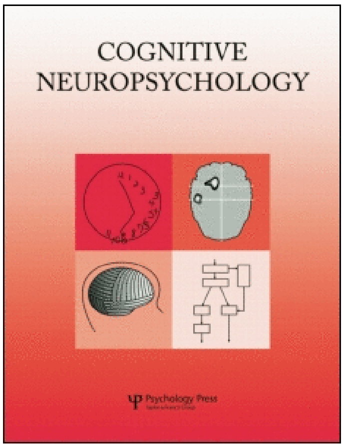

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Motion-induced positional biases in the flash-lag configuration

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Motion-induced positional biases in the flash-lag configuration

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When both stationary and moving objects are present in the visual field, localizing objects in space may become difficult, as shown by illusory phenomena such as the Fröhlich effect and the flash-lag effect. Despite the efforts to decipher how motion and position information are combined to form a coherent visual representation, a unitary picture is still lacking. In the flash-lag effect, a flash presented in alignment with a moving stimulus is perceived to lag behind it. We investigated whether this relative spatial localization (i.e., judging the position of the flash relative to that of the moving stimulus) is the result of a linear combination of two absolute localization mechanisms—that is, the coding of the flash position in space and the coding of the position of the moving stimulus in space. In three experiments we showed that (a) the flash is perceived to be shifted in the direction of motion; (b) the moving stimulus is perceived to be ahead of its physical position, the forward shift being larger than that of the flash; (c) the linear combination of these two shifts is quantitatively equivalent to the flash-lag effect, which was measured independently. The results are discussed in relation to perceptual and motor localization mechanisms.

Keywords: Flash-lag; Localization; Motion-position interaction; Visual illusion; Action perception.

Localizing objects in space is one of the most important functions of the visual system, both in building a veridical perceptual representation and in guiding successfully our own movements. Despite seemingly simple, visual localization is complicated by the fact that, in addition to the positional information of objects, various other sources of information must be taken into account, such as eye position, visual motion, or the position of our body in the environment (see Schlag & Schlag-Rey, 2002; Whitney, 2002). Combining motion and position signals generates a number of illusory phenomena. Fröhlich discovered that the initial position of a moving stimulus is mislocalized in the direction of motion (Fröhlich, 1923). In the flash-lag effect (FLE) the position of a stimulus

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that is flashed in alignment with a moving stimulus is perceived to lag behind it (Nijhawan, 1994). Although in the last decade there has been a renewed, rapidly growing interest for this topic, a unitary picture of the way the brain combines position and motion information is still lacking (Krekelberg & Lappe, 2001; Nijhawan, 2002).

Localization in the perceptual domain does not always correspond to localization in the motor domain. For example, hand or eye pointing are not always guided by the perceptual representation, and sometimes they do not demonstrate visual illusory effects (Burr, Morrone, & Ross, 2001; de'Sperati, Grimoldi, Bau-Bovy, & Jacomuzzi, 2006). One aspect that differentiates pointing movements from visual representations is that they are based upon different systems of coordinates. The brain deals with position of objects in space through both an egocentric and an allocentric system of coordinates. In the former case, the position of an object is represented in relation with some body reference, for example the direction of the eyes or the head, while in the latter case the relative distance among objects is the represented variable.[1] As a consequence, visual perception involves mostly an allocentric representation that accommodates the various objects in the visual field, while the motor system is based upon various egocentric representations (Stein, 1992). The way allocentric and egocentric representations interact may turn out to be an important distinction in the action–perception debate (Bruno, 2001).

The FLE is an interesting example of a faulty allocentric representation of the relative position between moving and stationary objects. In the last decade, this illusion has been closely examined by several research groups. The various interpretations that have been put forth to explain this phenomenon may be subsumed under two broad categories: Those focusing on spatial aspects and those focusing on temporal aspects. Among the former, motion extrapolation posits that the position of a moving objects is predictively extrapolated in space to compensate for neural delays of the flash (Nijhawan, 1994), while the motion-biasing model posits a postdictive shift (Eagleman & Sejnowski, 2007). Temporal mechanisms include attention capture (Baldo & Klein, 1995), motion integration (Krekelberg & Lappe, 2000), and differential latencies (Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998), which can cause important perceptual delays.

Most accounts of FLE focus on the way position is assigned to the moving stimulus, implicitly assuming that the absolute perceived position of the flash is coded correctly (see, however, Eagleman & Sejnowski, 2007). Yet, recent findings showed that visual motion can affect considerably the perceived position of flashed stimuli (Durant & Johnston, 2004; Hubbard, 2008; Watanabe, 2005; Watanabe, Sato, & Shimojo, 2003; Whitney & Cavanagh, 2000), whose position appears biased in the direction of motion. This "dragging action" exerted by visual motion suggests that the FLE could derive from the net sum of two components—that is, a position forward shift of the moving object and a smaller position forward shift of the flash. Depending on the balance between these two components, the size of the FLE may vary considerably. Alternatively, it could be that relative judgements such as the FLE are not the simple combination of individual absolute judgements (Brenner & Cornelissen, 2000) and that more complex, nonlinear mechanisms are at play. In this study we tested the two-component hypothesis by comparing the size of the FLE (a relative judgement) with measures of the perceptual localization of both the flash and the moving stimulus (absolute judgements), with the aim of mapping systematic motion-induced spatial distortions occurring in a region of space nearby the moving stimulus.

