Perisaccadic mislocalization of visual targets
by head-free gaze shifts: visual or motor?

Sigrid M.C.I. van Wetter and A. John van Opstal*

Radboud University Nijmegen,
Donders Centre for Neuroscience,
Faculty of Science,
Department of Biophysics
Geert Grooteplein 21
6525 EZ Nijmegen, The Netherlands

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*corresponding author.
E-mail: j.vanopstal@science.ru.nl
Tel: (+31) 243 614 251
Fax: (+31) 243 541 435

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ABSTRACT

Localization of a visual target flash is inaccurate when it is presented around the onset of a saccadic eye movement. Such perisaccadic mislocalization is maximal in the direction of the saccade, and varies systematically with the target-saccade onset delay. We have recently shown that under head-fixed conditions perisaccadic errors do not follow the quantitative predictions of current visuomotor spatial updating models that explain these mislocalizations in terms of spatial updating. These models all assume sluggish eye-movement feedback, and therefore predict that errors should vary systematically with the amplitude and kinematics of the intervening saccade. Instead, we reported that errors depend only weakly on the saccade amplitude. An alternative explanation for the data is that around the saccade the perceived target location undergoes a uniform transient shift in the saccade direction, but that the oculomotor feedback is, on average, accurate. This ‘visual shift’ hypothesis predicts that errors will also remain insensitive to kinematic variability within much larger head-free gaze shifts. Here we test this prediction by presenting a brief visual probe near the onset of gaze saccades between 40 and 70 deg amplitude. According to models with inaccurate gaze-motor feedback, the expected perisaccadic errors for such gaze shifts should be as large as 30 deg, and depend heavily on the kinematics of the gaze shift. In contrast, we found that the actual peak errors were similar to those reported for much smaller saccadic eye movements, i.e. on average about 10 deg, and that neither gaze-shift amplitude, nor kinematics plays a systematic role. Our data further corroborate the visual origin of perisaccadic mislocalization under open-loop conditions, and strengthen the idea that efferent feedback signals in the gaze control system are fast and accurate.

Key words:
Human – spatial perception – sensorimotor integration – efferent feedback – eye-head coordination - models
INTRODUCTION

Orienting the eyes toward a briefly flashed visual target in darkness requires the use of retinal as well as extraretinal signals, as any intervening change of gaze direction prior to the orienting response has to be accounted for. Thus, programming a saccadic eye movement needs to incorporate the changes in eye position since the target flash. The present study investigates the occurrence of systematic localization errors of head-free gaze shifts that were elicited by a double-step target flash in darkness, in which the second flash was timed around the first gaze-shift onset. We will first briefly review similar experiments, so far carried out under head-fixed conditions.

Spatial updating. Hallett and Lightstone (1976) showed that the human saccadic system accurately localizes a visual target, flashed before or during an intervening saccadic eye movement in darkness. To account for this behavior, the system is thought to use an extraretinal signal about intervening eye movements to transform the retinal target coordinates into an oculocentric reference frame (Jürgens et al., 1981; Scudder, 1988; Goldberg and Bruce, 1990; Scudder et al., 2002). Sparks and Mays (1983) demonstrated that accurate open-loop re-orienting even occurs when the intervening saccade is experimentally induced by microstimulation of the monkey midbrain superior colliculus (SC), which suggests that the extraretinal signal originates at or downstream from the stimulation site. Subsequent single-unit recordings showed that the saccade-related burst in the population of SC cells carried the oculocentric, updated coordinates of the target (Sparks and Porter, 1983), and therefore indicated that the spatial remapping of targets occurred upstream from the recorded cells. Indeed, later experiments have shown that the visual activity of cells in posterior parietal cortex (Duhamel et al., 1992), frontal eye fields (FEF; Umeno and Goldberg, 1997), and SC (Walker et al., 1995) signal the updated target coordinates, even before the onset of a planned saccade (predictive remapping). In an elegant series of electrophysiological experiments Sommer and Wurtz (2002, 2006) showed that FEF cells receive an efference copy of the eye movement from saccade-related SC cells (Sommer and Wurtz, 2002, 2006). A neural correlate of spatial updating in the human parietal cortex was recently demonstrated in an fMRI study by Medendorp et al. (2003).

Perisaccadic errors. However, a large number of studies have reported systematic localization errors of visual stimuli presented around the occurrence of an intervening
saccade, both in darkness under open-loop conditions, as well as in visual-perceptual studies in the light. This was first shown in a study by Matin and Pearce (1965), in which subjects had to report the location of a target flashed in otherwise darkness near the onset of a saccade. Their results indicated that the flash was mislocalized in the direction of the saccade, and that the size of the error depended on the timing of the flash relative to saccade onset (the target delay). Dassonville and colleagues showed that similar mislocalizations also occurred for the second saccade in a double-step trial, hinting at the possibility that the perceived direction of the flash and the actual saccade target may share common processing mechanisms. The size of the error varied systematically with the target delay, and could be as large as 70% of the first-saccade amplitude (Dassonville et al., 1992, 1995; Schlag and Schlag-Rey, 2002). This phenomenon has become known as perisaccadic mislocalization.

The programming of saccades also interferes with the perception of allocentric visual cues. Cai et al. (1997) showed that relative retinal locations of visual dots are perceived to shift with the saccade when a briefly presented probe dot is flashed near the saccade onset, suggesting that the oculomotor system also influences visual processing. Sogo and Osaka (2002) further demonstrated that when two targets are briefly flashed around a saccade, they are both mislocalized. However, the amount of their mislocalization not only depends on the target delay, but also on the inter-flash interval of the targets, suggesting that the mechanisms causing perisaccadic mislocalization also affect allocentric visual relationships.

Perisaccadic mislocalization of visual stimuli is not confined to open-loop conditions in darkness, but also occurs in the light. There is now clear evidence that in addition to mislocalization in the saccade direction, the perception of visual space becomes transiently compressed toward the saccade endpoint (Ross et al., 1997). Lappe et al. (2000) and Awater and Lappe (2006) argued that this apparent compression results from post-saccadic visual analysis by the perceptual system, in which the presaccadic visual relations are stored in memory and compared with the visual situation immediately after the saccade. Their results thus suggested that visual-spatial perception and saccade programming, like in the open-loop double-step paradigm, may invoke different mechanisms (Bridgeman et al., 1994; Deubel et al., 1998).

The question arises as to why the visuomotor system performs so poorly around the saccadic event. Couldn't it do any better? According to Niemeier et al. (2003, 2007) the visuomotor system may operate in a statistically optimal way. They argued that, due to
internal noise, or to poor stimulus conditions, the brain has to deal with different and varying uncertainties of the sensory and motor events. They proposed that the visuomotor system builds a statistical model of the sensory environment and of its own motor state, such that it can account for these uncertainties through optimal inference. Simulations showed that, as a consequence, the system will produce the type of error patterns observed for saccadic suppression of target displacement (Niemeier et al., 2003, 2007). A similar line of reasoning was forwarded by Binda et al. (2007), who demonstrated that perisaccadic visual compression nearly disappears when visual stimuli were paired with auditory targets. Apparently, the default dominance of vision over audition in localization tasks may reverse around saccades, when vision becomes less reliable. They used a Bayesian framework to explain their results.

**Visuomotor updating models.** Under open-loop conditions, post-saccadic allocentric visual cues are absent, and a spatially accurate representation of a visual target in eye-centered coordinates after an intervening eye movement is determined by:

\[
T_E = T_R - S_1
\]

where \(T_R\) is the initial retinal error of the target (i.e. prior to the gaze shift at the time of target presentation, and \(S_1\) is the intervening saccadic eye displacement since the target offset. Clearly, a localization error in a double-step experiment would occur when either of these two signals is not veridical. Several models have been proposed to explain perisaccadic mislocalization in the double step.

The oculomotor feedback model assumes that the internal representation of the eye movement in Eqn. (1) is a sluggish, low-pass filtered version of the actual oculomotor command, but that the visual signal is accurate (Dassonville et al., 1992; 1995; Honda, 1990; 1991; Schlag and Schlag-Rey, 2002). The perceived direction of the visual flash is therefore given by:

\[
T_{E}^P = T_R - S_1^P
\]

with \(S_1^P\) the internally perceived, sluggish extraretinal eye-movement that followed since the target disappeared. As a consequence, an error arises in the direction of the saccade that is given by the difference between the perceived and actual eye movement (figure 1A). Due to the dynamics of these signals, the predicted perisaccadic errors resemble those that were indeed observed experimentally.
Perisaccadic Gaze Errors

Recently, however, Pola (2004, 2007) argued that a brief visual probe actually produces persistent activity in the visual pathways and that, as a consequence, the use of such a temporally blurred signal results in errors of the perceived, extraretinal eye-movement signal. In his model, the extraretinal signal is determined by a weighting process of the persistent visual signal, $T_R(t)$, with the (accurate, slightly delayed) efference copy signal according to:

$$S^P(t_0) = \int_{t_0}^{t_1} T_R(t) \cdot S_1(t - \tau) dt$$

with $t_0$ and $t_1$ the visual persistence interval, and $\tau$ is the delay. He showed that the predicted localization error patterns were equivalent to those of the oculomotor model, and that this model was also able to account for the visual interactions observed in double flashes (Sogo and Osaka, 2002; Pola, 2007). Hence, perisaccadic localization errors could have a visual, rather than an oculomotor origin.

Finally, Ross et al. (1997) explained their more complex mislocalization results in the light by errors in both the visual and oculomotor representations. In their formulation, the internal target updating, required by Eqn. 1, was performed on the basis of:

$$T^P_E = C(M, \Delta S) \cdot T_R - S^P_1$$

in which $C(M, \Delta S)$ is a dynamic, nonlinear retinal compression factor (value between 0 and 1) that depends on the target probe’s instantaneous retinal eccentricity, $M=T_R-S_1\ (the\ dynamic\ motor\ error)$, as well as on the difference between the perceived and actual saccade, $\Delta S=S^P_1-S_1$ (Ross et al., 1997; see Van Wetter and Van Opstal, 2008, and Supplemental Material, for technical details). Clearly, when compressed visual-spatial information is combined with a sluggish eye-movement signal, the perceived oculocentric location of the target will be misjudged too.

