,14) = 17.5$, $p < 0.002$; 4-saccade sequences: $F(3,21) = 7.6$, $p < 0.007$).

Finally, as in the double-step session, it was possible to examine the relationship between successive saccades on a trial-by-trial basis. There was no correlation between the error of saccade $n - 1$ and that of saccade n (average of individual correlation coefficients, -0.01 ± 0.03), but there was a negative correlation between S_{n-1} error and the parallel component of S_n (average of individual slopes, -0.8 ± 0.1 , average of individual correlation coefficients, -0.7 ± 0.04).

Discussion

There are three main results. First, saccades in the double-step task use an extraretinal signal that conveys metric information about previously made movements on a trial-by-trial basis. Second, this extraretinal signal arises downstream of saccadic adaptation. Third, the extraretinal signal is not a direct estimate of eye position but rather a corollary discharge signal. These three results will be discussed successively.

Double-step saccades use an extraretinal signal

In both the double-step and multiple-saccade sessions, there was no correlation between first and second saccade errors. This result suggests that there was no error propagation from first to second saccades, and thus that the system has access to extraretinal information to program the second saccade. There was, however, a negative correlation between the error of the first saccade and the horizontal component of the second saccade, showing that an extraretinal signal is used on a trial-by-trial basis, that this signal closely resembles the metrics of the actual saccade, and that the second saccade compensated for about 75% of first saccade error.

These results confirm neurophysiological and neuropsychological findings. Sparks and Mays (1983) trained monkeys in the double-step task, and before a saccade to the first target could be initiated, the eyes were driven to another position by electrical stimulation of the superior colliculus. Monkeys nevertheless made correct saccades, showing that retinal information about target position was combined with an extraretinal signal and suggesting an origin of the signal downstream of the superior colliculus. Furthermore, temporary inactivation of a pathway carrying

corollary discharge from motor areas to higher areas (superior colliculus (SC)–mediodorsal thalamus (MD)–frontal eye fields (FEFs); Sommer & Wurtz, 2004a) leads to errors in the double-step task such as would be expected if the second saccade was executed to the remembered retinal location of the target (Sommer & Wurtz, 2004b). Lesions of this pathway in humans lead to a similar pattern of results (Ostendorf, Libermann, & Ploner, 2010).

Previous behavioral results are also in favor of an extraretinal signal in the double-step task (Bock, Goltz, Belanger, & Steinback, 1995; Ditterich, Eggert, & Straube, 1998; Joiner, FitzGibbon, & Wurtz, 2010; Munuera, Morel, Duhamel, & Deneve, 2009). Munuera et al. (2009) examined visually guided first saccades and memory-guided second saccades in a double-step task and introduced artificial motor errors on the first saccade by stepping the target randomly on a subset of trials. They measured the relative weights of visual feedback and extraretinal information in second saccade programming. Consistent with increasing motor noise with larger saccades, the weight of the extraretinal signal decreased with saccade amplitude. Recently, Joiner et al. (2010) examined the pattern of saccade endpoint error in the double-step task. By examining the relationship between first and second saccades, they showed that the second saccade compensated for first saccade variations. The present study replicates these results and extends them by showing that the first saccade variations that can be compensated include saccadic adaptation. Ditterich et al. (1998) reported both a positive correlation between first and second saccade errors (suggesting propagation of error and the absence of an extraretinal signal) and a negative correlation between first saccade error and the difference between the two errors (similar to the horizontal second saccade component used here). Their analysis revealed that this was due to the mix of two distinct populations of saccade sequences. The first population consisted of sequences with a long first saccade latency in which there was error propagation and the second of sequences with a short first latency in which there was compensation. They suggested two modes of sequence planning: an extraretinal mode and a pre-planning mode (i.e., memorizing vectors or spatial locations). In the present results, there was no correlation between first and second saccade errors, suggesting that the second population was not present. This may be due to the fact that Ditterich et al. (1998) examined only horizontal sequences. Perhaps pre-planning is possible for saccades with the same direction, but that this strategy is less used with saccades with many directions, as in the present experiment. The sequences in Ditterich et al. (1998) could also sometimes include saccades back and forth across the midline. This would imply transferring target location information across hemispheres, which may also have prompted their participants to sometimes use a pre-planning strategy.

