The spatial pattern of peri-saccadic compression for small saccades

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In the temporal vicinity of a saccade onset, visual stability is transiently disrupted and briefly flashed visual stimuli undergo a systematic perceptual mislocalization. Specifically, when a stimulus is flashed around saccade onset, localization judgments are grossly biased toward the saccade endpoint. This peri-saccadic compression increases with saccade amplitude. Previous studies of peri-saccadic compression have typically used rather large saccade amplitudes. In the present study, we investigate systematically the pattern of errors for small saccade sizes (2°–10°), taking into account both the amplitude of the saccade and the position of the flashed stimulus (11 positions tested from 1 to 12°). Our results show a weaker compression effect for the smallest saccades. Moreover, we found that the strength of the compression depends on both stimulus side and relative distance to the saccade target.

Keywords: small saccade, mislocalization, compression

Citation: Lavergne, L., Vergilino-Perez, D., Lappe, M., & Doré-Mazars, K. (2010). The spatial pattern of peri-saccadic compression for small saccades. *Journal of Vision, 10*(14):17, 1–12, http://www.journalofvision.org/content/10/14/17, doi:10.1167/10.14.17.

Introduction

Previous studies have shown that a stimulus flashed around the onset of a saccade is systematically mislocalized (see Schlag & Schlag-Rey, 2002, for a review). This fact has often been linked to mechanisms that combine visual signals with eye position signals to maintain perceptual stability across saccades. Two components underlie this mislocalization: a uniform shift of localization in the direction of the saccade and a "compression" of localization toward the saccade endpoint, i.e., a trend to localize the stimulus closer to the saccade endpoint than it really is. Indeed, when visual references are available, a stimulus flashed spatially before the saccade target is displaced in the direction of the saccade whereas a bar flashed spatially beyond the target is displaced in the opposite direction (e.g., Lappe, Awater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997). This peri-saccadic compression has been investigated by manipulating visual characteristics of stimuli such as contrast (Michels & Lappe, 2004), color (Lappe, Kuhlmann, Oerke, & Kaiser, 2006), luminance (Georg, Hamker, & Lappe, 2008), or by manipulating the modality of the localization report: verbal reporting of the position or the number of bars (Awater, Burr, Lappe, Morrone, & Goldberg, 2005; Matsumiya & Uchikawa, 2001; Morrone, Ross, & Burr, 1997), manual pointing (Bruno & Morrone, 2007), mouse pointing (Lappe et al., 2000; Ostendorf, Fischer, Finke, & Ploner, 2007; Reeve, Clark, & O'Regan, 2008), or saccade targeting (Awater & Lappe, 2006; Lappe, Michels, & Awater, 2009).

Although saccadic compression is a quite robust phenomenon, visual or motor factors can impact its strength. This includes the absence or presence of visual references (Lappe et al., 2000), stimuli contrast (Michels & Lappe, 2004), luminance adaptation state (Georg et al., 2008), and saccade amplitude (Kaiser & Lappe, 2004). This latter point is of particular interest for our study. Kaiser and Lappe (2004)

doi: 10.1167/10.14.17 Received April 14, 2010; published December 14, 2010 ISSN 1534-7362 © ARVO

showed that the magnitude of the mislocalization increased with saccade amplitude when they flashed a dot at various positions around the onset of 12° to 24° saccades. This effect was recently replicated by Richard, Churan, Guitton, and Pack (2009) with 14° to 30° saccades but modulated by the flashed stimulus position.