Similarities and differences. It is important to note that a common feature of the three different visuomotor schemes of Eqns. 2-4 is the use of a damped or blurred representation of the internal eye-movement signal, $S^P_1$. We have recently pointed out that, as a consequence, and despite their conceptual differences, these models all predict that the resulting localization errors depend in a systematic way on the properties of the intervening saccade, in particular on its amplitude and on its kinematics (Van Wetter and Van Opstal, 2008; see also Ostendorf et al., 2007). Moreover, our simulations with these models over a large range of model parameters showed that they
all predict equivalent error patterns (Pola, 2004; Van Wetter and Van Opstal, 2008). Figure 1A illustrates this point for the oculomotor model, by showing the expected error patterns for a small and fast (black line), vs. a slow and large saccade (red line).

Yet, the results from our double-step experiments indicated that the localization errors were unrelated to the variability in the intervening saccades, which suggested that the errors had a purely visual, rather than an oculomotor origin. We therefore proposed that around the saccade the visual representation of the target undergoes a transient shift in the direction of the saccade, but that the extraretinal feedback signal is, on average, accurate. The shift depends only mildly on the planned saccade amplitude. According to this simple idea localization errors saturate for saccades exceeding 10 to 15 deg, and the saccade kinematics do not play a significant role (figure 1B).

----- figure 1 about here -----

**Head-free gaze shifts.** Perisaccadic mislocalization has typically been studied under head-fixed conditions. A recent exception is Vliegen et al., (2004, 2005) who elicited double-step eye-head gaze shifts to visual-visual and visual-auditory double-steps presented around and during the first gaze shift. They observed that the localization errors were smaller than expected from Dassonville’s oculomotor model, but were unable to provide a conclusive explanation, as stimulus intensities and durations in their experiments differed considerably from the Dassonville et al. (1992, 1995) studies.

The present study is designed to test the predictions of the four different models mentioned above for large, and highly variable head-free gaze shifts. Under head-free orienting, the target representation should be invariant to eye- and head movements, and hence accurate updating of the oculocentric target coordinates now requires that

$$T_E = T_R - G_1 \quad \text{with} \quad G_1 = S_1 + H_1$$

(5)

in which $S_1$, $G_1$, and $H_1$ are the intervening eye-, gaze-, and head-displacement signals since target offset, respectively.

In principle, one could extend the visuomotor updating models described above in two different ways, depending on whether the perisaccadic errors were to result from a process that updates the gaze coordinates ($G_1$), or whether the errors are entirely due to a misrepresentation of the rapid eye-movement ($S_1$) signal. The former possibility assigns the errors to erroneous feedback of a gaze-displacement signal, which is currently supposed to have a collicular origin (e.g. Munoz et al., 1991; Galiana and Guitton, 1992; Guitton, 1992; Freedman et al., 1996; Goossens and Van Opstal, 1997).
In the latter case, localization errors would result from sluggish feedback of eye movement signals, which are considered to arise in the brainstem burst generator (e.g. Van Gisbergen et al., 1981; Scudder et al., 2002). The associated head movement is then assumed to be accurate.

Note, that the predictions of visuomotor updating will differ for these two scenarios, as gaze- and eye-displacement signals are typically dissociated under head-free conditions (Ron et al., 1993; Goossens and Van Opstal, 1997).

For the visual shift model, however, the predictions are the same, regardless the underlying motor programs. In particular, this simple model also predicts that localization errors should be similar to the patterns reported for much smaller head-fixed saccades (i.e. saturating at about 10 deg around the gaze-shift onset).

Here we test these predictions for large head-free gaze shifts (amplitudes between 40 and 70 deg) made to double-step visual flashes in otherwise complete darkness. In this paradigm the gaze-control system has to rely entirely on the retinal target coordinates, and on eye- and gaze-feedback signals, as no further visual cues are presented. Our data show that the errors are unrelated to the kinematics of the first gaze shift, and that, in line with the prediction of the visual-shift model, error patterns are similar to those generated under head-fixed conditions for much smaller saccades.
METHODS

Subjects
Six subjects (five male, one female, ages 20-49) participated in the experiments. Subject JO is one of the authors, subjects IL and BD were inexperienced in gaze control studies, but were involved in the design and analysis of the experiments. The other three subjects (TG, RW and PB) were naive regarding the purpose of this study. All subjects had normal uncorrected binocular vision, except for JO who is amblyopic in his right, recorded eye. Informed consent was obtained. Experiments adhered to the principles of the Declaration of Helsinki, and the US federal regulations for the Protection of Human Subjects.

Apparatus
Experiments were conducted in a completely dark room (WxLxH=2.5x3.5x2.5 m$^3$), in which two pairs of 2.5x2.5 m$^2$ coils were attached to the left/right walls and floor/ceiling to generate the horizontal (30 kHz) and vertical (40 kHz) magnetic fields needed for the scleral search coil technique (Robinson, 1963). The subject was seated in a chair with the head in the center of the magnetic fields. Vision was binocular, and the head was free to move in all directions. To provide the subject feedback about his/her posture during the experiment, a metal bar, fixed to the floor of the experimental room, softly rested against the lower part of the neck, without impeding the subject’s head movements.

Visual stimuli were provided by green light-emitting diodes (LEDs; $\lambda$=568 nm; Knightbright Electronics, L59EGW/CA; diameter 2.5 mm, corresponding to 0.2 deg viewing angle). The LEDs were powered with current pulses (frequency 150 Hz) and set to a relatively low intensity of 0.8 cd/m$^2$ (calibrated with a Minolta LS-100 luminance meter). To measure eye movements, the subject wore a search coil (Skalar Instruments, Delft, The Netherlands; Collewijn et al., 1975) on the right eye. Head rotations were measured with a custom made small coil that was attached to a light-weight (150 g) helmet. During calibration of the eye- and head coils, a 40 cm long thin aluminum rod protruded from the helmet, to position a red LED in front of the subject’s recorded eye. This red LED defined a head-fixed visual stimulus that provided the subject accurate visual feedback about head orientation. After the calibration run (see below), this rod was removed.
Perisaccadic Gaze Errors

Horizontal and vertical components of eye movements were extracted from the eye-coil signal by lock-in amplifiers (Princeton Applied Research, model 128A) that were tuned to the respective field frequencies. Horizontal and vertical head-movement signals were measured with PAR 120 lock-in amplifiers. Signals were low-pass filtered with a 4th order low-pass anti-aliasing filter (cut-off at 150 Hz) and amplified with custom-made amplifiers. Signals (four channels) were subsequently digitized at a sample frequency of 500 Hz/channel (Metrabyte, DAS-16) and stored on hard disk for further off-line analysis. Stimulus generation and data acquisition were controlled by a PC 486 that was equipped with a timer board (National Instruments, DT2817) and an I2C board to control the LEDs. LEDs (n=85) were mounted on a thin-wire hemisphere with a radius of 0.85 m. The LEDs were mounted at 7 different polar coordinate eccentricities, R, and 12 directions, √, with respect to the straight-ahead central LED ([R, √] = [0,0] deg) at R = [2, 5, 9, 14, 20, 27, 35] deg, and √ = [0, 30, 60, ......, 330] deg, where √=0 is rightward, and √=90 deg is upward with respect to the central LED.

Paradigms

Calibration paradigm.

Each experimental session started with a calibration run to obtain steady fixations of the eye-in-space (gaze), head-in-space and eye-in-head at all selected LED positions. Each trial started with fixation of the central LED for 600-800 ms. The subject had to align the red head-fixed LED with the central fixation spot. In this way, eye and head pointed roughly in the same direction. When this LED was extinguished, a peripheral LED, selected in pseudo-random order from one of 33 locations (target eccentricities at 0 deg (five times), at 9 deg (in the four cardinal directions), or at 20 or 35 deg (in all 12 directions)), was illuminated for 2.0 s. The subject was required to make an accurate gaze saccade to the new LED and to maintain fixation as long as it was illuminated. When this LED extinguished, the red head-fixed LED on the aluminum rod was illuminated for 500 ms. The subject had to make a saccade toward this second LED, while keeping the head stationary at its newly acquired orientation. In this way, the head-in-space orientation could be calibrated. From the five central LED trials, the eye-in-head offset position, E₀, with respect to the helmet LED could be determined (e.g. Goossens and Van Opstal, 1997, for more details). During calibration, the visual stimuli had an intensity of about 1.0 cd/m². After calibration, the rod was removed from the helmet to
Perisaccadic Gaze Errors

allow the subject to make natural eye-head gaze shifts without any restrictions or visual feedback about head movements.

Double-step paradigms.
In the double-step paradigm the initial fixation position was located at \([R_0, \sqrt{0}]=[27,180]\) deg, and presented for 600-1000 ms. The subject had to foveate this fixation spot (note: eye and head were not necessarily aligned in this experiment as subjects did not receive feedback about their head orientation). When the fixation spot extinguished, the first visual target (0.8 cd/m²) would appear after a 100 ms gap of darkness for a duration of 20 ms at either [27,30] or [27,330] deg, with respect to straight ahead, i.e. at a retinal location of \([R_1, \sqrt{1}]=[52, \pm15]\) deg from the initial fixation point. The subject had to make a natural gaze shift to this stimulus as fast as possible.

In 92% of the trials, a second brief visual target (0.8 cd/m²) would be presented for 15 ms. The onset of this stimulus was pseudo-randomly selected from \(\otimes T \in [100, 120, ...., 240]\) ms after the offset of the first stimulus, to ensure an approximately homogeneous distribution of stimulus delays relative to the first gaze shift onset (which typically had a latency of about 200 ms, see Table 1). This second stimulus could be presented at either one of ten different locations, pseudo-randomly selected from \([R_2, \sqrt{2}]=[20, 60], [20, 120], [27, 60], [27, 90], \) or [27, 120] deg, with respect to straight ahead in the upper visual hemifield, and the other five locations mirrored about the horizontal meridian in the lower visual hemifield, thus creating a variety of retinal target locations. In these trials the subject was required to refixate the perceived location of the second visual stimulus as fast and as accurately as possible. The remaining 8% of trials served as catch trials, in which only the first target was presented. One experimental run consisted of 108 trials: 100 double steps and 8 catch trials. A typical recording session contained two to three experimental double-step runs. Subjects participated in three to five recording sessions, taken on different days.

