Smooth anticipatory eye movements alter the memorized position of flashed targets

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Briefly flashed visual stimuli presented during smooth object- or self-motion are systematically mislocalized. This phenomenon is called the “flash-lag effect” (Nijhawan, 1994). All previous studies had one common characteristic, the subject’s sense of motion. Here we asked whether motion perception is a necessary condition for the flash-lag effect to occur. In our first experiment, we briefly flashed a target during smooth anticipatory eye movements in darkness and subjects had to orient their gaze toward the perceived flash position. Subjects reported to have no sense of eye motion during anticipatory movements. In our second experiment, subjects had to adjust a cursor on the perceived position of the flash. As a result, we show that gaze orientation reflects the actual perceived flash position. Furthermore, a flash-lag effect is present despite the absence of motion perception. Moreover, the time course of gaze orientation shows that the flash-lag effect appeared immediately after the egocentric to allocentric reference frame transformation.

Keywords: anticipation, smooth pursuit, saccades, localization, flash perception, flash-lag effect

Introduction

It seems natural that in our everyday life, we experience the visual environment to be spatially stable. However, when we orient gaze or move through the visual scene, self-motion induces an optic flow. Thus, for a stable space perception during self-motion, the central nervous system (CNS) has to use extraretinal signals to compensate for retinal motion. In this condition, the question arises, “How does the brain combine visual signals from the environment with internal signals related to self-motion?”

An interesting way to address the issue of a stable percept of the environment is to perform a localization task. To localize a flashed object, the brain has to integrate the object’s retinal location with an extra-retinal signal about the direction of gaze (Bridgeman, 1995; Festinger & Canon, 1965; Mergner, Nasios, Maurer, & Becker, 2001; Mon-Williams & Tresilian, 1998; van Beers, Wolpert, & Haggard, 2001). It is particularly difficult for the CNS to match moving and flashed stimuli because continuously changing variables (i.e., position and velocity signals) have to be matched at key events, although they are processed with different delays. A systematic bias of the perceived position shows the limits of this process (for a review, see Schlag & Schlag-Rey, 2002).

One condition in which localization errors happen is during smooth object- or self-motion. An impressive demonstration of such a perceptual mislocalization has first been conducted by MacKay (1958) and has later been rediscovered by Nijhawan (1994). In their experiment, two strobed segments that were flashed in alignment with a continuously lit rotating line lagged the moving object, and the size of the lag increased with angular velocity. This phenomenon is called the “flash-lag effect” and has been extensively studied using the original, rotational configuration (Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 1999; Lappe & Krekelberg, 1998; Purushothaman, Patel, Bedell, & Ogmen, 1998), as well as using constant linear motion (Brenner, Smeets, & van den Berg, 2001; Whitney, Cavanagh, & Murakami, 2000; Whitney & Murakami, 1998). However, the flash-lag effect is not restricted to moving objects but also appears during smooth pursuit eye movements (Kerzel, 2000; Nijhawan, 2001; van Beers et al., 2001). This is also the case for head or whole body movements (Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000). In both conditions, retinal signals about motion are absent. Even more spectacular is the finding that in certain conditions a flash-lag appears without any motion at all. Illusory motion perception can induce a perceptual bias of a flashed target (Cai,
The flash-lag effect shows two characteristic features. First, there is a difference in flash localization error depending on the retinal location of the flash with respect to the motion direction (i.e., a flash presented ahead or behind the gaze direction is mislocalized differently) (Kerzel, 2000; Nijhawan, 2001; van Beers et al., 2001; Whitney et al., 2000; Whitney & Murakami, 1998). Second, the final gaze orientation error depends linearly on the eye and/or target velocity at the moment of the flash (Brenner et al., 2001; Nijhawan, 2001; van Beers et al., 2001).