Besides these results on quite large saccades, it is not clear what happens for smaller saccades. Few studies have used small saccades and there is no consensus about the size of the effect expected with such saccades. Morrone et al. (1997) flashed a bar at random positions between −5° and 5° from screen center while subjects executed 2.5° saccades from −1.25° to 1.25°. Shortly before saccade onset, they found a compression pattern as bars were localized closer to the target than they were presented. However, no compression pattern was found in other studies in which saccades of 10° or less were used. Brenner, Mejer, and Cornelissen (2005) asked subjects to execute 5° saccades toward a jumping dot while two stimuli were briefly flashed. The reported location of these stimuli did not show a compression pattern. Reeve et al. (2008) asked their subjects to execute 10° saccades and to report either the location or the separation between two flashed bars. They showed a compression pattern on location but not on separation trials. One reason they discussed to explain their results was a too small saccade size. Awater and Lappe (2004), who used a 7° amplitude, found a weaker effect of compression than in previous studies with larger amplitudes and also suggested smaller saccade amplitude (7°) as a possible explanation. They further suggested that the strength of compression could also depend on the distance between the saccade target and the localization bar (3.5° in their experiment) with bars further from the target showing stronger compression. However, this alternative does not seem to fit with the results of Morrone et al. (1997) who found a clear compression pattern for 2.5° saccades when bars were flashed at a maximal distance of 3.75°. Richard et al. (2009) systematically tested the influence of both saccade amplitude and bar position for saccades of 14°, 20°, and 30° and showed that the influence of saccade amplitude on compression strength could be modulated by bar position. More precisely, for 20° and 30° saccades, they showed different patterns of compression depending on whether the bar's absolute position (i.e., relative to fixation cross) or relative position (i.e., relative to saccade target) was held constant. Whereas they showed a general increase of compression from 10° to 20° and to 30° saccades with equidistant bars to the target, they showed that when absolute bar position was held constant, compression decreased from 10° to 20° when bars spatially before the target were considered.

None of these studies had been specifically designed to analyze what happens for small saccades. Since small saccades are the prevailing type of saccade in everyday behavior, it is important to know whether similar compression effects exist for them as for large saccades. We thus conducted a study to clarify (1) whether saccadic compression does exist for very small saccades, i.e., for saccades shorter than those usually studied (2 to 10°) and (2) whether the distance of the flashed stimulus relative to the saccade target has any influence on the strength of compression.

Methods

Participants

Five subjects with normal or corrected-to-normal vision participated in the experiment. Three were authors, two were naive: one was familiar with eye movement recording and the other was familiarized with the eye tracking procedures before the experiment with a 70-trial session in which a saccade target was presented at a random position and to which the subject had to saccade. All gave their informed consent prior to starting the experiment, which was carried out according to the ethical standards of the Declaration of Helsinki (2004).

Instruments and eye movement recording

The experiment was conducted in a dimly lit room. Subjects were seated 57 cm away from the screen and their head kept stable with a submaxillar dental print and forehead rest. The stimuli were presented on an Iiyama HM240DT monitor with a refresh rate of 170 Hz and a resolution of 600 × 800 pixels. Eye movements were monitored by a Bouis oculomotor system (Bach, Bouis, & Fischer, 1983), with an absolute resolution of 6 arc minutes and a linear output over 12° of visual angle. Viewing was binocular, but only the movements of the right eye were monitored. Signal from the oculometer was sampled every 2 ms. Saccades were detected with an in-house program using Labview 7.1 by velocity (>40° s^{-1}), acceleration (>3000° s^{-2}), and minimal displacement (0.15°) thresholds. The detection occurred with a maximum delay of 5 ms (the duration of a 2° saccade is around 25 ms).

Stimuli

As shown in Figure 1, stimuli were displayed on a gray background (mean luminance: 5 cd m^{-2}).

Saccade targets ("STs") consisted of a white square (0.5° × 0.5°; luminance: 26 cd m^{-2}) displayed at various positions (2°, 3°, 4°, 5°, 6°, 8°, or 10°) right to the fixation cross (0.5° × 0.5°), which was displayed 6° left from the screen center on the horizontal meridian. The localization target ("LT") was a vertical green bar that was as high as the screen (0.3° × 27°; mean luminance: 4 cd m^{-2}) and that could appear at one out of 12 different positions (every degree between 1° and 12°). However, the LT

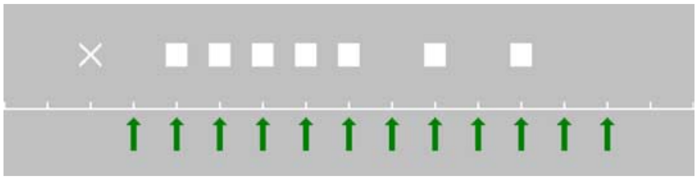


Figure 1. Spatial characteristics of stimuli. Seven possible positions at which the ST (0.5° × 0.5° white square) could be displayed in a trial (2, 3, 4, 5, 6, 8, 10°). Green arrows represent the position at which the LT could be flashed in a trial (every degree between 1 and 12° except target position).

could never be at the same location as the ST, so for one ST, the LT could only appear at 11 possible positions. In line with previous studies on compression, a ruler, i.e., a white horizontal line, with vertical tick marks (0.1°) every degree, was displayed during the entire trial 1° below the ST and initial fixation cross positions.