Data analysis
Calibration and saccade selection. Data from the eye coil were calibrated off-line by mapping the end-fixations of the 33 gaze-fixation points from the calibration paradigm onto their known locations. The optimal parameters that map the digitized voltages onto known degrees of eye rotation were found by training two feedforward neural networks for the horizontal and vertical components of the eye position signals, respectively (e.g.
Goossens and Van Opstal, 1997, and Vliegen et al., 2005). To calibrate the data, the neural networks were applied to the raw data samples. From the five central fixation trials in the calibration experiments, we determined the orientation of the eye, \( E_0 \), when it fixated the red LED on the rod, with respect to the central fixation spot. To calibrate the head-in-space orientation, we used the eye-coil calibration signals when the eye was fixating the head-fixed red LED, as ‘targets’ for the head. Subsequently, the head-in-space orientation was obtained by subtracting the offset, \( E_0 \), from the calibrated head-coil signals. Finally, the eye-in-head orientation was found by subtracting the calibrated head-in-space orientation from the calibrated gaze orientation: \( E_H = G - H \) (see Goossens and Van Opstal, 1997).

Gaze saccades were detected in the calibrated data on the basis of acceleration and velocity criteria for their on- and offsets that could be separately set, and adjusted, by the experimenter. First gaze-saccade responses with an onset latency of less than 80 ms, or longer than 500 ms and with an amplitude less than half the required gaze vector were excluded from the analysis. Second-saccade responses with a latency (relative to \( T_2 \)) exceeding 600 ms, amplitude less than half the motor error vector, and a directional error exceeding 45 deg were also excluded. Double-step trials in which the first saccade was not followed by a valid second response were not considered in the analysis. After passing the selection criteria subjects yielded between 460 and 660 successful double-step responses.

Because the eye-in-head saccade often terminated well before the gaze-saccade offset (see figure 3, for an example), we defined the offset of the eye-in-head saccade as the moment of maximum eye displacement during the gaze shift.

*Localization error.* The data were analyzed in the following way. First, the measured localization error vector of the second gaze saccade, \( \dot{\mathbf{E}}_2 \), was defined as the difference between the second target position and the end position of the second gaze saccade (figure 2A). To obtain the localization error in the direction of the first gaze-saccade vector, we computed

\[
\dot{E}_{2//G} = \dot{E}_2 \cdot \mathbf{G}_1
\]

(6)
with \( \hat{G}_1 \) the unit vector along the first gaze shift, and \( \mathbf{r} \) denoting the inner product. We also computed the component of the localization error vector along the first eye-in-head saccade vector, \( \mathbf{s}_1 \). In that case:

\[
E_{2,\perp,\mathbf{s}} = \mathbf{r}_2 \cdot \mathbf{r}_1 \tag{7}
\]

Because the gaze vector and the eye-in-head saccade may differ substantially (in size and direction), the errors predicted by the visuomotor updating models may differ too (figure 2B).

---- figure 2 about here ----

Note that the localization error of Eqns. 3 and 4 may contain two contributions: (i) an error due to a systematic (preprogrammed) undershoot in the direction of the motor error vector for the second gaze shift \( \mathbf{M}_{G,2} = \mathbf{r}_2 - \mathbf{G}_1 \), which is unrelated to the timing of the second target, but could be a fixed proportion of the motor error amplitude, and (ii) the putative perisaccadic localization error in the direction of the first gaze- or eye saccade, which is presumably due to an error in the visual-motor remapping process (Eqn. 2). The latter varies systematically with the target delay, and (according to the visuomotor updating models) also with the kinematics of the primary gaze shift.

Because the target configurations in our experiments were such that the amplitude of the first gaze shift and the size of the motor error vector for the second target could be correlated, we incorporated both potential factors in our multiple regression analysis (see below, Eqn. 9, and Van Wetter and Van Opstal, 2008).

**Running averages.** To visualize the average trend of the errors as function of the target onset delay, a running average was computed by convolving the errors, ranked according to delay \( t_0 \), with a Gaussian filter (standard deviation 5 data points; total window width 20 points).

**Residual errors.** Error data obtained from the double-step series were pooled to determine a grand running average, \( \bar{E}_{2,\perp}(t_0) \), as function of the flash delay, \( t_0 \). To obtain the so-called *residual errors*, we removed the mean systematic trend in the data (see Results, e.g. figure 9B) by subtracting this grand running average from the measured errors (separately for first gaze- and eye-in-head saccades):

\[
E_{2,\text{res}}(t_0) = E_{2,\perp}(t_0) - \bar{E}_{2,\perp}(t_0) \tag{8}
\]
Perisaccadic Gaze Errors

According to the visual-motor feedback models, these residual errors are expected to contain systematic contributions that are due to the trial-to-trial variability in the first-saccade properties (in gaze or eye-saccade amplitude, and in mean gaze- or eye velocity). In our previous study we showed that the influence of saccade amplitude and velocity is highly dynamic, as it varied strongly with the flash delay. Thus, to quantify these potentially dynamic contributions, we performed a multiple linear regression analysis on the residual errors according to:

\[ E_{2,\text{res}}(t_0) = a(t_0) \cdot \hat{G}_1 + b(t_0) \cdot \hat{V}_{G1} + c(t_0) \cdot \hat{M}_{G2} \quad (9) \]

in which \( \hat{X} = (X - \mu_X) / \sigma_X \) is the normalized (dimensionless) variable (z-score), and parameters \([a(t_0), b(t_0), c(t_0)]\) are the dynamic (dimensionless) partial correlation coefficients obtained at delay \( t_0 \).

Illustration of the analysis procedure. Figure 3A-C shows how the analysis of Eqns. 6-9 is applied on model saccades (see Van Wetter and Van Opstal, 2008, and Supplemental Material for details). In this example we simulated a large set of gaze saccades that were subjected to the visual persistence mechanism of Pola (2004, 2007; Eqns. 3 and 13). In this simulation, horizontal gaze shifts with amplitudes between 40 and 70 deg were generated by a simplified version of Robinson's feedback model, in which the asymptote of the nonlinear burst generator was varied to yield both fast (peak at 750 deg/s) and slow (peak at 350 deg/s) saccades (amplitudes and peak velocities were randomly selected). Target-flash locations were selected at random from [-14, 0, +14] deg, and presented at a random delay between -220 and +220 ms around the saccade onset. In these simulations, it was further assumed that the second gaze shift would always undershoot the target by 10\%, which imposed a systematic localization error, proportional to the motor error, across the entire delay interval. We applied Pola's (2004, 2007) visual persistence model (Eqn. 3) to predict the additional perisaccadic localization error as function of target delay. To that end, the visual probe (a 5 ms pulse) was delayed (by \( \tau_V \) ms, here 20 ms) and low-pass filtered (order \( n_V \), and time constant \( T_V \), here 15 ms; see Eqn. 10) to produce the retinal persistence signal, \( T_R(t) \). The internal representation of the gaze shift was identical to the actual gaze shift, but delayed by \( \tau_G \) ms (here 30 ms). In these example simulations, we used two different visual filters, to generate different patterns of predicted gaze-localization errors. For the red symbols
Perisaccadic Gaze Errors

(and red line, which represents the running average through the 500 data points) the filter was of order \( n_V = 4 \) (parameters similar as in Pola 2004; see legend figure 3A), whereas for the blue symbols, \( n_V = 2 \). Figure 3A shows the predicted error patterns for the two implementations. The point of this panel is that the predicted patterns strongly depend on the precise parameter values (e.g. the mean peak error dropped from 22 to 10 deg). We then determined the residual errors for these two data sets, by subtracting from each data point the running average at that delay (Eqn. 8). The result is shown in figure 3B. The two data sets now scatter around the zero line (both running averages are on the zero line), but an increase in error variability before and during the saccade can also be observed. Presumably, this is caused by the variability in the saccade parameters. To assess the influence of the gaze shift kinematics, we then subjected these data to the regression analysis of Eqn. 9. Figure 3B illustrates the numerical results for the red data set selected in three different time windows, centered around \( t_{on}=[-150, -40, +70] \) ms. Finally, figure 3C shows the behavior of the regression parameters for both data sets across the entire delay interval (the three moments of figure 3B are also indicated). The main point here is that, despite some quantitative differences between the two model implementations, the qualitative dynamic behaviors of the parameters are remarkably similar: for amplitude, the dependence is monophasic, while the velocity dependence follows a clear biphasic pattern. As a consistency check, the reconstructed influence of the motor error was negative, and nearly constant across the entire delay interval (due to the fixed 10% undershooting strategy). In Van Wetter and Van Opstal (2008) we demonstrated that these curves are a hallmark for all models that assume an inaccurate, sluggish perceived eye-movement signal (Eqns. 2-4, see also Eqns. 10-11), regardless the exact properties of the underlying saccades, and of the visuomotor feedback mechanisms.

Figure 3 about here

Since the eye- and gaze-saccade trajectories and kinematics can be substantially different in natural gaze shifts (e.g. figures 4 and 5), the regression analysis was performed separately for residual gaze errors measured as function of the kinematics of the first gaze shift (gaze amplitude, \( G_1 \), and gaze velocity, \( V_{G1} \)), and of the first eye-in-head saccade (eye amplitude, \( S_1 \), and eye velocity, \( V_{S1} \)), respectively.
Perisaccadic Gaze Errors

To obtain the dynamic regression parameters for the measured responses, we adopted the same procedure as illustrated in figure 3 (Van Wetter and Van Opstal, 2008). The regression was thus performed over consecutive 100 ms wide time bins, shifted in 10 ms steps along the [-250,+250] interval, with centers running from [-200, +200] ms (i.e. 41 regressions with 90 ms overlap). Regression was performed only when the bin contained at least 20 data points.

Predicted localization errors of gaze shifts and eye saccades.
Visuomotor updating models. The same data analysis as in figure 3 was run on perisaccadic gaze errors that were predicted by the different models (see Introduction). In our previous study we ran various versions of the visuomotor updating models on our data, and showed that the actual parameter values for the retinal stimulus filter, the eye-movement filter, or the combination of both, were not critical for the regression results. Indeed, a given error pattern could be obtained with all versions of these models, albeit each with its own parameter settings (Pola, 2004; Van Wetter and Van Opstal, 2008).