Decomposing the FLE in its constituents may help understanding where localization becomes faulty. Also, if the relative position judgement of the moving and the stationary stimulus turns out

[1] Throughout the article we use the term "relative" as a synonym of "allocentric". By contrast, the term "absolute" is used as synonym of egocentric.

to result from the combination of absolute positional coding of the two stimuli, it will become possible to probe the perceptual FLE in terms of separate pointing localization errors to the flash and the moving object.

EXPERIMENT 1

In this experiment we measured mislocalization of the flash and mislocalization of the moving arc (Figure 1) in a sequential pointing task. We used circular motion around a fixation point to avoid possible differences of position judgement in foveofugal and foveopetal linear movements (Mateeff et al., 1991). Four parameters were calculated (Figure 2 A): the arc forward shift (AFS), the flash forward shift (FFS), the flash-to-arc distance (FTA), and the flash eccentric shift (FES). Furthermore, a measure corresponding to the traditional flash-lag was derived, which we called virtual flash-lag (VFL).

Method

Participants

A total of 12 participants (3 females, 2 left-handed, with a mean age of 27.6 years) participated in this experiment. They had normal or corrected-to-normal vision. Except for 2 participants, they were naïve as to the purpose of the experiment. Informed consent was requested before the beginning of the experiment.

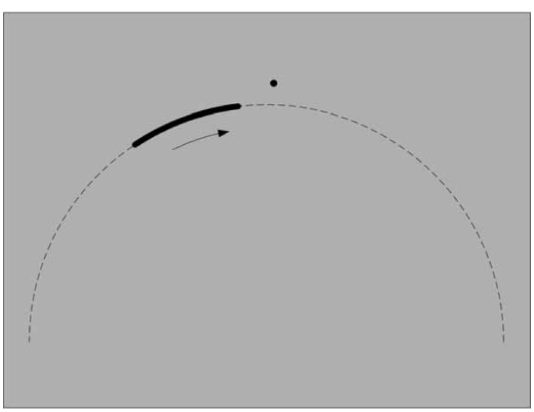

Figure 1. *Sketch of the stimulus configuration. The arc revolved in the clockwise direction. A flash was displaced in proximity of its leading edge. The arrow and the dashed semicircle were not part of the actual stimulus.*

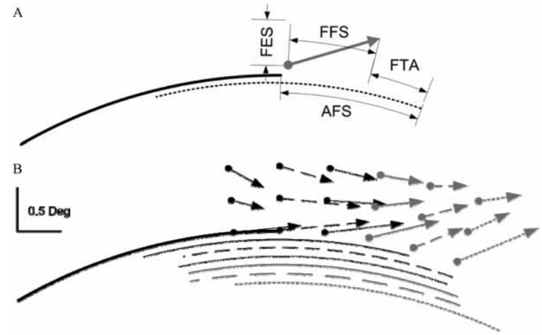

Figure 2. *(A) A schematic illustration of four parameters: the arc forward shift (AFS), the flash forward shift (FFS), the flash eccentric shift (FES), and the flash-to-arc distance (FTA). The small circular spot represents the objective flash position, and the arrow indicates the position shift, with the tip denoting the reported positions of the flash. The bold arc represents the objective position of the moving arc at the time of the flash. Underneath the arc is the perceived arc position at the time of the flash. (B) Positional shifts in Experiment 1. The circular spots represent the 18 objective flash positions, with 18 arrows denoting the corresponding perceptual position shifts. Underneath the bold arc, the reported positions of the arc are shown in cascade for the six flash offset conditions, averaged across the three eccentricity values (dark-solid, dark-dashed, dark-dotted, grey-solid, grey-dashed, grey-dotted). Data from all repetitions along the circular trajectory are pooled together.*

Stimuli and task

The stimuli were displayed on a 17″ CPD-4402 Triniton CRT monitor (1,024 × 768 resolution; 85-Hz frame rate) and were controlled by Matlab and the Psychtoolbox (Brainard, 1997) with an Intel Pentium III PC in a dimly lit experimental booth. The background of the display was dim grey (luminance: 0.45 cd/m^2). A grey fixation cross (1.37 cd/m^2) subtending 0.12° of visual angle was displayed at the centre of the screen. At the beginning of each trial, a grey circular arc with a length of 30° (subtending 3.1° of visual angle; 1.37 cd/m^2) appeared in a random position along a circular trajectory (eccentricity: 6.0°) and started to revolve clockwise at 3.142 rads/s (0.5 cps). After a random period of 700–1,000 ms, a white spot (0.1° of visual angle, 73.4 cd/m^2) was flashed for 1 video-frame near the moving arc (Figure 1). Relative to the head of the moving arc, the flash appeared displaced along the circular trajectory by one of the six following values: −0.52, 0, 0.52, 1.04, 1.56, or 2.08° of visual angle. The flash eccentricity was one of the three following values: 6.0, 6.3, or 6.6°. Note that in the 6° eccentricity condition the flash was located on the circular trajectory. After the flash, the moving arc continued to move for a random time (500 to 800 ms) before disappearing.