Procedure and design

The experiment was divided into 30 blocks. Within a block, each experimental condition was presented twice (7 ST × 11 LT) in random order. The design was a 7 × 11 factorial design in which LT position was different for each of the 7 STs. Each block began with a full calibration procedure during which subjects had to saccade to five bars presented successively from left to right in steps of 3°. Reference measures were taken for each of the 5 bars. If the variability of each measure was below a threshold (0.4 V) and if they were linear, the calibration was considered successful and the experiment started. Calibration was checked at the beginning of each trial: a bar appeared 6° left from the center of the screen and subjects had to fixate it. If the recorded value was different from full calibration (±0.1°), the calibration was automatically renewed.

When successful fixation was detected, the initial fixation cross was presented at 6° left from the center of the screen, indicating the beginning of the trial (see Figure 2). After a brief period of fixation (600–1500 ms, random), the initial fixation cross disappeared and the ST was shown for 50 ms at a random position among 7 possible ones (see Stimuli section). The subject had to execute a saccade toward the ST. At an unpredictable time after ST extinction (the inter-stimulus interval was calculated individually on the basis of mean saccade latency in the previous block to be between −100 and +100 ms of saccade onset), the LT was flashed for 5 ms at one of the 11 possible positions. After 1100 ms, a mouse pointer appeared between 1° and 12° right from initial fixation cross, 2° below the ruler. Subjects were asked to report the perceived position of the bar by mouse click and could freely move their eyes at this point. When the LT was not perceived at all, the subject had to click on a pre-defined area (top left of the screen) and the trial was discarded from further analysis. In each trial, only one saccade target and one bar position was shown. Subjects performed 4620 trials, distributed in 30 blocks of 154 trials.

Data analysis

Blinks (0.3%) as well as all trials in which the latency of the saccade was not between 80 and 800 ms (2.4%), the saccade amplitude was below 1° (1.1%), the bar was not perceived (1.7%), or the time to saccade onset was outside the period of interest (5.2%) were excluded from further analysis. A total of 10.7% of data was excluded.

Results

Saccade latencies and landing positions

The data in Table 1 present mean saccade latency and position for each ST averaged across the 11 LTs. LT

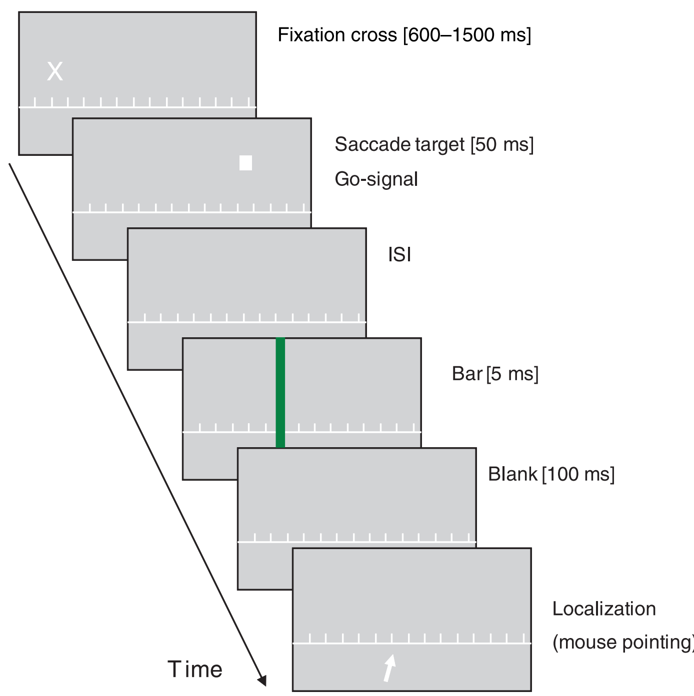


Figure 2. Temporal characteristics of a trial. At the beginning of each trial, the subject fixated a cross 6° left of the sagittal plane. After a random time between 600 and 1500 ms, the fixation cross disappeared (go signal for the saccade) and the saccade target appeared for 50 ms at one of 7 possible positions right to the fixation cross. After a random inter-stimulus interval (ISI), a vertical bar (LT) appeared at one of 11 positions for one video frame (5 ms); 1100 ms later, a pointer appeared with which subjects reported the LT position they perceived.