Although the predicted amplitude of the localization errors depends strongly on the model parameters (e.g. figure 3A and figure 10A, the results of the normalized multiple linear regression analysis on the residual errors (Eqn. 9) do not (figure 3C). Thus, the dynamic parameter behaviors were very similar for the different visuomotor models, as well as for considerable variations in the parameters of each of these models (see Van Wetter and Van Opstal, 2008, their figure 5, and also figures 3 and 9 in this study).

To predict the gaze errors, we here report on data from the oculomotor feedback model of Dassonville et al. (1992), rather than from the other visuomotor models. Computations with this model are more straightforward, because the only signal needed to be filtered is the measured gaze shift or eye movement (see below).

To that end, we filtered each measured gaze- and eye-in-head movement trajectory toward the first target, \( G_1(t) \) and \( S_1(t) \), respectively, with a LP filter. The default parameters of this filter were taken from our earlier eye movement experiments (Van Wetter and Van Opstal, 2008). The impulse response of this filter is given by:

\[
h_s(\tau) = \frac{\tau^{n_s-1}}{(n_s-1)!} \cdot e^{-\tau/T_s} \tag{10}
\]

with \( T_s=20 \) ms, the filter’s time constant, and \( n_s=5 \), the order of the filter. The perceived gaze-displacement, or eye-movement trajectory is thus given by the convolution:
Perisaccadic Gaze Errors

\[ G_i^p(t) = \int_{0}^{t} G_i(t + T_{\text{lead}} - \tau) \cdot h_i(\tau) d\tau \quad (11) \]

The internal movement signal had a default lead of \( T_{\text{lead}} = 150 \text{ ms} \). The expected localization error for each trial is then determined by the difference between the internally perceived (Eqn. 2) and the actual location (Eqn. 1) of the target in oculocentric coordinates:

\[ E_{2,i} = T_{E}^p - T_{E} \quad (12) \]

In the gaze-motor feedback model, the retinal target location, \( T_{Ri} \), in Eqn. (5) is perceived correctly. Therefore, the predicted perisaccadic error is given by the difference between perceived and actual gaze- or eye-displacement signals at the time of the flash (figures 1B, 2B):

\[ E_{2,i,G}^{\text{pred}}(t_0) = G_1^p(t_0) - G_1(t_0) \]
\[ E_{2,i,S}^{\text{pred}}(t_0) = S_1^p(t_0) - S_1(t_0) \quad (13) \]

The resulting pattern of simulated errors (applied to measured gaze- and eye-in-head saccades) was subjected to the same regression analysis as the measured errors (Eqns. 8 and 9; figures 9 – 11).

Visual shift model. We also predicted the errors for the visual shift model (Van Wetter and Van Opstal, 2008). According to that idea, the errors arise as a result of a transient perceived shift, \( \oplus \), of the location of the visual target, which is in the direction of the saccade. It depends on the delay, \( t_0 \), of the target with respect to the gaze-shift (or eye-saccade) onset, and slightly on the gaze- or eye-saccade amplitude. We described this dependence by the following heuristic equation:

\[ \beta(t_0, G_i) = E_{\text{max}} \cdot (1 - \exp(-\alpha \cdot G_i)) \cdot \exp(-\gamma \cdot t_0^2) \quad (14) \]

We took \( E_{\text{max}} = 10 \text{ deg}, \langle =0.2 \text{ deg}^{-1}, \) and \( \oplus =4.1e-4 \text{ ms}^{-2} \) (i.e. a temporal width of 35 ms), to get a reasonable approximation of the eye-movement data of Van Wetter and Van Opstal (2008; figure 1B).

Statistics. Large gaze shifts toward dim and briefly illuminated targets are endowed with considerable inherent variability in their end points, even in the case of single visual targets (see e.g. figures 4-6). Thus, to assess whether the observed error patterns around the gaze-shift onset were due to a real effect of perisaccadic processing, we performed the following statistical analyses on the error data.
Perisaccadic Gaze Errors

First, we estimated the regular distribution of gaze endpoint errors by computing their mean, $\mu_E$, and standard deviation, $\sigma_E$, outside the perisaccadic delay interval, which was set at $t_0 \in [-100, +60]$ ms around gaze-shift onset. We then generated 100 sets of random data points from a Gaussian distribution, each with the same mean and standard deviation as the data. Each set of random errors, $E_{\text{RND}}$, had the same number of points as the original data set, and were assigned the same delays. Finally, two-dimensional Kolmogorov-Smirnov (2D-KS) statistics were computed between the actual errors and each of the random data sets for all data points belonging to the perisaccadic interval. The 2D KS test determines whether or not the random data set ($t_0$, $E_{\text{RND}}$) and the original set of measured errors, ($t_0$, $E_{\text{2,1}}$), are drawn from different distributions. The procedure thus yielded 100 values for the $d$-statistic, which is a distance measure for the two distributions, and 100 $p$-values, out of which average values were determined. When the average $p<0.01$ the two data sets were assumed to be drawn from different distributions (Press et al., 1992). As a consistency check, we also determined the 2D-KS statistics for the data outside the perisaccadic interval, for which the random data and the measured errors should be indistinguishable.

The KS test was also performed on the running averages through the data sets. In that case, the data could be ranked as function of the target onset delay, out of which cumulative distributions were determined. The one-dimensional (1D) KS test then measures the distance between the two cumulative distributions and its associated $p$-value.

As a third method, we determined the dynamics of the $t_u$-statistic (Student t-test on the means of two data sets, for which the variance need not be the same; Press et al., 1992) for the randomly generated noise and the measured error data. To that end, the data sets were binned in 50 ms-wide windows with 40 ms overlap (i.e. the window was shifted in 10 ms steps, from $t_0=-220$ to $+220$ ms). For each time bin the significance of a difference in the means was determined, thus yielding 45 $t_u$- and $p$-values as function of the target onset delay, $t_u(t_0)$ and $p(t_0)$, respectively (see Figure 7B,C, for results).
RESULTS

A representative example of a combined eye-head motor response in a double-step trial from one of our subjects is shown in figure 4. Figure 4A presents the spatial trajectories of the gaze-in-space (red) and head-in-space (blue) movements toward both targets, as well as the first eye-in-head saccadic eye movement (black trace, plotted in head-centered coordinates; the onset position was roughly in the center of the head). Gaze shifts toward the first and second visual stimulus were goal-directed. The oblique dashed lines demarcate the error of the second gaze shift (E2//G = 6.7 deg), measured along the overall direction of the first gaze shift, which was -20 deg relative to the rightward horizontal direction. Figure 4B shows the temporal trajectories of the horizontal (solid) and vertical (dashed) movement components, as well as the stimulus events (thick black lines in top panel). Note that all movements were executed under open-loop conditions, as visual targets were extinguished before the onset of the first gaze shift.

Two points are worth mentioning: first, the eye-in-head saccade (bottom panel) terminated well before the end of the first gaze shift. As a consequence, during the second portion of the gaze shift the eye-in-space was carried toward its goal by the head movement, which can also be observed in the spatial trajectories. Second, both gaze shifts terminated well before the head movements (center panel). Thus, after gaze-shift offset, the VOR was fully operational.

---- figure 4 about here ----

In our analysis, we determined separate model predictions for the gaze localization errors as function of the first gaze-in-space movement, G1(t), or of the first eye-in-head saccade, S1(t) (see Introduction and Methods, figure 2). To verify that these two movements, and hence the model predictions, were indeed different, figure 5 shows their amplitudes plotted against each other. Figure 5A shows data from subject jo. Clearly, the amplitudes are very different, and not positively correlated (we even obtained a negative correlation of r = -0.20). Typically, the eye-movement amplitudes were much smaller than the total gaze-shift amplitudes. Four subjects displayed qualitatively similar behavior, and were termed ‘head-movers’, as their gaze shifts were associated with relatively large head movements (cf. figure 4). Two of our subjects (pb and rw), however, followed a different movement strategy, in that their eye-saccades were positively correlated with the gaze saccades. Figure 5B shows the data for subject pb (r = 0.77). As the head movements during the gaze shift of these two subjects were
Perisaccadic Gaze Errors

typically smaller than for the head-movers (because they often started later, or were slower), they were termed 'eye-movers' in this study.

---- figure 5 about here ----

Because the visual targets were dim (0.8 cd/m²), very brief, and presented at large retinal eccentricities, it is important to verify that subjects were indeed able to do the double-step task under these conditions. To that end, figure 6 shows the first- and second gaze responses of subject tg. In figure 6A it can be seen that the endpoints of the first gaze shifts landed near the (extinguished) target locations, although substantial errors also occurred. Part of these errors could be explained by target averaging, as the largest localization errors of the first target were found when the delay, t₀, of the second target was less than -100 ms, i.e. when both targets were presented well in advance of the first gaze onset and therefore hardly influenced by perisaccadic mechanisms. Indeed, in line with this observation the target delay and amplitude of the first gaze shift error vector were negatively correlated for all subjects (Table 1). Figure 6B shows that the horizontal component of the second gaze shift correlated well with the horizontal motor error (r=0.85). Yet, a systematic overshoot may be observed, which may partially be attributed to the delay-dependent gaze mislocalizations (see below).

---- figure 6 and Table 1 about here ----

In order to perform meaningful regressions on the influence of the amplitude and kinematics of the first gaze shift and the first eye-in-head saccade on the delay-dependent gaze localization errors, the respective variables should be widely distributed. Figure 7 shows the typical distributions that were obtained in these experiments (subject bd). The localization errors in the direction of the first gaze shift, E₂∥G, have a positive mean (top panel), which is to be expected if a systematic effect of target delay is present at all. The independent variables are all broadly distributed around a single peak that is close to the mean.

---- figure 7 about here ----

Perisaccadic mislocalization in head-free gaze shifts? To assess whether also head-free gaze shifts to visual flashes were endowed with perisaccadic localization errors, we performed a statistical analysis on the error data according to the procedures described in Methods. The results of these analyses are shown in Figure 8 and in Table 2. Figure 8A shows the measured errors in the direction of the first gaze shift of subject tg (red
Perisaccadic Gaze Errors

symbols), together with the running average through the data (thick red line). The blue dots correspond to random noise, that was generated with the same mean and standard deviation as the measured errors outside the [-100,+60] ms delay interval. The blue line shows that the running average through the random noise data meanders around zero deg. We then computed the 2D and 1D KS statistics for these two independent data sets for the delay intervals of interest. The numerical results of this analysis are provided in Table 2. In five/six subjects the differences between the distributions in the perisaccadic interval [-100,+60] ms were highly significant. Only the data of subject il failed to reach significance. As a consistency check, the data distributions outside the perisaccadic interval were indeed statistically indistinguishable for all subjects. The 1D KS statistic that was performed on the running averages was significant for all subjects.