In all previous studies of the flash-lag effect, it could be hypothesized that it was exclusively due to the perception of motion. In these experiments, a perception of motion was induced either by target motion, self-motion, or illusory motion. Is motion perception necessary to evoke a flash-lag? Here we tested whether a flash-lag could be induced by self-motion but in the absence of motion perception. This was done by testing subjects in a situation where there is no perception of motion despite smooth anticipatory eye movements. In our first experiment, we designed a paradigm inducing smooth anticipatory eye movements that were not perceived by subjects (Kowler & Steinman, 1979). During these smooth eye movements, we presented briefly a flashed target and asked subjects to orient gaze toward the remembered target position. In our second experiment, we validated our gaze orientation approach by a perceptual localization task. As a result, we rule out the hypothesis that the bias in spatial perception is due to motion perception. Indeed, we show that spatial perception of human subjects can be altered by self-motion in the absence of the sense of motion.

# Methods

## Experiment 1

### Experimental set-up

Healthy human subjects without any known oculomotor abnormalities participated in the experiment after informed consent. Among the seven subjects, three were completely naïve of oculomotor experiments. Mean age was 29 years, ranging from 22 to 36 years. All procedures were conducted with approval of the Université catholique de Louvain Ethics Committee, in compliance with the Helsinki declaration (1996).

Experiments were conducted in a completely dark room. Subjects sat in front of a 1-m distant tangent screen, which spanned about ±45° of their visual field. Their heads were restrained by a chin-rest. A horizontally moving 0.2° red laser target was back-projected onto the screen. The target was controlled via an M3-Series mirror galvanometer (GSI Lumonics) and by using a dedicated computer running LabViewRT (National Instruments, Austin, TX, USA) software. Movements of one eye were recorded with the scleral coil technique, Skalar Medical BV (Collewijn, van der Mark, & Jansen, 1975; Robinson, 1963).

## Paradigm

Recording sessions were composed of a series of blocks, each containing 40 trials. During the first block of trials, the moving target was always present. These trials were used to build up an anticipatory response and will be referred to as build-up trials. After one block of build-up trials, several blocks of test trials randomly mixed with build-up trials were presented.

Build-up trials (Figure 1A) started with an 800-ms fixation period at the center of the screen. After a 300-ms target extinction period (gap), the target moved from the center of the screen for 800 ms at 40°/s, always in the same direction. The trial ended with another 500-ms fixation period. The gap duration was chosen to provide an optimal smooth anticipatory eye movement (Morrow & Lamb, 1996).

![Figure 1. Experimental paradigm. A. Build-up trials. After an 800-ms fixation and a 300 ms gap period, the target moved for 800 ms at 40°/s, always in the same direction. B. Test trials. Test trials started like build-up trials with an 800-ms fixation. After a variable gap of 100-500 ms, a 10-ms flash appeared at a random position between -15° and 15°.](https://example.com/figure1.png)
In the second part of the recording session, build-up trials were randomly interleaved with 30% of test trials (Figure 1B). Test trials started in the same way as build-up trials with an 800-ms fixation period in the center of the screen. Afterwards, instead of the fixed gap followed by a ramp target motion, the target disappeared for a random duration lasting between 100 and 500-ms. This variable gap was followed by a 10-ms flash presented at a random position ±15° around the expected eye position (= target position of build-up trials). All trials lasted for 2400-ms. Subjects were instructed to follow the target as accurately as possible during build-up trials, and to orient gaze to the memorized target (flash) position during test trials.

**Data acquisition and analysis**

Eye and target position were sampled at 500-Hz and stored on the hard disk of a PC for offline analysis with Matlab (Mathworks) scripts. Position signals were low-pass filtered using a zero-phase digital filter (autoregressive forward-backward filter, cutoff frequency: 50-Hz). Velocity and acceleration were derived from position signals using a central difference algorithm.

In our analysis, only test trials were considered. We were interested in the gaze orientation mechanism toward the flashed target. Position error (PE) and eye velocity (EV) signals were measured at the moment of the flash. The position error is the difference between target (T) and eye (E) position at a given moment in time: PE=T–E. All trials were aligned on the flash onset. In order to describe the flash localization process, PE was measured every 50-ms starting at the end of the first saccade until 1000-ms after the flash (see Figure 2).

**Experiment 2**

**Experimental set-up**

Three out of the seven subjects of Experiment 1 participated in this experiment after informed consent. All procedures were conducted with approval of the Université catholique de Louvain Ethics Committee, in compliance with the Helsinki declaration (1996).