The extraretinal signal carries information about adaptation

Adaptively reducing the amplitude of the first saccade modified the second saccade such that it corrected for first saccade adaptation. This suggests that the extraretinal signal carries information about saccadic adaptation, and therefore, that it may be generated at a level downstream from adaptation (Panouillères, Urquizar, Salemmé, & Pélisson, 2009). This result replicates findings in both humans and monkeys. Doré-Mazars, Vergilino-Perez, Collins, Bohacova, and Beauvillain (2006) adapted single saccades and then tested a two-saccade sequence within spatially extended objects. When second saccades aimed for a new object, they corrected for first saccade adaptation. When second saccades explored the same object, they did not correct for first saccade adaptation. The present experiment extends these results by examining the effect of first saccade adaptation on the second saccade in a paradigm with point targets and vertical saccades. In monkeys, Tanaka (2003) examined the same double-step as used in the present experiment: a first horizontal saccade and a second vertical saccade. After adaptation of the horizontal saccade, the vertical saccade acquired a horizontal component, thus maintaining the accuracy of the second saccade. As in the present results, the correction was not complete.

Incomplete compensation may indicate the use of several extraretinal signals, not all of which carry information about adaptation. Some extraretinal signals may originate upstream of adaptation and their use would tend to propagate first saccade adaptation onto second saccades. In studies where double-step performance was disrupted by lesions of the SC–MD–FEF pathway (Ostendorf et al., 2010; Sommer & Wurtz, 2004b), the deficit was only partial, also suggesting that several corollary discharge pathways may contribute, the SC–MD–FEF pathway being only one of these. It is currently a matter of debate whether the colliculus could give a corollary discharge signal carrying information about adaptation (Frens & van Opstal, 1997; Takeichi, Kaneko, & Fuchs, 2007). Another possibility is that adaptation occurs in the cerebellum, and that the corollary discharge signal would originate there and be sent to higher areas via the thalamus. In support of this, patients with lesions of the cerebellar thalamus showed reduced adaptation relative to patients with thalamic lesions not involving the cerebellar thalamus and controls (Gaymard, Rivaud-Pechoux, Yelnik, Pidoux, & Ploner, 2001). Whatever the neurophysiological underpinnings, the current results fit well with the idea of several corollary discharge pathways being implicated in the double-step task.

The present results have implications for the perceptual effect of adaptation. Several studies have shown that adaptation is accompanied by a proportional shift in the localization of visual targets (Awater, Burr, Lappe,

Morrone, & Goldberg, 2005; Bahcall & Kowler, 1999; Bruno & Morrone, 2007; Collins, Doré-Mazars, & Lappe, 2007; Collins et al., 2009). Awater et al. (2005) used verbal reports and Bruno and Morrone (2007) a pointing response, and both showed a shift of perceived target location in the direction of adaptation. In Collins et al. (2009), participants had to report whether a post-saccadic target was to the left or right of the pre-saccadic target. Reports shifted in the direction of adaptation. This could arise because of a mismatch between the expected post-saccadic target location, based on an unadapted extraretinal signal, and the actual post-saccadic target location. A second possibility is that the extraretinal signal carries information about adaptation because it is based on a mislocalized target. Although adaptation does not seem to influence localization during fixation but only when the target is flashed during saccade preparation (Georg & Lappe, 2009), the present study used memory-guided saccades that have different effects on visual localization (Zimmermann & Lappe, 2010). If the target is mislocalized, there is no mismatch between expected and actual post-saccadic target locations if the target steps during the saccade. Although the present study did not test the effect of adaptation on perception, the results are in favor of the second hypothesis (see Collins et al., 2009).

The extraretinal signal is a corollary discharge

The variability of endpoints to a target increased with the number of saccades. Control experiments ruled out that this increase was due to perceptual or memory requirements. The variability of saccades to a target increased slightly when subsequent targets had to be memorized, and not when the target simply had to be held in memory for a short period. Other studies have shown an increase of variability with increased delay (White, Sparks, & Stanford, 1994), but the delays used were much longer. Variability due to memorizing several targets could not explain the total variability. Instead, the increase of variability is due to the use of several extraretinal signals.