We also ran a third analysis to assess the temporal evolution of the difference between the two data sets. To that end, we performed windowed \( t_u \)-tests, in which a 50 ms window was shifted across the entire delay range in 10 ms steps. On the data sets within each window we performed a \( t_u \)-test (see Methods). Figure 8B shows the result for the data of subject tg. Blue symbols correspond to the significant \( t_u \)-statistics, which shows a large peak around the gaze-shift onset. The grey symbols are \( t_u \)-values that were not significant (\( p>0.05 \)). The red symbols indicate the significance (\( p \)-value) of each \( t_u \)-statistic. Clearly, all values were highly significant within the perisaccadic interval. Figure 8C shows the significant \( t_u \)-values for all six subjects. Despite idiosyncratic differences, all subjects yielded qualitatively similar results, in that a significant difference was obtained around and during the gaze shift onset. From these results we conclude that, like head-fixed saccadic eye movements, also head-free gaze shifts suffer from perisaccadic localization errors. In what follows, we will analyze the strength of this effect, by comparing the measured results to the predictions yielded by the different visuomotor updating models.

--- figure 8 and Table II about here ---

Figure 9A shows the localization errors of the second gaze shifts of subject jo in the same format as figure 8A. Despite the considerable scatter, also for this subject a clear systematic trend can be observed in these errors. For delays around the gaze-shift onset, between about -140 and +80 ms, errors are positive on average. The peak localization error occurs around the gaze-saccade onset, reaching a mean amplitude of
about 10 deg. In figure 9B we show the running averages obtained for all six subjects (identified by different colors), together with the running average determined for the pooled data of all subjects (black line; N=3187 responses). Despite idiosyncratic differences, also apparent from the results of the statistical analysis in figure 8C, the overall trend in the data is consistent, and appears to be qualitatively similar to the results obtained from head-fixed experiments. To illustrate this latter point, figure 9C includes the data from the four subjects who participated in our recent oculomotor study (adapted from Van Wetter and Van Opstal, 2008). Here, the eye-movement data have been pooled across all saccade amplitudes (ranging from 5-35 deg; individual subjects indicated by different colors. Black line: pooled for all four subjects, N=3750 saccades).

To assess whether the measured error patterns can be understood from the assumption that efferent feedback of either the first gaze shift, or the first eye-in-head saccade, is inaccurate, we used the actually measured gaze- and eye saccades to predict the localization errors (see Methods, and figures 1 and 2). Figure 10A shows the results for the data from subject bd in the same format as figures 8A and 9A, together with the running average through the data (solid red line). The size of the predicted effects depend strongly on the particular model parameters. To illustrate this point, we ran the oculomotor feedback model with twelve different parameter sets. The results of these twelve simulations are indicated by the running averages, as black and grey solid lines. Results obtained with the visual persistence model (Eqn. 3) and the visual compression model (Eqn. 4) were similar (not shown here, but see Supplemental Material). Obviously, many parameter sets do not yield an adequate description of the actual data. This observation also holds for the predicted curve obtained with the default set of parameters that were taken from other studies (Pola, 2004; Dassonville et al., 1992, 1995; indicated by DEF). Note that when $T_{lead}$ is reduced from -150 to -120 and -90 ms, respectively, the amplitude of the predicted errors decreases substantially (light-gray and dark-gray curves, respectively). On the other hand, when either the order of the low-pass filter, or the filter time constant is decreased, the predicted errors increase. There will exist a particular set of parameters, to be found for example by brute force, or by a least-squares fit procedure, for which the measured localization errors could be described best.
However, the critical prediction of the different visuomotor schemes is that the variability in the errors should depend in a systematic way on the gaze-(or eye-)saccade properties (Van Wetter and Van Opstal, 2008). To test this more sensitive prediction, the regression analysis of Eqn. 9 should be performed on the data after removing the primary effect of the stimulus delay, on both the original data, and on the predicted data sets. To that end, we applied Eqn. 8 to determine the residual errors, by subtracting the running averages from the measured data, and from each of the twelve different predicted data sets (figure 10B). We then performed the dynamic multiple linear regression analysis of Eqn. 9 on the residual errors, as described in Methods. In brief, the data were binned in 100 ms time-windows that were shifted between \( t_0 = [-200, +200] \) ms in 10 ms steps. The regression thus yields the dynamic influence of the primary gaze-saccade amplitude, \( a(t_0) \), its mean gaze velocity, \( b(t_0) \), and the second gaze-shift motor error, \( c(t_0) \), as function of the flash delay, \( t_0 \).

The result of this regression on the data of subject bd is shown in figure 10C. Two points are worth noticing. First, although the regression curves differed in a quantitative sense for each particular parameter set, the overall patterns in the regression results were remarkably similar and appeared to be quite robust against large variations in the model parameters. This finding held for all three versions of the visuomotor updating schemes (not shown here, but see Van Wetter and Van Opstal, 2008, for specific examples). Second, the regression parameters found for the measured data (black curves) did not follow these model predictions in any way. The 1d ks-test performed between each of the three parameter curves from the experimental data, and each of the corresponding twelve curves of the model simulations always indicated that these parameter curves were highly dissimilar (\( p<1e^{-6} \)). In conclusion, the data do not follow the predictions of the visuomotor updating models in any way.

--- figure 10 about here ---

Figure 11 shows the results for all six subjects. The left-hand panels show the dynamic regression parameters for the measured residual errors (to be compared with the black curves in figure 10C), while the right-hand panels show the results for the predicted errors (based on the oculomotor feedback model with default parameters; compare with the thick colored curves in figure 10C). On the basis of the results in figure 5 (and Table 1) we grouped our subjects in head movers (\( n=4 \), figure 11A,B) and eye movers (\( n=2 \);
Perisaccadic Gaze Errors

Figure 11C,D), respectively. For the head movers we show the results of the analysis for the first gaze-saccades (figure 11A,B), while for the eye movers we provide the results for the eye saccades (figure 11C,D). Thin lines provide the regression results (blue: \(a(t_0)\), amplitude, red: \(b(t_0)\), mean velocity, green: \(c(t_0)\), motor error of second gaze shift) as function of flash delay, \(t_0\), for each individual subject, while the fat solid lines give the results, averaged across subjects. The pattern of results for the eye-saccades (head movers) and gaze saccades (eye movers) were very similar (see Supplemental Material).

The predicted data show a clear and consistent modulation of the regression parameters as function of stimulus delay for all subjects. The measured residual errors, however, did not follow any of these predicted patterns in our subjects, irrespective of their movement strategies (figure 11A,C). Thus, like for head-fixed saccades, the systematic localization errors around a head-free gaze-shift cannot be explained by an erroneous, low-pass filtered version of the actual eye- and gaze saccades.

--- figure 11 about here ---

Figure 12 compares the measured error data with the predictions from the visual-shift model (Eqn. 13). Figure 12A shows the raw error data for subject bd (gray circles), together with the running average through the data points (red line), and the model prediction (black line). Although we have not attempted to optimize the parameters of this simple model with a least-squares fit, it did a decent job in describing the average trend through the data, despite the large variability in the underlying gaze-shift amplitudes and kinematics (e.g. figure 6). Figure 12B shows the running averages for the six subjects, together with the grand running average (red), and the model prediction for the overall averages. In figure 12C we show the results of applying this model to the dynamic regression analysis on the residual errors (Eqns. 8 and 9). The model predicts nearly flat curves across the relevant delay interval, which is also observed in the actual data (compare with figure 10C, black curves).

--- figure 12 about here ---
DISCUSSION

Summary. This paper studied the pattern of perisaccadic mislocalizations of visual targets flashed around large head-free gaze shifts. We showed that, like head-fixed saccades, head-free gaze shifts consistently mislocalize visual targets in the direction of the primary gaze shift, when the brief flash is presented near gaze-shift onset (figure 8). According to visuomotor updating models (Dassonville et al., 1992, 1995; Pola, 2004, 2007; Ross et al., 1997), the errors should vary with the amplitude and kinematics of the primary gaze- (or eye-)saccade as function of the second target delay (Van Wetter and Van Opstal, 2008; figures 1A, 10C, 11B,D). Instead, our data show that the gaze-shift properties have a negligible influence on perisaccadic gaze-localization errors (figures 10C, 11A,C). According to the alternative visual-shift hypothesis, gaze errors should be similar as observed for much smaller head-fixed saccades (figure 1B), and not depend on the movement kinematics. Our results support this simple idea, which yields a better description for the observed error patterns (figure 12). We conclude that our data provide further support for the hypothesis that perisaccadic localization errors under open-loop orienting conditions have a visual-spatial, rather than a dynamic motor origin.

Related studies. Our experiments set out to test the hypothesis that a sluggish representation of extraretinal gaze-position would underlie perisaccadic mislocalization. This idea was forwarded by Dassonville et al. (1992, 1995) and Schlag and Schlag-Rey (2002) for head-fixed saccadic eye movements, and provided an adequate model to predict the error data. Recently, Pola (2004) argued that visual mechanisms could explain the error patterns equally well. In his model, the brief target flash is not transmitted as such through the visual system, but produces prolonged activity in the visual pathways. Thus, even when the oculomotor feedback itself would be accurate, the internal estimate of eye position at the time of the flash becomes inaccurate, as it would be determined by a temporal weighted ('blurred') average. This mechanism causes the perceived estimate of eye position to be similar as the sluggish, low-pass filtered signal of Dassonville’s model (Pola, 2004; Dassonville et al., 1992, 1995; Honda, 1990, 1991; Eqn. 8). As a consequence, both models predict equivalent localization errors.

In the model proposed by Ross et al. (1997), localization errors are due to errors in both the visual and oculomotor representations. In their model the saccade distorts (compresses) visual space by a compression factor that depends on the target's retinal eccentricity and on the difference between internal and actual eye positions. This leads
Perisaccadic Gaze Errors

to an erroneous estimate of the actual retinal error, $T_E$, provided the internal eye position estimate is inaccurate too. If the extraretinal signal would be veridical, visual compression vanishes. Thus, to explain the observed localization errors, the extraretinal signal was modeled as a slow dynamic representation of final and initial eye-position estimates (see Ross et al., 1997, for details).