Experiments were conducted in a completely dark room. Subjects sat in front of a 0.4-m distant, 21 in. Sony GDM-F520 computer screen on which we presented either a 0.5° red circular target or a white vertical cursor. The screen refresh rate and resolution were 100-Hz and 640 x 480 pixels, respectively. Subjects were asked to use a computer mouse to move the cursor. The cursor was composed of two vertical 0.1° large and 1.0° high bars that were aligned horizontally and separated vertically by 0.65°. Target and cursor presentation were controlled in real time by a VSG2/5 Visual Stimulus Generator (32MB VRAM) (Cambridge Research Systems Ltd).

Subjects’ heads were restrained by a chin-rest. Their eye movements were recorded using a Chronos eye tracker, Skalar Medical BV, which is based on high-frame rate CMOS sensors (Clarke, Ditterich, Druen, Schonfeld, & Steineke, 2002).

**Paradigm**

We used a paradigm similar to the one used in Experiment 1, except that we had to reduce the range of the flash position to −10°...10° because of the limited screen size. Recording sessions were composed of a series of blocks containing 40 trials each. Each block started with three build-up trials (Figure 1A). Afterwards, build-up and test trials (Figure 1B) were mixed with 50% probability. However, in contrast with Experiment 1, after each test trial there was a perceptual localization task (Figure 3) and the next trial was always a build-up trial. Afterwards, there was again a 50% probability for either a build-up or a test trial to appear.

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**Figure 2.** Data analysis. After the occurrence of the first orientation saccade, eye position error (PE) was sampled every 50 ms. Dotted black lines represent the initial fixation point and the flash position. The star stands for the flash. The red line represents eye position (saccades in bold). At the moment of the flash, position error (PEflash) and eye velocity (EVflash) were also measured.

**Figure 3.** Perceptual localization task. The trial started with an 800-ms fixation period, a 100-500-ms gap and a 10-ms flash at a random position −10°...10°. After each test trial, subjects localized the memorized perceived position of the flash by means of a cursor. The cursor position could be adjusted by a computer mouse, and subjects had to press the mouse button to validate their choice of the perceived flash position.
The perceptual localization task consisted of the alignment of the cursor with the memorized perceived position of the flash. Subjects had to press the mouse button to validate their choice of the position of the cursor.

**Data acquisition and analysis**

The target position was sampled at 100-Hz and stored on the hard disk of a PC. Images of the eyes were sampled independently of the target at 100-Hz and stored on the hard disk of a second PC. The eye position was extracted offline from the eye images using the polar correlation algorithm for an ellipse approximation of the iris (Clarke et al., 2002), as implemented in the Iris software (Skalar Medical BV). The cursor position of the perceptual localization task was also recorded. Synchronization between eye and target signals was performed by means of a TTL signal.

In this experiment, four parameters of interest were extracted from the recording files (i.e., position error PE_{\text{flash}} and eye velocity EV_{\text{flash}} at the moment of the flash as well as the actual and perceived [= cursor] position of the flash).

**Results**

**Experiment 1**

**General observations**

At the end of each trial, the eyes pointed at the perceived location of the flashed target. Figure 4 shows four typical trials that illustrate the behavior and the gaze orientation performance. If the eyes move toward the flash, the condition is called foveopetal (FP); otherwise, we will refer to it as foveofugal (FF). The smooth eye displacement during the latency period of the first orientation saccade resulted in an overshoot of the first saccade in the FP condition, whereas first saccades in FF trials undershot. Although in Figure 4B and 4D the flash localization is rather precise (FF condition), in Figure 4A and 4C, we observe a remaining error on the final eye position (FP condition). In fact, in the FP condition, subjects generally localized the flash ahead of its actual position. When asked after the experiment, subjects reported that they had no sense of performing smooth anticipatory eye movements during the gap. This is in accordance with previous findings (Kowler & Steinman, 1979).