ST position	2°	3°	4°	5°	6°	8°	10°
Latencies (ms)	189 (25)	184 (14)	182 (10)	183 (10)	184 (9)	189 (11)	194 (13)
Landing positions (°)	1.6 (0.2)	2.4 (0.3)	3.2 (0.3)	4.0 (0.2)	4.9 (0.2)	6.7 (0.5)	8.4 (0.8)

Table 1. Characteristics of saccades: Mean latencies (milliseconds) and landing position (degrees) as a function of saccade target positions. Values in brackets are standard deviations.

position did not affect mean saccade latency ($F(11,44)$ = 1.07, ns) or mean landing position for each ST (all Fs, ns). As expected, ST position had no effect on saccade latency ($F < 1$; mean value = 186 ± 4.3 ms, see Table 1 for details) but significantly affected saccadic landing positions ($F(6,24) = 214.9$, $p < 0.0001$).

Overall perceived position patterns

Individual mean LT perceived positions were computed as a function of time, for each 7 ST × 11 LT condition, in 25-ms bins. Mean results over all subjects are plotted in Figure 3.

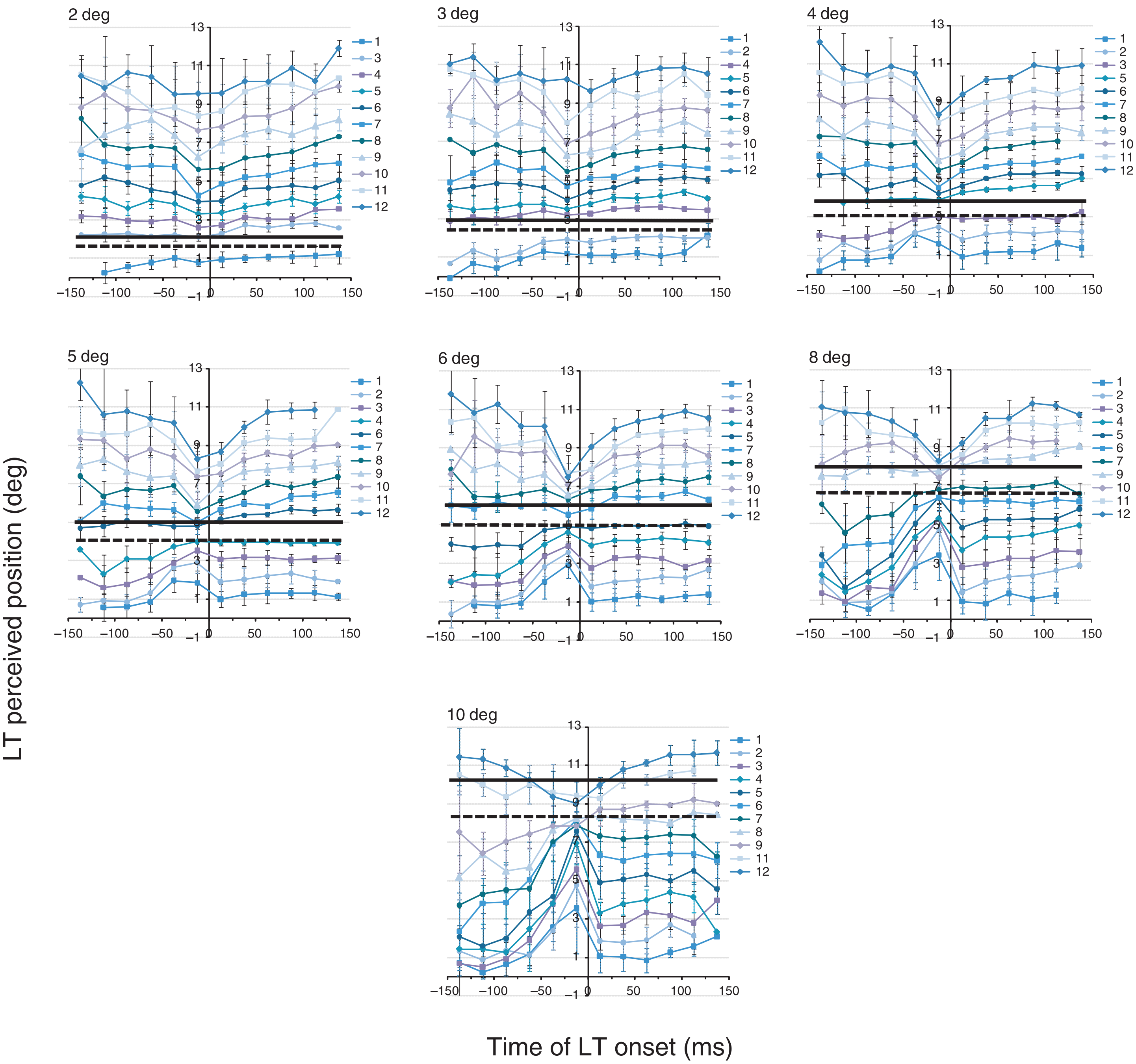
A pattern of compression of LT localization judgments emerges for all STs. That is, LTs are mislocalized in the direction of the saccade when presented left of the ST, i.e., spatially before the ST, and in the direction opposite from the saccade when presented right of the ST, i.e., beyond the ST. As in other studies, localization error size (i.e., the difference between perceived positions long before and after a saccade when compression does not occur and near saccade onset when it does) is maximal between 25 and 0 ms before saccade onset. For each ST, LTs that are more distant from ST are more mislocalized than the LTs that are closer to the ST. As expected, the strength of compression (i.e., the maximal error of localization) decreases with saccade size (i.e., ST). Note however that LTs are rather compressed toward the saccade landing position that slightly undershoots real ST position. This is particularly clear for 8° and 10° ST positions and is in accordance with the results of Awater et al. (2005) and Awater and Lappe (2004).