Participants sat in front of the monitor and fixed their head on a chinrest with a viewing distance of 67 cm. They were instructed to keep central fixation until the moving arc disappeared. Immediately thereafter, the arc reappeared in a random position along the circular trajectory. By means of the mouse, participants had to place the arc where they perceived it to be at the time of the flash. The movement of the arc was constrained along the circular trajectory. Participants were encouraged to be as precise as possible and to use adjustments. They had to confirm the judgement by pressing the right mouse button. The arc remained in that position until the end of the trial. As a subsequent task, participants also had to point the mouse cursor (a spot identical to the flash appearing in the centre of the monitor) to the perceived position of the flash. Again, participants were encouraged to be as precise as possible and to confirm the judgement by pressing the right mouse button. The next trial began 1 to 1.5 s after the participants' decision.

Each combination of conditions was repeated 10 times, for a total of 180 trials for each participant (6 flash offsets × 3 flash eccentricities × 10 repetitions), randomly interleaved.

Results and discussion

The results obtained from all participants showed a similar pattern and were averaged across subjects. Figure 2B shows the reported positions of the moving arc and the flash together with their objective positions. The moving arc was reported to be shifted in the direction of motion with a mean arc forward shift (AFS) of 2.06° ± 0.178. A repeated measures analysis of variance (ANOVA) showed that AFS depended on the offset of the flash, especially for extreme values, $F(5, 55) = 14.743$, $MSE = 0.282$, $p < .01$, but was independent of its eccentricity, $F(2, 22) = 1.713$, $MSE = 0.109$, $p = .204$. The interaction Offset × Eccentricity was nonsignificant, $F(10, 110) = 0.98$, $MSE = 0.143$, $p = .465$ (Figure 3A). Because the contribution of eccentricity to the reported positional shift of the moving arc was negligible, in Figure 2B we collapsed the eccentricity conditions and showed the mean arc forward shift for the six offset conditions.

The flash shift can be decomposed into two components—namely, flash forward shift (FFS) and flash eccentric shift (FES). Overall, the FFS was 0.65° ± 0.11. A repeated measures ANOVA for FFS showed that eccentricity was significant, $F(2, 22) = 12.266$, $MSE = 0.185$, $p < .001$, but the offset was nonsignificant, $F(5, 55) = 2.273$, $MSE = 0.269$, $p = .059$ (Figure 3B). The interaction was also nonsignificant, $F(10, 110) = 0.865$, $MSE = 0.134$, $p = .568$. This means that the flash forward shift depended only on the flash eccentricity: The closer the flash to the trajectory of the moving arc, the further its position was perceived to be shifted in the direction of motion. As for the FES, a repeated measures ANOVA indicated that both offset and eccentricity were significant, $F(5, 55) = 32.192$, $MSE = 0.016$, $p < .001$, and $F(2, 22) = 11.318$, $MSE = 0.126$, $p < .001$, respectively, but with no interaction, $F(10, 110) = 0.944$, $MSE = 0.008$, $p = .497$ (Figure 3C). This indicated that FES increased with flash offset and decreased with flash eccentricity.

We then derived the magnitude of a "virtual" flash-lag effect (VFL, Figure 3D). Analogous to the perceptual FLE, which is normally calculated by estimating the objective flash-to-moving stimulus distance at which the flash appears to be aligned with the moving stimulus, here linear regression has been used to estimate the flash-to-arc distance at which the perceived position of the flash is identical to the perceived position of the head of the arc. This corresponds to the (virtual) flash offset at which the