![Figure 4](https://jov.arvojournals.org/)

Figure 4. Typical trials. Black solid and dotted lines represent the fixation target and the flash position, respectively. The star stands for the flash. Eye position (red lines) and saccades (bold red lines) are shown for four different conditions. A and C. Flash presented at a foveopetal (FP) position during medium (A) and high (C) eye velocity. B and D. Flash presented at a foveofugal (FF) position during medium (B) and high (D) eye velocity.
On average, subjects needed 2–3 saccades to orient their eyes to the memorized position of the flash. The general properties and dynamics of this orientation process have been previously described in detail (Blohm, Missal, & Lefèvre, 2003). Here we will concentrate on the directional bias in space perception, which results from the fact that the eyes were moving at the moment of the flash.

To quantify smooth eye velocity after the flash, we provide in Figure 5A the mean behavior and raw data. Panel B shows the smooth eye displacement, which is the eye displacement after removing saccades. The smooth eye displacement is thus the integration of the smooth eye velocity. The total smooth eye displacement depended on the eye velocity at the moment of the flash: the higher the eye velocity at the moment of the flash, the larger the total smooth eye displacement.

In our analysis, we will consider only the eye position PE\textsubscript{flash} and velocity EV\textsubscript{flash} at the moment of the flash. Indeed, PE\textsubscript{flash} is the only retinal signal that is available to the system to localize the flash (see “Discussion”).

**Localization error**

We examined in this section the two characteristic features of a putative flash-lag effect. Table 1 summarizes the different parameters that were analyzed. Note that -PE\textsubscript{end} (PE\textsubscript{end} = PE(1000-ms)) will be the measure of the perceptual offset. If -PE\textsubscript{end} > 0 (and thus PE\textsubscript{end} < 0 ), the flash is perceived ahead of its actual position in the direction of the smooth eye movement.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Case</th>
<th>Values (mean ± SD)</th>
<th>Range [25...75]%</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>PE\textsubscript{flash}</td>
<td>FF</td>
<td>6.643 ± 4.100</td>
<td>[3.061...9.578]</td>
<td>765</td>
</tr>
<tr>
<td></td>
<td>FP</td>
<td>6.530 ± 3.775</td>
<td>[3.454...9.515]</td>
<td>762</td>
</tr>
<tr>
<td>EV\textsubscript{flash}</td>
<td>FF</td>
<td>10.115 ± 8.595</td>
<td>[4.535...14.246]</td>
<td>765</td>
</tr>
<tr>
<td>-PE\textsubscript{end}</td>
<td>FF</td>
<td>0.587 ± 1.068</td>
<td>[0.129...1.070]</td>
<td>765</td>
</tr>
<tr>
<td></td>
<td>FP</td>
<td>1.592 ± 2.212</td>
<td>[0.559...2.692]</td>
<td>762</td>
</tr>
</tbody>
</table>

FP indicates foveopetal; FF, foveofugal.

The two signatures of the flash-lag phenomenon are analyzed in Figure 6. Figure 6A represents the perceptual offset of the flash for the different flash locations on the flash position relative to fovea (deg).

![Figure 5. Smooth eye movement. A. Mean and SD of smooth eye velocity (solid and dotted black lines) aligned on the flash onset. All foveofugal (FF) and foveopetal (FP) conditions are pooled. B. Mean and SD of the smooth eye displacement (solid and dotted black lines) accumulated since the flash onset. Gray lines show individual trials. Trials were aligned on flash onset (time zero).](image)

![Figure 6. Final gaze orientation toward flashed targets during smooth anticipation. A. Dependency of the perceptual offset (-PE\textsubscript{end}) on the retinal target position relative to the fovea. B. The perceptual offset depends strongly on the eye velocity at the moment of the flash EV\textsubscript{flash} in foveopetal (FP) condition. In foveofugal (FF) condition, only a weak influence of the smooth eye velocity is observed. Whiskers indicate the SEM (see text for details). Bins of 2.5° (panel A) and 5°/s (panel B) are centered on the binning interval.](image)
retina in the gaze orientation experiment. Figure 6A clearly shows that there is an asymmetric perceptual bias in the flash localization. Thus, a flash presented during smooth anticipatory eye movements is mislocalized in the same way as a flash presented during smooth pursuit.