Effect of saccade size

Compression strength

In line with previous studies, we computed individual compression indexes (e.g., Awater & Lappe, 2004; Lappe et al., 2000) in order to examine the effect of saccade size on compression strength. For a given saccade target, the compression index is defined as the standard deviation across all mean perceived LT positions when localization error size is maximal (i.e., when compression is maximal), normalized to the standard deviation across LTs when no compression occurs (i.e., baselines of perceived position outside the temporal window of compression). For each subject, maximal localization error for each LT was defined as the smallest or highest value of localization when the LT was presented spatially before or beyond ST, within the critical period when compression is known to occur ([−75; 0 ms] to saccade onset). Following the same rationale, the same LT's baseline was defined as the individual trial-weighted mean value of localization within periods when compression is known not to occur ([−150; −100 ms] and [100; 150 ms] to saccade onset). This index is thus close to 0 when compression is maximal (i.e., all LTs seen at the same position) and increases when compression decreases. Figure 4A plots the mean compression index for each ST. We conducted an ANOVA on compression index with ST position as a within-subject factor. For 2° to 8° ST, the value decreases from 0.79 ± 0.12 to 0.45 ± 0.06 indicating that compression strength increases with saccade size ($F(6,24) = 12.43$, $p <$ 0.00001). Unexpectedly, the index increases between 8° and 10° ST (0.44 to 0.55 ± 0.11, respectively, $F(1,4)$ = 833.14, $p = 0.0001$), indicating a decrease of compression strength. This seemed paradoxic because the localization data (see Figure 3) seem to show the opposite: overall size of the error appears larger in the 10° compared to the 8° condition.