We have demonstrated that all three proposals produce equivalent error patterns, regardless the details of the underlying mechanisms. Even the dynamics of the regression parameters (Eqn. 6, figures 10 and 11) were insensitive to the specific differences in model implementations (e.g. figures 3 and 10; Van Wetter and Van Opstal, 2008). Consequently, the predictions of models relying on inaccurate motor feedback are unequivocal: the variability in the perisaccadic localization errors should systematically vary as a function of target delay and, moreover, depend on the primary gaze-shift amplitude and kinematics.

The only study so far that acknowledged the influence of saccade kinematics on perisaccadic mislocalization is by Ostendorf et al. (2007). They demonstrated that intersubject variability in saccade kinematics correlated with the amount of visual compression. However, they reported no effect of the saccade amplitude on compression. Moreover, like in our previous eye-movement study (Van Wetter and Van Opstal, 2008), they did not find an effect of the first-saccade properties on the forward perisaccadic errors. Although these latter results corroborate our own findings, several points are worth noticing. First, the variability in the saccade amplitudes in their study was relatively small, as the first target was fixed at 10 deg eccentricity. Second, when performing an overall regression analysis on the influence of saccade amplitude and velocity (i.e. pooling data across the entire delay range, rather than performing a windowed analysis), the expected effect of amplitude and kinematics may in fact be quite small (Van Opstal and Van Wetter, 2008). Thus, given the substantial random noise in response error distributions, a small effect of amplitude or velocity may easily get unnoticed. Indeed, also in the present data set the correlation of this overall multiple regression model was low ($r \approx 0.3$; not shown), indicating that most of the variability in the data was due to random noise within the gaze control system. Third, the effects of saccade variability described in the present study concern the dynamic variability within individual subjects, rather than across subjects.

Perisaccadic mislocalization around head-free gaze shifts has not been studied in detail so far. Only two recent studies (Vliegen et al., 2004, 2005) have addressed this
Perisaccadic Gaze Errors

issue, albeit indirectly. In their double-step sound-localization study Vliegen et al. (2004) showed that the audio-motor system generated accurate gaze shifts toward brief noise bursts presented before and during a large intervening eye-head gaze shift. In that situation, the auditory system has to incorporate dynamically changing auditory localization cues (due to the ongoing head movement), as well as gaze- and head-movements following the presentation of the sound. The results indicated that localization of the noise burst in the dynamic double-step was indistinguishable from single-target sound localization without the intervening gaze shift. This suggested that the motor feedback signals, needed to update the coordinates of the auditory target into a body-centered reference frame, were accurate. These results are therefore in line with our hypothesis that systematic perisaccadic localization errors are due to a visual, rather than to a motor feedback mechanism.

Also the subsequent study of Vliegen et al. (2005) on localization of a visual target flash in double-step gaze-shifts indicated that the errors were, on average, much smaller than expected from sluggish motor feedback. In that study, however, the target flash was substantially longer (50 ms) than employed in the experiments of Dassonville and colleagues (2 ms). Although the sluggish motor-feedback hypothesis has no specific role for the sensory properties of the stimulus (neither its modality, nor its saliency), the alternative proposal of Pola (2004, see above), as well as our visual-shift model, could be accommodated to produce smaller localization errors when the visual target duration or intensity increases. We recently showed that, indeed, longer stimulus durations had a negative effect on perisaccadic localization errors (Van Wetter and Van Opstal, 2008).

Binda et al. (2007) recently provided further support for the visual origin of perisaccadic errors. They demonstrated that localization errors of a visual target diminished in the presence of an auditory stimulus, possibly because the dominance of vision over acoustic input was reversed in the perisaccadic interval. Indeed, such a strategy would be beneficial, because auditory stimuli are not systematically mislocalized around saccades (Vliegen et al., 2004; Binda et al., 2007).

Note that the visual stimuli in our experiments were presented under open-loop conditions, were very brief (15 ms), dim (0.8 cd/m²), small (0.2 deg), and presented at large retinal eccentricities (52 deg for the first target flash, and between 27–36 deg for the second flash). These factors all contribute to an increased (but not systematic) variability in the responses when compared with longer-duration and brighter stimuli (e.g. Vliegen et al., 2005). Nevertheless, subjects made goal-directed responses to both
targets (figure 5), and the systematic pattern of perisaccadic localization errors stood out in all subjects (figures 8 and 9). In addition, our study on head-fixed saccades yielded comparable error patterns for much smaller saccades (figure 9; Van Wetter and Van Opstal, 2008), and the errors were also comparable to those observed in other studies (Dassonville et al., 1992; 1995). By increasing the saliency of the targets one could, of course, reduce the random response noise (like in Vliegen et al., 2005). However, as argued above, such a manipulation would have had a detrimental effect on the size of the perisaccadic localization errors.

The only response parameter that contributed significantly to the observed errors in Van Wetter and Van Opstal (2008) was the motor error vector for the second saccade, $M_2$. Since head-fixed eye movements have a well-known tendency to undershoot visual targets by about 10%, this parameter yielded an expected negative partial correlation coefficient, which did not vary with the flash delay. In the present study, the contribution of motor error was substantially smaller than observed for head-fixed saccades (figures 10 and 11). Apparently, the tendency to undershoot visual targets is weaker when the head is free to move.

*Double-flash interaction?* Although two visual flashes in rapid succession served to elicit gaze shifts, our paradigm differs in several ways from the double-flash experiment of Sogo and Osaka (2002). In their study the flashes were both presented around the onset of the first saccade, which was elicited by a different, third, target. The target eccentricities used in their study were between 4-12 deg (as opposed to more than 30 deg in this study), the intervening saccade was 8 deg (here between 40-60 deg), and pointing was measured using a post-saccadic ruler, instead of gaze shifts. When the brief (2 ms) flashes were both presented around the saccade onset, they were both mislocalized, but their mislocalization was not simply understood from the effects to each target flash in isolation. Sogo and Osaka (2002) reported that the two targets appeared to interact, creating a different mislocalization pattern for the second target flash, and hence a perceived change in the allocentric relations between the flashes. The interaction was significant when the flashes occurred within 120 ms, and nearly disappeared when the inter-flash interval (IFI) exceeded 200 ms. This interaction could be understood from the visual persistence model of Pola (2007), whenever the two visual activities would overlap in time. Note, however, that also Pola’s visual persistence model creates a sluggish extraretinal signal through Eqn. 3, and therefore predicts a
similar strong dependence of the localization errors on the first saccade amplitude and kinematics as the other visuomotor updating models described in the Introduction (see figure 3).

In our experiments, the first target flash served to elicit the gaze shift, and therefore was presented well before the gaze shift onset (on average about 200 ms, which is well outside the perisaccadic interaction interval; see Table 1). Yet, the IFI’s in our experiments were roughly between 100 and 240 ms, which includes the interaction interval reported by Sogo and Osaka (2002). Note, however, that at the shortest IFI’s (around 100 ms) the perisaccadic localization errors of the second gaze shift were not systematic, as they fell at the edge of the perisaccadic error range (between -100 and +100 ms onset delays; Figs. 8-10). The peak localization errors occurred at, or slightly after, the gaze-shift onset, corresponding to typical IFI’s of 200 ms, or more. One of our subjects (PB) had shorter first-saccade response latencies, but the peak amplitude of his perisaccadic errors did not deviate significantly from the other subjects. Thus, in our experiments, the interactions due to IFI were expected to be small around the gaze-shift onset. We have assessed the potential role of the IFI by incorporating this parameter in our normalized multiple linear regression analysis by extending Eqn. 9 with \( d(t_0) \cdot \text{IFI} \) as an additional regressor. In five subjects, the dynamic contribution of IFI to the residual localization errors was insignificant across the entire delay interval of [-250, +250] ms. Only subject PB, yielded a small positive contribution for \( d(t_0) \) for long negative delays (where the IFI was shortest) that declined to zero near the gaze-shift onset (data shown in Supplemental Material). In line with this analysis, the first target in our experiments was localized consistently (apart from the typical undershoot, see figure 6).

Yet, we did observe a small effect on the first-saccade errors that depended on the IFI (see the consistent negative correlations in Table 1). Since this effect was maximal at the shortest IFI’s, for which the perisaccadic errors of the second gaze shifts were minimal (rather than increased), we suggest that it could be due to a different mechanism. When two visual targets are presented in close spatial and temporal proximity, the saccade is often directed toward the center of gravity of the two locations (e.g. Ottes et al., 1985). Thus, the longer the stimulus lead (negative delays), the shorter the IFI, and the more likely that the first saccade could be affected by such spatial averaging. As a result, the goal of the first target would be shifted in the direction of the second target flash, whereby the first-saccade error increases. It is possible that target averaging may also have been a factor in the Sogo and Osaka (2002) study, but in order
to assess such an effect also saccades toward the first target flash should have been measured.

**Statistical models.** Recently, Niemeier et al. (2003, 2007) proposed a different explanation for perisaccadic localization errors, which is based on statistical optimal inference. This concept holds that errors are an unavoidable consequence of the fact that the visuomotor system has to deal with dynamically changing uncertainties in both visual and (oculo-)motor processing. Especially around a saccade, these uncertainties (internal noise) might grow. Rather than assuming errors in the mapping process of Eqn. 1, the principle of optimal inference holds that the system optimizes its behavior against conflicting constraints and internal noise. Niemeier et al. (2003) showed that saccadic suppression of displacement (SSD) could be well explained by this principle.

Interestingly, the threshold for SSD increases with the saccade amplitude, an effect that is also successfully predicted by the optimal inference model (Niemeier et al., 2003). It may thus be expected that optimal inference would predict a similar amplitude and velocity dependence of perisaccadic errors in the double-step task as the other visuomotor models described by Eqns. 2-4 (see figures 3C, 10C and 11B,D). Indeed, the endpoint variability of saccades is known to increase nearly linearly with saccade amplitude, an effect that has been related to a decreasing retinal resolution at large visual eccentricities (Van Opstal and Van Gisbergen, 1989). However, our data on head-free gaze shifts (figure 10A,C), and also on head-fixed saccades (Van Wetter and Van Opstal, 2008) indicate that, beyond about 10-15 deg, the gaze shift amplitude and kinematics do not influence the size of the perisaccadic errors. Thus, to explain our results in terms of optimal inference, other statistical uncertainties should somehow compensate this amplitude-dependent effect. A further complication for applying the optimal inference model is the complex and variable coordination of the eye- and head-motor systems in head-free gaze shifts. Further study of the optimal inference hypothesis is therefore needed to analyze its consequences and predictions also for these more complex and dynamic conditions.