A closer look at this asymmetrical perceptual effect is provided in Figure 6B. Here we separated the data into two populations (i.e., foveopetal [FP] and foveofugal [FF] flash presentations). We observed a clear effect of the smooth eye velocity at the moment of the flash \( EV_{\text{flash}} \) on the perceptual offset for the FP condition (see Equation 2), whereas the effect was much more attenuated for the FF condition (see Equation 1).

\[
\begin{align*}
\text{FF: } & -PE_{\text{end}} = 0.163 + 0.029 \cdot EV_{\text{flash}} \quad (N = 765, R = 0.1393, p = .023) \\
\text{FP: } & -PE_{\text{end}} = -0.073 + 0.129 \cdot EV_{\text{flash}} \quad (N = 762, R = 0.3781, p < .001)
\end{align*}
\]

Equation 1

Figure 6B shows separately the dependence of the final gaze orientation error on the smooth eye velocity \( EV_{\text{flash}} \) at the moment of the flash for both FF and FP conditions. Individual analyses of the data for all subjects resulted in regression coefficients that varied between -0.021...0.064 (\( N = 765 \)) and between 0.070...0.234 (\( N = 762 \)) for the FF condition in Equation 1 and between 0.070...0.234 (\( N = 765 \)) for the FP condition in Equation 2.

Taken all together, we showed that targets flashed during smooth anticipatory eye movements are affected by a flash-lag illusion. This was the case although subjects had no perception of any eye movements when the flash occurred.

**Temporal evolution of the error**

After having shown in the previous section that an anticipatory smooth eye movement distorts the perceived space when tested with a short flash, we wondered whether we could reveal the temporal evolution of the flash-lag effect. Therefore, we performed the following regression analysis independently for both FF and FP conditions and for each time step during gaze orientation:

\[
PE(t) = \alpha(t) - \beta(t) \cdot EV_{\text{flash}}
\]

Equation 3

The results of the regression in Equation 3 are represented in Figure 7. Individual regression coefficients for each time step and FF or FP condition ranged from \( R = 0.1393...0.7597 \) (\( p < .001...0.023 \)). The nonzero offset \( \alpha \) in the early orientation (Figure 7A) was essentially due to the saccadic undershoot strategy (Gellman & Fletcher, 1992) and the system compensated for this error later on in the orientation process.

Figure 7B shows the evolution of the error dependence on \( EV_{\text{flash}} \) over time. Interestingly, in the earlier orientation process, there was no difference between FP and FF relationships (\( p > .05 \)). Indeed, Blohm et al. (2003) showed that the first orientation saccade did not take into account the smooth eye displacement. Therefore, at this time, the gain element \( \beta(t) \) is the same in the FP and FF condition (t test, \( p > .05 \)). However, afterwards, the \( p \) level that quantifies the difference of the regression parameter \( \beta(t) \) between FP and FF conditions decreased. After 450-ms, the regression parameters \( \beta(t) \) became significantly different (\( p < .05 \)) and even highly significantly different after 650-ms (\( p < .001 \)). Furthermore, in Figure 7, the 95% confidence intervals of the regressions for FP and FF conditions separately also decrease, which indicates that individual regressions improve over time. Hence, although Equation 3 is not a signature of the flash-lag effect, the resulting separation of both FP and FF populations in Figure 7B shows the relevance of this analysis in characterizing the temporal evolution of the flash-lag effect.

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**Experiment 2**

To demonstrate that the final gaze orientation reflects the perceived position of the flash, we performed a perceptual localization experiment. As in Experiment 1, subjects reported to have no sense of performing any smooth eye movements during the gap period.
Table 2 summarizes the results of this experiment. Here the cursor localization error \( \text{ERR}_{\text{loc}} \) replaces the eye position error \( \text{PE}_{\text{end}} \) of Experiment 1. We verified that the overall eye velocity at the moment of the cursor appearance was small (EV = \(-0.043 \pm 0.928°/s\), mean ±SD).

Table 2. Mean Values and Ranges of Parameters That Characterize the Perceptual Localization Data Set in Experiment 2.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>(</td>
<td>\text{PE}_{\text{flash}}</td>
<td></td>
<td>FF</td>
<td>5.902 ± 3.568</td>
</tr>
<tr>
<td>FP</td>
<td>4.299 ± 3.251</td>
<td>[1.924...6.875]</td>
<td>284</td>
<td></td>
</tr>
<tr>
<td>( -\text{ERR}_{\text{loc}}</td>
<td></td>
<td>FF</td>
<td>0.602 ± 1.310</td>
<td>[-0.325...1.619]</td>
</tr>
<tr>
<td>FP</td>
<td>1.957 ± 2.021</td>
<td>[0.403...3.934]</td>
<td>284</td>
<td></td>
</tr>
</tbody>
</table>

FP indicates foveopetal; FF, foveofugal.