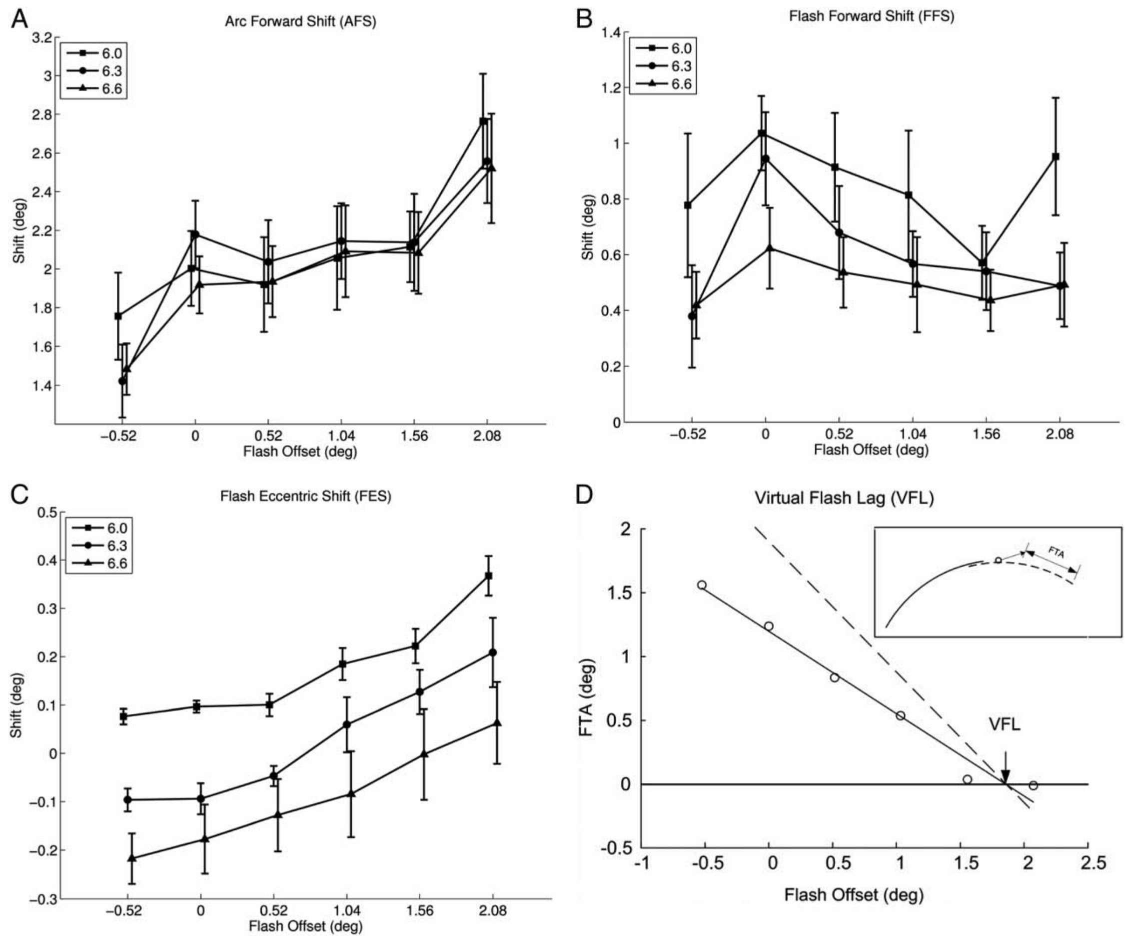

Figure 3. *Results of Experiment 1 (sequential judgement). (A) Mean arc forward shifts (AFS), grouped for flash eccentricity and plotted against flash offset. The error bars indicate the* SEM. *(B) As (A), but for flash forward shifts (FFS). (C) As (A), but for flash eccentric shifts (FES). (D) Virtual flash-lag (VFL) for the flash eccentricity = 6.3°. The circles represent the mean values of the perceived flash-to-arc distance (FTA, see inset) at each flash offset. The solid line is the regression line, and the dashed line denotes the theoretical constant flash-lag in the direction of motion (see text). VFL was estimated as the value of the flash offset at the zero-crossing of the regression line.*

objective flash position plus its perceptual shift (FFS) is identical to the objective arc head position plus its perceptual shift (AFS)—that is, when the perceived flash-to-arc distance (FTA) was zero. The obtained mean VFL values across subjects were 1.49° ± 0.13, 1.88° ± 0.20, and 1.87° ± 0.21, respectively, for eccentricities of 6.0, 6.3, and 6.6°. Pair-wise comparison tests showed that the VFL at eccentricity = 6.0° was significantly lower than that at the other two eccentricities, $t(11) = -3.258$, $MSE = 0.121$, $p < .01$, and $t(11) = -2.327$, $MSE = 0.162$, $p < .05$, for 6.3° and 6.6°, respectively. This was mainly due to the largest FFS when the flash was displayed on the circular trajectory.

It is interesting that there was a significant mismatch between the obtained regression line and the theoretical, unitary-slope line, which represents a constant flash-lag effect (slope: −0.645 deg/deg, with a 95% confidence interval from

−0.778 to −0.511). Therefore, this finding would seem to suggest that the magnitude of the flash-lag depends on the offset between the flash and the moving stimulus.

The procedure we used to measure the perceived shift of both the flash and the arc could have introduced some distortions due to the time span between the stimulus presentation and the response. In fact, it is known that spatial representations are subject to deterioration starting very soon after stimulus offset (Werner & Diedrichsen, 2002). Although we did not measure them, response times were actually in the order of 2–3 s. Important delays are inherent in most stimulus–response paradigms, and there is no way to avoid them. Also the FLE is often measured with psychophysical methods that involve large delays, so our procedure is similar in this respect and resembles the cursor adjustment method employed previously (Müsseler, Stork, & Kerzel, 2002). Thus, it seems unlikely that this bias corrupted our localization measures more than if we had used a traditional psychophysical method. In fact, the comparison between VFL and an equivalent measure obtained through the constant-stimuli method gave an almost identical result (see Experiment 3). On this basis, we take the above values to reflect mainly perceptual mechanisms, without important spatial distortions introduced by the delayed pointing procedure (see also the General Discussion section).

Another possible response bias could derive from the motor component of the response. In this case, systematic distortions could arise in the motor space. However, first, the fact that we used closed-loop responses and not direct pointing should minimize motor errors. Second, because of the random distribution of the stimuli, the entire range of stimulus positions and of motion tangential directions has been sampled, so as to cancel out possible residual motor asymmetries.