Interestingly, Binda et al. (2007) have provided evidence that statistical optimization principles could underlie perisaccadic visual compression, which is observed in perceptual localization experiments in the light (Ross et al., 1997). When the visual target is combined with an auditory stimulus, the effect of visual compression nearly disappears. Binda et al. (2007) explained this by a Bayesian model of auditory-visual
Perisaccadic Gaze Errors

integration that weights the different and continuously varying reliabilities of visual and auditory inputs. According to their hypothesis, the auditory input increases its weight around saccades, as auditory stimuli are not influenced by perisaccadic errors (Vliegen et al., 2004; Binda et al., 2007).

Other optimization principles to understand oculomotor behavior have been proposed too. For example, the tendency for saccades to undershoot the target (figure 6A) could be understood from optimizing speed-accuracy trade-off, in combination with the kinematic constraint that saccade durations increase with saccade amplitude, and that the endpoint scatter increases with amplitude (Harris, 1995). It has recently been argued that the nonlinear main sequence of saccades could be understood from principles that aim to minimize movement duration, given the internal noise in the system (Harris and Wolpert, 2006; Tanaka et al., 2006). We have recently provided evidence that the midbrain superior colliculus could thus be regarded as an optimal saccade controller by specifying a vectorial gaze-velocity command that obeys the main sequence (Van Opstal and Goossens, 2008).

Model specifics. In the present study, most simulations with the visuomotor models were restricted to the sluggish oculomotor feedback proposal of Dassonville et al. (1992, 1995; Eqns. 10-12) using default parameters (i.e. a lead time of 150 ms, and a fifth-order low-pass filter with a time constant of 20 ms; see also Pola, 2004). This model described the oculomotor error data for mid-range saccadic eye movements (10-15 deg amplitude) quite well (Van Wetter and Van Opstal, 2008). A series of simulations with different implementations of the visuomotor models showed that varying the model parameters strongly affects the size of the predicted errors (see figures 3A and 10A, cf. with figure 3 of Van Wetter and Van Opstal, 2008), but that it has only a small effect on the results of dynamic regression on the error residues (Eqns. 8-9; figures 3C and 9B). Therefore, although the predicted errors of the default implementation of the visuomotor feedback model deviate greatly from the actually measured data (figure 10A, curve DEF), the results shown in figures 3C, 10C and 11B,D should be considered canonical for the predictions of all visuomotor models that employ sluggish gaze-motor feedback.

The predicted patterns in the regression parameters of the visuomotor feedback schemes for head-free gaze shifts (figures 10 and 11) differ from those reported for head-fixed saccades (Van Wetter and Van Opstal, 2008). In that study, the expected influence of the first-saccade amplitude on the residual errors followed a single-peaked
positive-only relation with a lead starting well before saccade onset, while mean eye velocity displayed biphasic (positive/negative) behavior. In contrast, for head-free gaze shifts the expected dynamics of the regression parameters depended on the adopted movement synergies. Head movers displayed a single-peaked relation for both gaze- and eye-velocity, while the influence of gaze- and eye-saccade amplitude started well after gaze-shift onset (figure 11B). The results for the eye-movers were qualitatively more similar to the head-fixed predictions, albeit that also in this case the influence of eye-saccade amplitude was delayed (figure 11D).

Our conclusion that our heuristic visual-shift hypothesis provides a better description of the data than the different visuomotor updating models is not based on its better performance in describing the actual errors (figure 12A,B), but on the crucial difference between the more sensitive dynamic analyses of figures 3C, 10C, 11B,D (sluggish motor feedback) and figure 12C (visual shift). The visual shift hypothesis yields a dynamic behavior of the regression parameters that is qualitatively comparable to the actual data (figure 11A,C).

**Gaze vs. eye-in-head.** Because the different visuomotor feedback models were developed to explain the data obtained under head-fixed conditions, there are different ways to extend them to head-free gaze shifts. If errors are due to the internal eye-movement signal only (i.e. the head-movement estimate is, on average, correct), the oculomotor feedback signal is supposed to originate from the brainstem (e.g. from the saccadic burst generator; Van Gisbergen et al., 1981; Scudder, 1988; Scudder et al., 2002). In subjects denoted as ‘head-movers’, the eye-in-head saccade was typically much smaller than the overall gaze-shift amplitude (figure 5A), because the head covered a substantial part of the gaze trajectory. As a result, the size of the predicted errors for the eye-in-head saccades was of the same order of magnitude than the actually measured errors (data not shown). However, the variation in neither the eye-saccade amplitude, nor the kinematics, was related to the dynamic error patterns (figure 11).

A more parsimonious extension of the visuomotor updating models would be to attribute the observed localization errors to a **gaze-feedback** signal. A serious candidate for providing efferent feedback has been identified as the midbrain superior colliculus (Sommer and Wurtz, 2002, 2006). The SC has a well-established role in the generation of saccadic eye-head gaze shifts (e.g. Munoz et al., 1991, in cat; Freedman et al., 1996,
in monkey), indicating that the signal emitted by the SC is a gaze-displacement command, rather than an oculomotor command.

Recently, Goossens and Van Opstal (2006) proposed that the spatial-temporal distribution of SC activity faithfully encodes the planned trajectory and kinematics of the saccade. Their recordings suggested that the collicular signal contains an accurate dynamic representation of saccades with a lead time of about 20 ms (Van Opstal and Goossens, 2008). Although their analysis has so far been restricted to saccadic eye movements only, the approach predicts that SC cells encode the planned gaze trajectory when the head is free to move. If true, the SC signal would represent a veridical gaze-motor command that could be combined at upstream levels with visual inputs to transform the coordinates of the target into a stable and accurate oculocentric reference frame. Note, however, that the signal represented by the SC can, under certain conditions, be dissociated from the actual eye movement. For example, Frens and Van Opstal (1997) showed that SC responses are unaffected by short-term adaptation of the saccade vector, indicating that the movement fields of SC cells change during adaptation. Hence, the signal responsible for adaptation is thought to affect saccade motor signals downstream from the SC. Interestingly, Awater et al. (2005) demonstrated that the visual compression effect (Ross et al., 1997) incorporates the actual, adapted, saccade vector, rather than the intended, unadapted, saccade vector. If one assumes that this result would also hold for open-loop orienting in darkness, it would further support the notion that spatial updating relies on accurate motor feedback, rather than on some derived, sluggish or even erroneous version of the oculomotor command. Since the SC does not provide the actual motor command under all conditions, the feedback signal for spatial updating could require integration from several sources that not only include the SC, but also motor signals that originate downstream from the site of adaptation. The distributed nature of the feedback could explain why disruption of the SC corollary feedback path induces only a partial deficit of spatial updating in the double-step paradigm (Sommer and Wurtz, 2002).

**The visual shift hypothesis.** Our visual-shift explanation of the data assumes that the remapping process of Eqns. 1 and 5 uses a kinematically correct representation of the eye- and gaze-displacement vectors. Thus, to cause the observed perisaccadic errors, the only remaining possibility is a dynamic shift of the perceived retinal location around the saccade with a time course that is dictated by the measurements. In that sense, the
Perisaccadic Gaze Errors

model seems to be a post-hoc heuristic explanation of the data, which, however, calls for new and different mechanisms than low-pass filtering of the gaze-displacement command. Note that although the hypothesis entails a spatial visual origin of the effect, the shift itself is contingent upon the planning process of saccades, and hence, some form of a dynamically varying signal (in combination with information of the upcoming saccade) into the visual system is needed to cause this shift. We propose that this saccade-related signal differs from the actual gaze-displacement feedback signal. The latter is supposed to be kinematically accurate, whereas the former does neither reflect the saccade kinematics, nor the saccade amplitude, as it saturates at about 10 deg. For example, it is conceivable that there might be an extraretinal process with an anticipatory component representing the size and direction of the upcoming response, but that has little or nothing to do with the actual kinematics of the saccade. It is also conceivable that the dynamics of the retinal shift could reflect the type of perisaccadic processing that would emerge from optimal inference (e.g. Niemeier et al., 2003, 2007), or Bayesian reasoning. Thus, the shift may be related to the amount of visual positional uncertainty in the presaccadic epoch. The observation that errors decrease with increasing probe duration (Van Wetter and Van Opstal, 2008) or stimulus luminance (Georg et al., 2008), might follow from such a statistical framework, since the visual signal becomes more reliable when its saliency increases. In addition, the absence of mislocalization errors to auditory stimuli (Vliegen et al., 2004; Binda et al., 2007) strengthen the idea that the gaze-motor signals are, on average, accurate, but that the perisaccadic errors are caused by visual processes.

Neural correlates. Since the visual-shift hypotheses outperforms the different visuomotor feedback schemes, the question arises at which stage these errors might be introduced. It is well established that motor signals influence visual receptive fields within several cortical and subcortical visuomotor areas. For example, visual receptive fields in posterior parietal cortex have been described as multiplicative gain fields, by which cells modulate their visual-spatial tuning with static changes in eye position (Andersen et al., 1985). Similar eye-position modulations have been reported for saccade-related cells in the midbrain superior colliculus (Van Opstal et al., 1995), in primary visual cortex (Weyand and Malpeli, 1993), and on the tuning curves of auditory cells in the monkey inferior colliculus (Groh et a., 2001; Zwiers et al., 2004). Such gain fields could mediate the transformation of retinal coordinates into a head-centered reference frame (Zipser
Perisaccadic Gaze Errors

and Andersen, 1988; Van Opstal and Hepp, 1995), or vice versa, from a head-centered acoustic reference frame into an oculocentric reference frame (Zwiers et al., 2004).

Later experiments have shown that parietal cells are also modulated by changes in head orientation, so that these cells could represent the visual target location in body-centered (Brotchie et al., 1995, in monkey, 2003, in human), or even in absolute world coordinates (Snyder et al., 1998).