The presence of increasing endpoint variability with the number of saccades rules out the hypothesis that the extraretinal signal used in the double-step task is a direct eye position estimate. Such an estimate could have been provided by proprioceptive signals from the extraocular muscles. It is known, however, that proprioception plays only a minor role (if at all), in online movement execution. Indeed, monkeys performed correctly in the double-step task when proprioceptive afferents were cut (Guthrie, Porter, & Sparks, 1983). Artificially changing eye position just before a saccade by stimulating the extraocular muscles did not lead to compensation by subsequent saccades, as if they were programmed from

the initial, pre-stimulation position (Sparks, Mays, & Porter, 1987). Finally, proprioceptive signals seem to arrive too late to be used in the double-step task (Wang et al., 2007; Wurtz, 2008). An alternative direct eye position estimate could come from the neural integrator that holds information about current orbital eye position on the basis of neuronal inflow to the extraocular muscles. Evidence in favor of a direct eye position estimate was recently presented by van Grootel and van Opstal (2009) in a study using audio-guided saccades. They asked participants to fixate a dot and then make saccades freely in darkness as soon as it disappeared. After several seconds of delay, a tone played from a particular location and participants were required to saccade to it. The variability of the audio-guided saccade did not depend on the number of previous saccades, prompting the authors to propose that the eye position signal was a direct input. However, several important differences between that study and the present study can explain the divergence of results. First, the target was auditory. It is possible that when programming an audio-guided saccade, the transformation of head-centered coordinates to eye-centered coordinates uses a direct estimate of orbital eye position. Second, the saccade to the target was not memorized. It may be that memory-guided saccades exhibit a strong dependence on corollary discharge because sensory feedback cannot guide movements. When the immediate sensory information is available to guide a movement, the system may sample eye position the moment that stimulus is presented and use a more precise position estimate that is not prone to accumulated error.

Karn, Møller, and Hayhoe (1997) reported increased variability with increasing numbers of intervening saccades in a multiple-step task similar to that used here. Because they observed a similar increase in a condition where exocentric information was available to localize the final target, they attributed the increase to non-specific factors like memory decay and concluded that the eye position signal was a direct estimate. Their participants were explicitly instructed to keep a target location in memory and learned the possible target locations as shown by a decrease in variability to targets within a session. This means that the observed variability increase was actually underestimated. Because they did not measure the effect of variability due to memory decay, total variability increase cannot be safely attributed to this factor alone.

In summary, the present findings show that the saccadic system keeps track of its own movements by using a corollary discharge signal representing the direction and amplitude of intervening movements. The signal carries information about the metrics of the saccade including information about saccadic adaptation. The evidence for the signal being a corollary discharge comes from small errors in the tracking process that accumulate as more saccades are made. As a result, memory-guided saccades made after many intervening saccades are noisier than after fewer

intervening saccades. This increase of variability was not due to the perceptual or memory requirements of maintaining several targets in memory, which were estimated independently and did not explain total variability.

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Footnotes

¹Several different terms have been used when talking about information about previous eye movements in oculomotor planning. The following will be used here. “Extraretinal signal” refers to any non-retinal information about eye movements (proprioceptive, direct estimate, vector copy). This term does not make any assumptions about what kind of information is vehicled by the signal nor about its origin. The terms “efference copy” and “corollary discharge” make assumptions about the nature and the origin of the signal, which carry metric information (amplitude, direction) about the upcoming saccade vector. The term corollary discharge will be used in this way here.

²In all ANOVAs reported hereafter, when Mauchly’s test was significant and sphericity could not be assumed, Huynh–Feldt adjustments to the degrees of freedom were used (although uncorrected dfs are reported in the [Results](#) section).

³The relationship between first and second saccades was examined separately for baseline and test saccades, to make sure that the adaptation of the first saccade was not the source of its relationship to the second saccade. The same analyses as above were run on test saccades and revealed similar results (negative correlation between first saccade error and second saccade horizontal component: $r = -0.76 \pm 0.04$; no correlation between first and second saccade errors: correlation coefficients not significantly different from 0, $ps > 0.099$). The negative correlation here indicates that the more the first saccade was adapted (i.e., the more it undershot the target), the greater the second saccade’s horizontal component in the opposite direction (see below).

⁴Because only six of eight participants were able to run the memory-delay session, averages, SEM, and ANOVAs were calculated on these six. For the subtraction analyses, the average value was used for the two remaining participants.

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