A third possible source of spatial distortions may derive from the requirement to perform a sequential double judgement, which may be different from judging the two locations separately. This issue was addressed in Experiment 2.

EXPERIMENT 2

Experiment 1 showed that the perceived position of both the moving arc and the flash appeared shifted forward in the direction of motion. In that experiment, we used a double sequential pointing task. In this experiment we used independent measures of mislocalization for the flash and the arc, thus excluding possible interferences. This experiment was run after Experiment 1.

Method

Participants

A total of 11 participants (5 females, 1 left-handed, with a mean age of 29.2 years) participated in this experiment. They had normal or corrected-to-normal vision. Except for 7 participants who had participated in the previous experiment, they were naïve as to the purpose of the experiment. Informed consent was requested before the beginning of the experiment.

Stimuli and task

The experiment was identical to Experiment 1, but the pointing task was performed in two different sessions, separately for the flash and the moving arc. The two sessions were counterbalanced across subjects. Also, at variance with Experiment 1, a dim circle (1.37 cd/m^2) representing the entire circular trajectory was displayed when the moving arc disappeared, to provide a visual reference. This was made to control the tendency to locate the perceived position of the flash toward the fovea in the absence of visual landmarks (van der Heijden, van der Geest, de Leeuw, Krikke, & Musseler, 1999).

Results and discussion

Figure 4 illustrates the shifts of the reported positions of the moving arc and the flash relative to their objective position, showing an overall pattern of mislocalization very similar to that in Experiment 1. On average, the moving arc was perceived shifted in the direction of motion, with

Figure 4. *Positional shifts in Experiment 2. The circular spots represent the 18 objective flash positions, with 18 arrows denoting the corresponding perceptual position shifts. Underneath the bold arc, the reported positions of the arc are shown in cascade for the six flash offset conditions, averaged across the three eccentricity values (dark-solid, dark-dashed, dark-dotted, grey-solid, grey-dashed, grey-dotted). Data from all repetitions along the circular trajectory are pooled together.*

a mean AFS of 1.79° ± 0.27 (Figure 5A). A repeated measures ANOVA on AFS showed that the flash offset had a significant effect, $F(5, 50) = 3.207$, $MSE = 0.505$, $p = .014$, while eccentricity did not, $F(2, 20) = 3.027$, $MSE = 0.277$, $p = .071$. The interaction was not significant, $F(10, 100) = 1.195$, $MSE = 0.134$, $p = .304$.

The flash was again perceived shifted in the direction of motion, with a mean FFS of 0.433° ± 0.139 (Figure 5B). A repeated measures ANOVA on FFS showed that two main factors, offset and eccentricity, were significant, $F(5, 50) = 4.126$, $MSE = 0.204$, $p < .01$, and $F(2, 20) = 6.132$, $MSE = 0.191$, $p < .01$, respectively, but the interaction was nonsignificant, $F(10, 100) = 1.358$, $MSE = 0.108$, $p = .211$. Thus, as in Experiment 1, the FFS decreased for larger eccentricities. However, in this experiment the FFS also depended on the flash offset: The more the flash was displayed ahead of the moving arc, the further it was perceived shifted in the direction of motion. Another repeated measures ANOVA was conducted on FES, again confirming a similar pattern of results as in Experiment 1 (Figure 5C): The two main factors were significant, $F(5, 50) = 11.705$, $MSE = 0.029$, $p < .001$, and $F(2, 20) = 5.39$, $MSE = 0.126$, $p = .013$, for offset and eccentricity, respectively, but the interaction was not significant, $F(10, 100) = 0.725$, $MSE = 0.033$, $p = .7$.

Also the VFL was very similar to that in Experiment 1. The mean VFL values across subjects were 1.60° ± 0.49, 1.41° ± 0.68, and 1.44° ± 0.32, respectively, for eccentricities of 6.0, 6.3, and 6.6°. A repeated measures ANOVA showed that VFL did not change significantly with eccentricity, $F(2, 20) = 0.194$, $MSE = 0.624$, $p = .826$.

Thus, this experiment replicated the findings of Experiment 1 except that the FFS increased with the flash offset. As a consequence, and at variance with Experiment 1, the regression line was indistinguishable from the theoretical, unitary-slope line (Figure 5D, slope: −1.080, with a 95% confidence interval from −1.292 to −0.868). This suggests that the magnitude of the flash-lag is in fact fairly constant regardless of the offset between the flash and the moving arc.

EXPERIMENT 3

The results of the previous two experiments showed that both the position of the flash and the position of the moving object were perceived shifted in the direction of motion, which suggested that the classic FLE may be the result of a combined mislocalization of the flash and the moving object. This experiment was aimed at measuring the FLE with a classic psychophysical procedure, so as to compare it with the VFL values obtained in Experiment 1 and Experiment 2.

Method

Participants

The same participants as those who had participated in Experiment 2 took part in Experiment 3. Experiment 3 was run after the Experiments 1 and 2. Informed consent was requested before the beginning of the experiment.