To better understand this unexpected finding, we restricted the analysis to localization errors of the 2 LTs symmetrically equidistant from 1° or 2° to each ST, i.e., the two immediately before the ST (−1° and −2° relative to ST) and the two immediately beyond ST (+1° and +2° to ST). Indeed, previous studies (e.g., Awater & Lappe, 2004; Richard et al., 2009) suggested an influence of LT–ST distance on compression strength. Note that the analysis could not be conducted for the 2° ST as there was only one LT spatially before ST. This way, for each 3° to 10° ST, the compression index was calculated on the same basis as described earlier but only across 4 different—equidistant—LTs. As shown in Figure 4B, index value now continuously decreases (ANOVA conducted on the compression index with the saccade target position as a within-subject factor: $F(5,20) = 15.43$, $p < 0.00001$), indicating an increase of compression strength with saccade size, which is coherent with patterns of localization presented in Figure 3. Maximal mislocalization (i.e., minimal index value) occurred in the 25-ms bin, i.e., in the time between 0 and 25 ms before saccade onset for all saccade targets (see Figure 4C). No temporal difference appeared between STs, but a general effect of saccade amplitude, as already shown in Figure 4B, can be seen. However, the binning of our data leaves the possibility of small differences in timing. Indeed, our experiment was designed to examine the size of the effect, not its temporal



Bin	Mean	Range	Bin	Mean	Range	Bin	Mean	Range
–150 ; –125	10	(8–18)	–50 ; –25	60	(51–64)	50 ; 75	54	(46–57)
–125 ; –100	20	(15–24)	–25 ; 0	62	(53–68)	75 ; 100	48	(41–59)
–100 ; –75	44	(38–51)	0 ; 25	67	(53–73)	100 ; 125	29	(22–39)
–75 ; –50	62	(51–69)	25 ; 50	68	(60–75)	125 ; 150	13	(3–49)

Figure 3. Mean LT perceived positions as a function of time relative to saccade onset. Data are presented in 25-ms bins. Each graph corresponds to an ST, and each curve corresponds to one bar position. Each continuous black line represents the ST position, and each dashed black line represents the mean saccade landing position. The table below the figure plots the mean number of trials and range (averaged over STs and LTs) per bin for a single subject and a given ST.