Figure 8 illustrates the results of the perceptual localization experiment. Panel A shows the dependence of the localization error on the retinal location of the flash. Compared to the gaze orientation experiment in Figure 6, the flash-lag is qualitatively the same, although the effect is more selective concerning the eye position error at the moment of the flash (see “Discussion”).

Figure 8B recapitulates the effect of the eye velocity (EV\( _{\text{flash}} \)) at the moment of the flash on the perceptual localization of the target. Qualitatively, we obtained the same results as for Experiment 1: FP flashes are mislocalized in the direction of the eye movement whereas this behavior is much reduced for FF flashes. This is expressed in the following regression equations:

\[
\text{FF}: \quad -\text{ERR}_{\text{loc}} = 0.053 + 0.023 \cdot \text{EV}_{\text{flash}} \quad (N = 312, R = 0.0831, p = .094) \quad (4)
\]

\[
\text{FP}: \quad -\text{ERR}_{\text{loc}} = 0.451 + 0.116 \cdot \text{EV}_{\text{flash}} \quad (N = 284, R = 0.1967, p = .002) \quad (5)
\]

Individual values of the regression coefficients for all subjects ranged from 0.017…0.029 (\( N = 84…131, p = .143…0.697 \)) for the FF condition in Equation 4 and 0.083…0.154 (\( N = 81…128, p = .015…0.072 \)) for the FP condition in Equation 5. However, we would like to point out that this perceptual localization task was conducted to confirm that the final gaze orientation really represents the perceived position of the flash. We claim that our results show that both localization procedures reveal the same phenomenon.

**Discussion**

A flash presented during perceived movement is perceptually mislocalized (Schlag & Schlag-Rey, 2002). Such a bias has previously been observed for targets presented briefly during smooth self-, object-, or illusory-motion and is called “flash-lag.” Here we asked whether the observed asymmetrical perceptual offset might be due to motion perception. Therefore, a briefly flashed target was presented during unperceived smooth anticipatory eye movements in darkness, and subjects had to localize the flash. This revealed the presence of a self-movement induced flash-lag illusion despite the absence of the sense of self-movement. Thus, space perception is decoupled from movement perception, although a perceived movement might influence the perceived space (Cai et al., 2000; Nishida & Johnston, 1999; Watanabe et al., 2002).

**Gaze orientation and perceptual localization**

Our gaze orientation and perceptual localization results show the same trend (i.e., almost the same dependency of the perceptual offset on the eye velocity at the moment of the flash and a very similar behavior for the influence of retinal flash position). However, we observed slightly different shapes and regression
parameters in the gaze orientation task and the perceptual localization experiment. There might be a difference between gaze orientation and manual localization motor strategies. Indeed, it has been shown that visually guided manual pointing to remembered targets leads to an overshoot for small target eccentricities, whereas larger distances are more likely to be undershot (Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995; Medendorp, Van Asselt, & Gielen, 1999). Furthermore, a comparison of gaze orientation and perceptual localization of briefly presented targets reveals systematic undershoots for gaze orientation compared to an overshoot in perceptual localization (Egbert, Ditterich, & Straube, 2001; Egbert, Sailer, Ditterich, & Straube, 2002). However, despite these possible differences, we observe very similar regression coefficients in Equations 1 and 2 compared to Equations 4 and 5.

The perceptual localization task allowed us to validate our approach and to confirm that the final gaze direction reflects the perceived position of the flashed target. In addition, the position of the cursor when the mouse button was pressed gave us direct information on the perceived flash position.