Stimuli and task

The stimuli were identical to those in Experiment 1, except that we used only one eccentricity (6.3°) and eight flash offsets (0.52°, 0.78°, 1.05°, 1.31°, 1.57°, 1.83°, 2.08°, 2.34°). The smaller offset step (0.26°), as compared to those in the previous experiments, was used to gain a better spatial resolution. By means of constant-stimuli method, participants judged whether the flash was leading or lagging the

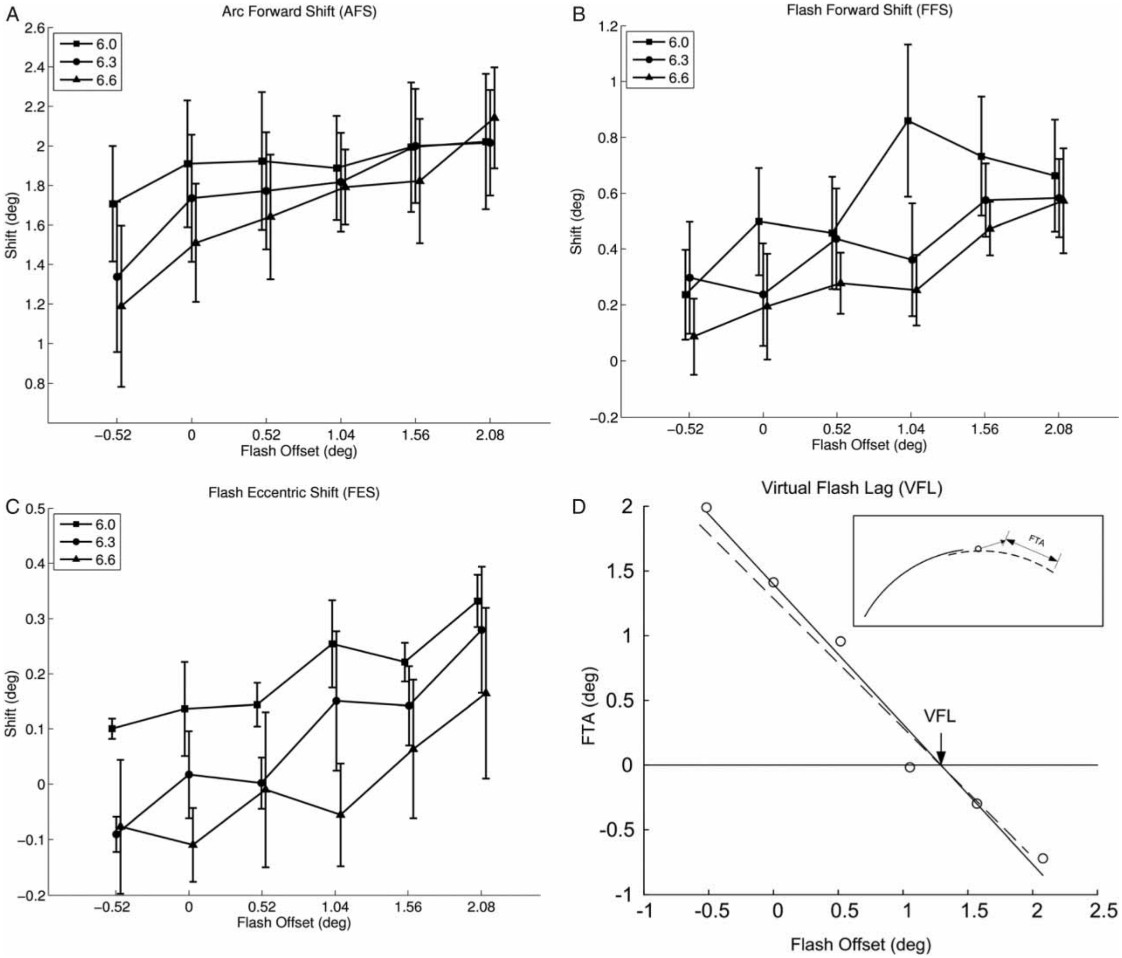

Figure 5. *Results of Experiment 2. (A) Mean arc forward shifts (AFS), grouped for flash eccentricity and plotted against flash offset. The error bars indicate the* SEM. *(B) As (A), but for flash forward shifts (FFS). (C) As (A), but for flash eccentric shifts (FES). (D) Virtual flash-lag (VFL) for the flash eccentricity = 6.3°. The circles represent the mean values of the perceived flash-to-arc distance (FTA, see inset) at each flash offset. The solid line is the regression line, and the dashed line denotes the theoretical constant flash-lag in the direction of motion (see text). VFL was estimated as the value of the flash offset at the zero-crossing of the regression line.*

head of the moving arc. The two responses "Flash is ahead" and "Flash is behind" were given by pressing the left or the right mouse buttons. A total of 240 trials (8 flash offsets × 30 repetitions) were administered to each participant.

Results and discussion

The psychometric curve for "flash is ahead" responses is plotted in Figure 6, together with the point of subjective equality (PSE). Each value is the mean of all observations for a given flash offset. Across subjects, the mean PSE was 1.49° ± 0.09 (range: 1.15° to 1.96°), which thus represents the offset that must be imposed to the flash to be perceived aligned with the moving arc—that is, the value at which the illusion is nullified. This value is taken as the size of the FLE.