It is, however, unclear whether a gain field mechanism could underlie perisaccadic mislocalization, visual compression, or both, because the responses of these cells have so far been studied under static changes in eye and head position only.

An alternative mechanism that has been proposed to underlie visuomotor spatial updating is predictive remapping in which visual receptive fields shift prior to saccade initiation in a direction that compensates for the retinal displacement of the target by the saccade. Predictive remapping occurs within several cortical and subcortical saccade-related regions, like posterior parietal cortex (Duhamel et al., 1992), frontal eye fields (Umeno et al., 1997), and SC (Walker et al., 1995). Predictive shifts in receptive fields have also been observed in regions involved in visual object processing and visual attention, like area V4 (Tolias et al., 2001). In predictive remapping, receptive fields shift in a direction opposing the saccade (Eqn. 1). Thus, perisaccadic errors in the direction of the gaze shift could emerge when feedback about the upcoming gaze displacement would fall short of the actual gaze shift, or when the retinal representation of the target would transiently shift. Recent evidence suggests that the dynamics of visual-receptive field shifts might be linked to perisaccadic localization errors, as parietal neurons respond to stimuli presented in both the original and the future receptive field during the perisaccadic interval, thereby effectively increasing the receptive field size in the saccade direction (Kusunoki and Goldberg, 2002). Whether this effect can be quantitatively connected to the measured mislocalization patterns, is still unclear.

It would therefore be interesting to test whether this expansion disappears for target flashes of longer durations, or may even reverse sign, as observed in monkeys for 100 ms flashes (Jeffries et al., 2007), and whether the receptive field shifts are nearly invariant to large variations in saccade amplitudes and kinematics.

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Perisaccadic Gaze Errors


Perisaccadic Gaze Errors

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Properties of primary gaze shifts. Onset latencies of first gaze shifts fall in the normal range of about 200 ms. For most subjects (‘head movers’, n=4) the eye-in-head saccade was poorly related, or even negatively correlated, with the gaze-shift amplitude. For two subjects, however, a significant positive correlation was obtained (‘eye movers’, n=2). For all subjects, a negative correlation resulted between the flash delay and the localization error of the first gaze shifts: the longer the flash delay, the larger the error. This feature may be indicative for target averaging. N: number of responses.
Kolmogorov-Smirnov tests on the gaze-localization error data as described in Methods. The 2D tests were performed on all individual data points, in the [-100,+60] ms delay interval (2D KS IN; left), and in the complementary interval (2D KS OUT; center). The 1D test was run on the running averages in the [-100,+60] ms interval (right). d: KS-statistic between random noise and measured error distributions. p: statistical significance. n.s: not significant. N: number of data points.
Perisaccadic Gaze Errors

Figure 1
Different models explaining perisaccadic localization errors for gaze shifts. (A) In visuomotor updating models, errors arise as a result of a damped representation of the actual gaze shift, $G_1$ (dashed lines, $G_1^P$; $T_{lead}$: lead time of the internal signal). These models predict a systematic relation between the localization errors and the primary saccade kinematics, here illustrated for a small and fast (black) vs. a large and slow (red) gaze shift. $E_2$,$G$: error in the direction of the first gaze shift. (B) According to the visual shift hypothesis, the retinal representation of the flashed target, $T_2$, transiently shifts by $\hat{\theta}(t_0)$ deg in the direction of the primary gaze shift (blue) to $T_2^*$, reaching the largest shift of about 10 deg near gaze-shift onset. The resulting error patterns are invariant to changes in the primary gaze-shift properties.

Figure 2
(A) Double-step paradigm (inset) and associated gaze shifts, $G_1$ and $G_2$ toward flashed targets $T_1$ and $T_2$, respectively. Target $T_2$ is flashed at delay $t_0$ before the first gaze-shift onset. The primary gaze displacement consists of a head movement, $H_1$, and an eye-in-head saccade, $S_1$. The localization error of $G_2$ is $E_2$, which can be projected along the gaze shift ($E_2$,G), or along the eye-in-head saccade ($E_2$,S). For clarity, the systematic undershoot has been omitted. (B) According to the visuomotor updating models (figure 1A), predicted error patterns for the gaze shift (red) and the associated eye-in-head saccade (blue) are different, because of their different amplitudes and kinematics.

Figure 3
(A) Simulated gaze errors for two realizations (red and blue symbols and running averages, respectively, see legend) of the visual persistence model of Eqn. (3). Gaze amplitudes (40-70 deg), gaze-shift kinematics (350-750 deg/s), second flash location and flash timing were all selected at random, thus generating 500 responses for each model. (B) Residual errors for the two models after subtracting the running averages from each data point. Multiple regression was performed on these residues, for which three analysis windows (at -150 ms, -40 ms, and +70 ms) are highlighted with the resulting fit parameters. (C) Parameter dynamics for the two models across the entire delay interval. Note similarity of the curves, despite the large differences in absolute error predictions (see A).
Perisaccadic Gaze Errors

Figure 4
An example of spatial and temporal gaze, head and eye trajectories in the flashed gaze-double-step paradigm (subject bd). (A) F: fixation spot; V₁ and V₂ target locations. The gaze localization error, measured in the direction of the first gaze shift, G₂//, is indicated (black-dotted lines). Eye-in-space (gaze) and head-in-space trajectories are similar. The eye-in-head trajectory (black line) is therefore dissimilar from the gaze- and head trajectories. For clarity, only the first eye-in-head saccade is shown. In the data analysis, the first gaze-in-space and eye-in-head trajectories are used to predict the gaze localization error, G₂// (see Methods). (B) The movements are executed under open-loop conditions, as both stimuli (V₁ and V₂) are extinguished before the first-gaze onset (fat black lines in top panel). Note that the eye-in-head movement duration (bottom panel) is shorter than the first gaze shift (measured by the on- (green) and offset (red) lines). After eye-movement offset, the eye-in-space is carried toward the goal by the head. In turn, the gaze duration is shorter than the head movement. Thus, the eye stays on target through the operation of the VOR.

Figure 5
Dissociation of eye- and head movement contributions to head-free gaze shifts for a typical head mover (jo) (A) and eye mover (pb) (B). For the head mover, the amplitude of the eye-in-head saccade and the gaze-in-space saccade do not correlate well, and the eye-movement is much smaller than the total gaze shift. For the eye mover, the eye- and gaze amplitudes have a positive correlation; the head-movement contribution to the gaze shift is typically smaller than for the head movers.

Figure 6
First (A) and second (B) gaze shifts are goal-directed. First gaze shifts end near the first target location (blue: responses for lower target; red: responses for upper target). Largest inaccuracies were found for largest negative delays, which may be caused by target averaging (Table 1). Second gaze-shift amplitudes correlate well with the component motor error, although a systematic overshoot is observed (most data points above the diagonal). This overshoot is partially explained by the delay-dependent gaze mislocalizations. Data from subject tg.
Perisaccadic Gaze Errors

Figure 7
Gaze-in-space and eye-in-head saccade parameters are broadly distributed. Subject bd.

Figure 8
Statistical analysis on localization errors. (A) Gaze-localization errors in the direction of the first gaze shift (red data points, subject TG), together with running average (red solid line). Blue data points are random data, generated with the same mean and standard deviation as the measured errors for which \( t_0 < -100 \text{ ms} \) or \( t_0 > +60 \text{ ms} \). Blue line is the running average through the noise. (B) Behavior of the tu-statistic (gray (n.s.) and blue (significant) points) and p-value (red points: \( p<0.05 \)) as function of delay. The statistics were computed in 50 ms-wide windows (see Methods). Note that highly significant differences were found in the perisaccadic epoch. (C) Results of the tu-statistic for all six subjects.

Figure 9
(A) Localization errors for subject jo (raw data), together with the running average through the data (red line). Same format as figure 8A. (B) Running averages for all six subjects, together with their grand average (taken over pooled gaze shifts; black line). (C) Data from the 4 subjects in our previous eye-movement study, together with the grand average of pooled saccades (black line). Note that the magnitude and time course of the head-free gaze- and head-restrained eye-movement errors are remarkably similar.

Figure 10
Sensitivity analysis of the visuomotor model predictions. (A) The predicted error patterns (here illustrated for twelve different parameter sets of the gaze-motor feedback model, Eqns. 7-9) depend strongly on the model parameters (lead time and filter characteristics indicated on right-hand side). The prediction for the default model (solid black curve, identified by DEF) deviates strongly from the measured data (red curve, DATA, running average through data points). Note that some model parameters lead to a better approximation of the data. (B) Residual errors (Eqn. 8) were computed by removing the average trend in the data (red) and in the different model predictions (black/gray lines) from the data points. All curves now nearly superimpose on the zero line. The multiple regression analysis of Eqn. 9 was then performed on these data sets (\( n=13 \)). (C) The predicted dynamic influence of gaze amplitude (\( a(t_0) \), blue), mean gaze velocity (\( b(t_0) \), red) and gaze motor error (\( c(t_0) \), green) is not very sensitive to the different model
Perisaccadic Gaze Errors

parameters. Bold colored curves: default model parameters; thin curves: the eleven other parameter sets shown in (A). Black curves: regression results on the measured data of subject bd, shown in (B). The data do not follow any of the model predictions.

Figure 11
Dynamic regression analysis (Eqn. 9) for all six subjects. (A-B): head movers (n=4). (C-D): eye movers (n=2). Left column: results of regression on the measured data. Right column: results of regression on the data predicted on the basis of the first gaze saccade (B), or the first eye-in-head saccade (D), by taking the default parameters. The model predictions are very different from the measured values for all subjects, regardless their movement strategies.

Figure 12
Prediction of perisaccadic errors (individual data points and running average, red line) for large head-free gaze shifts with the visual shift model of Eqn. 10 (black line). Parameters were set to $E_{\text{max}}=10$ deg, $\langle \rangle = 0.2$ deg$^{-1}$, and $\otimes = 4.1\times10^{-4}$ ms$^{-2}$. (A) Data from subject bd. (B) Running averages for each subject (thin lines, see legend), the average across all subjects (thick red line), and the prediction of the visual shift model (black). (C) Dynamic multiple regression on the visual-shift predictions shown in (A). The results qualitatively agree with the experimental data of figure 11A,C.