Time course of the flash-lag illusion

Our analysis in Figure 7 answered the question about the timing of the flash-lag effect in more details. Indeed, we showed when the visual illusion begins affecting the eye movements. This is in accordance with previous results showing that the first orientation saccade does not take into account any movement-related information but is only based on the position error PE_\text{flash} at the moment of the flash (Blohm et al., 2003). Furthermore, Blohm et al. (2003) revealed a 400-ms delay to account for the smooth eye displacement. If the eye moved smoothly in darkness, the system corrected for this smooth eye displacement around 400-ms later by means of a corrective saccade. Thus, the 400-ms delay represents the time needed for the manifestation of the egocentric to allocentric reference frame transformation. This finding can be compared to the transition period for the visual illusion to influence the ocular orientation process we found here. Indeed, we observe a separation of FF and FP data immediately after the 400-ms delay (Figure 7B). We conclude that the early localization of the flash is not affected by the visual illusion, but once the flash position has been transformed in allocentric coordinates, eye movements reflect the actual perceived flash location. Thus, the bias in space perception might be due to an erroneous reference frame transformation.

The relatively long delay for egocentric to allocentric reference frame transformation may also account partly for the observation that target motion can influence the flash-lag effect even some time after the flash occurred. Durations between 60-ms and 600-ms have been previously proposed for this process (Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000).

Next we discuss the egocentric to allocentric reference frame transformation and propose candidates for the possible underlying neural structures of the flash-lag effect.

Origin of the perceptual bias

The asymmetry between FP and FF conditions suggests a hemifield effect, whereas the time course of the flash-lag effect could indicate the involvement of two different pathways. It has been suggested (Blohm et al., 2003) that the early orientation involves a direct pathway from the primary visual areas to the saccade generator (for a review, see Krauzlis & Stone, 1999). Therefore, first orientation saccades are coded in an egocentric reference frame. A second pathway involving middle temporal (MT) and medial superior temporal (MST) areas and the posterior parietal cortex (PPC) has been proposed to compensate for the smooth eye displacements (Blohm et al., 2003). PPC is also known to code the egocentric to allocentric reference frame transformation (Andersen, Essick, & Siegel, 1985; Pack, Grossberg, & Mingolla 2001; Heide, Blankenburg, Zimmermann, & Kompf, 1995) and areas MT/MST contain neurons that are direction and speed selective (Born & Tootell, 1992; Mikami, Newsome, & Wurtz, 1986; Newsome, Wurtz, & Komatsu, 1988; van Wezel & Britten, 2002) and that carry information about eye movements (Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Eifuku & Wurtz, 1998; Komatsu & Wurtz, 1988a, 1988b; Newsome et al., 1988; Squatrito & Maioli, 1997). Interestingly, Krekelberg, Kubischik, Hoffmann, and Bremmer (2003) recently showed that areas MT/MST are strongly involved in the spatial localization of a flashed target, and the neural activity in these areas codess the persaccadic mislocalization of flashes. Therefore, we propose that the same brain regions might be responsible for the flash-lag effect.

Our manual localization data strongly support this hypothesis, whereas the gaze orientation results might reflect other, more complex mechanisms (see “Gaze Orientation and Perceptual Localization”). It has been suggested that other visual illusions, such as the Filehne illusion, might also be mediated by area MST (Erickson & Thier, 1991). It would be interesting to test the hypothesis that MT/MST neurons might code the flash-lag effect as it has been shown for persaccadic flashes (Krekelberg et al., 2003).

Conclusions

The sense of motion was a common factor in all previous experiments on motion-related visual illusions. Here we showed that motion perception is not a necessary condition for such a bias in space perception. Indeed, a flash-lag illusion was observed during unperceived smooth anticipatory eye movements. Furthermore, we showed that gaze orientation to briefly
presented targets follows the perceptual localization of the flash. In addition, the gaze orientation analysis reveals the time course of the flash-lag effect. We suggest that this reflects the time needed by the CNS to perform the egocentric to allocentric reference frame transformation.

**Acknowledgments**

This work was supported by the Fonds National de la Recherche Scientifique; the Fondation pour la Recherche Scientifique Médicale; the Belgian program on inter-university poles of attraction initiated by the Belgian state, Prime Minister’s office for Science, Technology and Culture (SSTC); and internal research grant (Fonds Spéciaux de Recherche) of the Université catholique de Louvain. Commercial relationships: none.

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