Having defined the VFL as the flash offset at which the perceived position of the flash and the

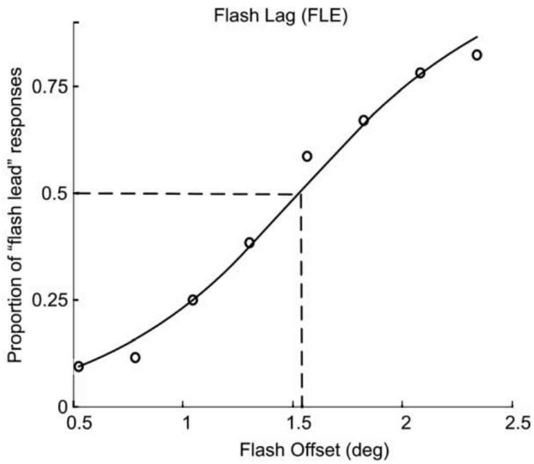

Figure 6. *The flash-lag effect (FLE). The psychometric curve of the experimental data obtained in Experiment 3 is plotted, together with the point of subjective equality (PSE).*

perceived direction of the arc correspond, we could compare the FLE directly with the values of the VFL at eccentricity = 6.3° obtained in the previous experiments (Figure 7). A one-way ANOVA did not reveal significant differences between FLE and VFL across experiments, $F(2, 31) = 0.411$, $MSE = 1.836$, $p = .667$. We also performed a paired t test in those participants who participated in both Experiments 2 and 3, and again there was no significant difference between the size of FLE and the VFL, $t(10) = -0.115$, $MSE = 0.701$, $p = .91$. These data showed that the VFL, obtained from either sequential or independent measures, corresponded to the perceptual FLE.

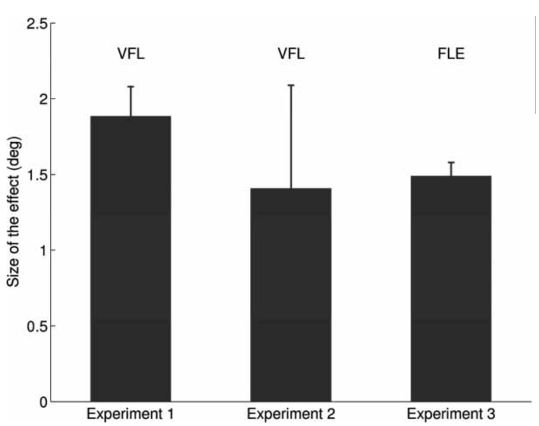

Figure 7. *Across-experiments comparison of the mean values of virtual flash-lag (VFL) and flash-lag effect (FLE). Data refer to the condition with eccentricity = 6.3°. The error bars indicate the* SEM.

GENERAL DISCUSSION

We found that the position of the moving arc at the time of the flash appeared shifted by about 2° of visual angle in the direction of motion. The flash was also shifted in the direction of motion, although to a lesser extent.

The size of the flash forward shift was about 25% (Experiment 1) or 30% (Experiment 2) of the size of the arc forward shift. The magnitude of these illusory mislocalizations varied as a function of the position of the flash relative to the arc. On average, a flash displayed behind the head of the moving arc was subjected to a smaller perceptual shift than that for a flash displayed ahead. The same general tendency for larger shifts of more forward flash offsets was seen for the arc. Importantly, by combining these mislocalizations into a quantity equivalent to the FLE (the VFL), we obtained an accurate estimate of the FLE, identical in size to the FLE measured with the constant-stimuli method in Experiment 3. Thus, although the flash appeared to lag relative to the moving stimulus, both the flash and the moving stimulus were reported to lead their physical position at the time of the flash.

Consider the common description of the FLE: When a flash is presented in physical alignment with a moving stimulus, it is perceived as lagging—hence the name, flash-lag. Yet, the size of the FLE is normally measured as the physical distance between the flash and the moving stimulus at which the illusion disappears (PSE). As long as there are no spatial asymmetries, this measure corresponds, also quantitatively, to the description of the FLE: When the flash is displayed aligned with the moving stimulus, the same lag arises. However, in the presence of FLE asymmetries in the motion direction, measuring the distance that nullifies the illusion is not equivalent to measuring the perceived spatial separation between the two stimuli when they are physically aligned. Our data suggest that the size of the flash-lag was fairly constant regardless of the flash offset in Experiment 2, but not in Experiment 1. In fact, in Experiment 2 the regression line of FTA was almost coincident with the theoretical line that represents a constant flash-lag effect (Figure 5D). In Experiment 1 there was instead a mismatch between the regression line and the theoretical, constant-flash-lag line. Thus, with independent flash and arc measures, the estimated flash-lag was constant along motion direction, while in the presence of the arc as a visual reference when locating the flash the estimated flash-lag became asymmetric—that is, smaller when the flash was displayed backward relative to the head of the moving arc than when it was displayed forward. This is reminiscent of other leading-trailing asymmetries induced by visual motion (Watanabe et al., 2003) or by smooth pursuit eye movements (Mitrani & Dimitrov, 1982; Tanaka, Yoshida, & Fukushima, 1998; van Beers, Wolpert, & Haggard, 2001; van Donkelaar, 1999; Van Donkelaar & Drew, 2002), or saccades (Ross, Morrone, & Burr, 1997), or even by invisible motion (de'Sperati & Deubel, 2006; Watanabe et al., 2003). The asymmetry that we found in Experiment 1 could be a sign that indeed there was an interference in estimating the flash position due to the presence of the arc in the visual display when locating the flash. This suggests that using visual references to study the flash-lag effect could introduce a positional bias. Conversely, Experiment 2 was closer to the traditional experiments on flash-lag, where no visual references are used. As a consequence, it would appear that the size of the flash-lag does not depend on the relative position between the flash and the moving stimulus.

Prima facie, our data seem to support quite directly the hypothesis that the moving arc underwent a form of spatial extrapolation, as originally suggested by Nijhawan (1994) to explain the flash-lag effect. Given the revolving speed, the amount of extrapolation corresponded to a delay of about 100 ms, which is in line with previous estimations (Nijhawan, 1994). However, we have no means of ascertaining where exactly participants saw the moving arc at the time of the flash. An alternative hypothesis to perceptual extrapolation would be that, due to the difficulty of judging the instantaneous position of a moving object (Whitney, 2002) and to the rather indirect judgement required of the participants in Experiments 1 and 2, participants added cognitively (for example, in imagery) a portion of trajectory, so that the AFS reflected a mixture of perceptual and cognitive processes. However, this explanation does not fit easily with the fact that the VFL predicted accurately the size of the FLE, which was measured with a classical psychophysical method. For the alternative hypothesis to hold, we should additionally admit that both the flash and the moving arc underwent the same distortion in a postperceptual stage, so as to maintain constant the spatial relationship between them. This could happen if, despite the instructions given in Experiment 1 and 2, participants judged the flash position always relative to the arc position (Eggert, Ditterich, & Straube, 2001), either perceived (Experiment 3) or cognitively mediated (Experiments 1 and 2): In this way, the same relative position would be preserved between the two visual objects, but only in the second case would a spatial shift be introduced afterwards. Despite being plausible in principle, this explanation seems at present a bit gratuitous, especially because in Experiment 2 the position of the flash was judged in independent trials.

Extrapolation has been suggested to occur within motor neuronal structures but not in the visual system (Kerzel & Gegenfurtner, 2003). The rationale of this proposal is that extrapolation would be needed for motor interceptive behaviour to successfully compensate for neural delays. By contrast, as long as our motor systems are capable to respond appropriately to moving stimuli, there would be no need for "online" extrapolation in visual perception, for its function is to build a representation of the world for "offline" cognitive elaboration. The observation that hand reaching, but not visual perception, codes the future position of a disappearing moving stimulus (Kerzel & Gegenfurtner, 2003) supports this hypothesis, but would seem at odds with the present data, as well as with the existence of the clear perceptual spatial shift of drifting Gabor patches (De Valois & De Valois, 1991) and with phenomena such as the representational momentum (Freyd & Finke, 1984; Hubbard, 2008). Another possibility is to posit that, somewhat similarly to the postdiction hypothesis (Eagleman & Sejnowski, 2007), extrapolation in the visual system is performed "on demand", when position needs to be extracted from motion, while it is an "intrinsic feature" in motor systems, because they must be able to respond very quickly to potentially useful or dangerous aspects of the visual world. If so, when motion disappears suddenly (as in Kerzel & Gegenfurtner, 2003), the visual system would have nothing to extrapolate any longer, while motor systems could still rely on their own online, automatic extrapolation procedure. Conversely, with ongoing motion a time marker such as a visual flash can start perceptual extrapolation, which is then incorporated in the final percept.

Due to important differences in the experimental conditions, stimuli, and tasks across studies, a comprehensive view accommodating the growing body of experimental results on the flash-lag effect still seems out of reach. One very basic problem is comparing heterogeneous measures of a given perceptual phenomenon (e.g., Bruno, 2001; Franz, 2001; Kerzel & Gegenfurtner, 2005). Using pointing movements is a simple way to measure localization errors. However, pointing movements are directed to only one object at a time, thus seemingly precluding the analysis of allocentric perceptual representations such as the FLE, which involve multiple objects. Yet, the fact that we were able to decompose the FLE into its constituents encourages the use of pointing measures, which could be fruitfully associated to more traditional psychophysical measures of FLE. Furthermore, if localization errors are probed by means of rapid, open-loop pointing movements (e.g., saccades), in the future it could become possible to reveal not only the static spatial map of FLE, but also its temporal evolution. In fact, motion-induced localization errors in the saccadic system take up to a few hundred milliseconds to build up, a time that may be necessary for the coherent, final percept to stabilize (de'Sperati, Grimoldi, Baud-Bovy, & Jacomuzzi, 2006). Saccades may thus represent a precious tool to sample the passage from the motor map to the perceptual map of FLE in the subsecond range.

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