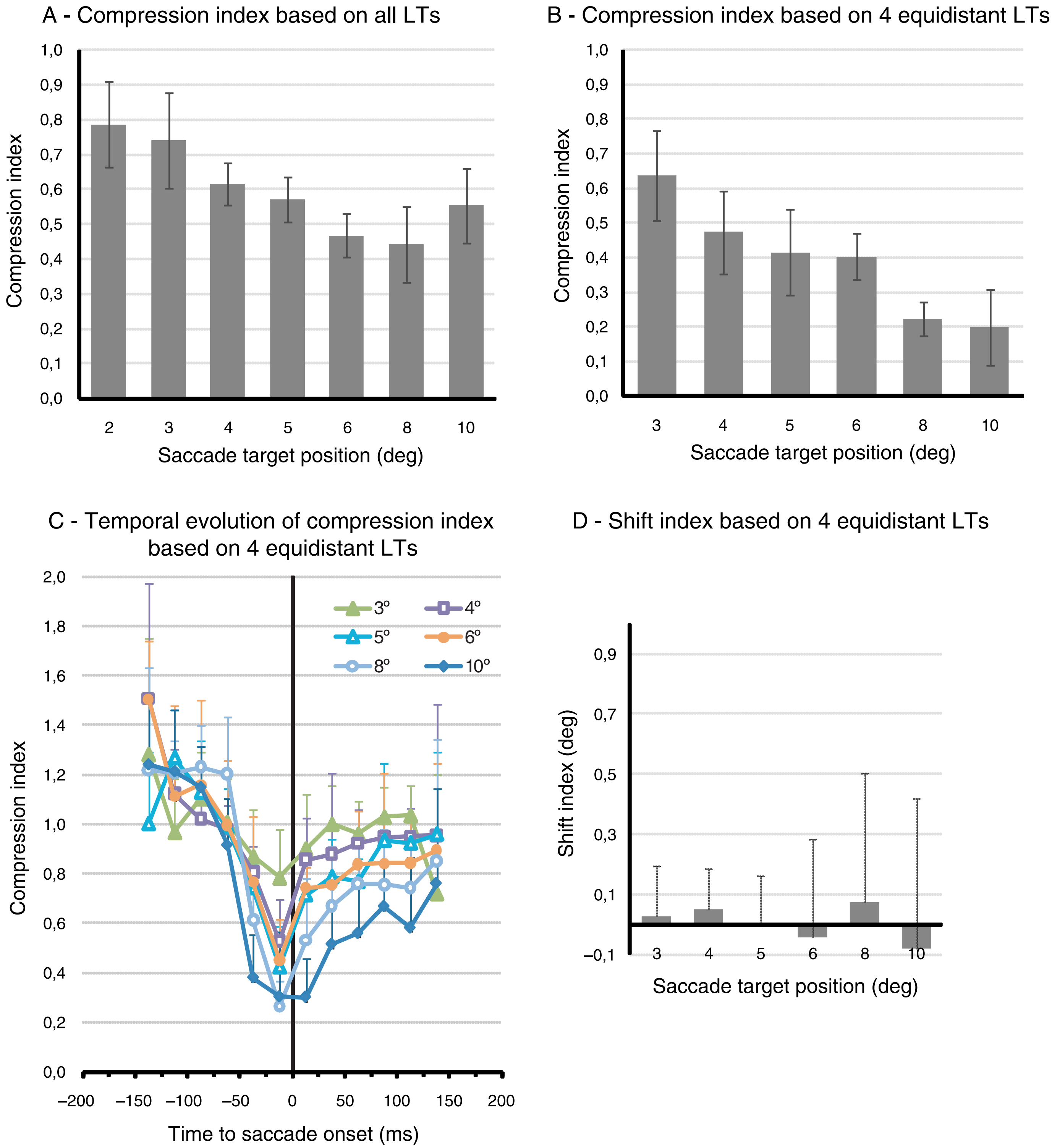


Figure 4. Mean compression index across all subjects for each ST position, calculated (A) over all 11 absolute LT positions and (B) over 4 LTs equidistant to ST position. (C) Temporal evolution of compression index based on 4 equidistant LTs. Data are presented in 25-ms bins and one curve corresponds to one saccade target. Compression indexes that are higher than 1 are due to the heterogeneity between localization values in the two temporal windows used to calculate the LT baseline value of the index (i.e., [−150; −100 ms] and [100; 150 ms] to saccade onset). (D) Mean shift index across all subjects for each ST position calculated over 4 LTs equidistant to ST position. For all figures, vertical thin or dashed lines represent standard deviations.

properties. Examining the temporal aspect would have needed more than 60 trials per condition, with a more systematical inter-stimulus interval larger than the small time window that we used.

Shift strength

Peri-saccadic mislocalization is composed of two effects, compression and a uniform shift. The relative contributions of these two effects to the mislocalization vary between different experimental settings. In order to examine the contribution of the uniform shift on the mislocalization pattern in our data set, we computed a shift index for each ST, which is defined as the difference between the mean perceived position of the 4 equidistant LTs (i.e., −2°, −1°, +1°, +2° relative to each ST) when mislocalization is maximal and to the mean perceived position of the same LTs when no compression occurs, i.e., baselines of perceived position more than 100 ms before or after the saccade (e.g., Awater & Lappe, 2004; Lappe et al., 2000). As shown in Figure 4D, the shift strength did not depend on saccade size (ANOVA with ST position as a within-subject factor: $F < 1$) and was quite small (0.03 ± 0.04°) in our experiment. The small values that we obtained for the shift index might partly be due to differences in the localization baselines between before and after the saccade. However, even compared to only the pre-saccadic baseline (100 ms before saccade onset) or only the post-saccadic baseline (100 ms after saccade end) the shift did never exceed 0.8°, even for the largest saccade amplitudes. The small values of shift can also be linked to the fact that our shift index is computed on the basis of the four equidistant bars (i.e., −2°, −1°, +1°, +2° relative to each ST). So, the shift, computed as the difference between mean perceived position when compression is maximal and when no compression occurs, is necessarily small with these localization bars. In other studies, such as Lappe et al. (2000) for instance, where a 2° shift has been found, bars used for the computation were between 3.6° and 9° distant from the ST. Thus, the data in this experiment are strongly dominated by the compression and show only a small uniform shift.

Effect of bar position

Absolute errors

Figure 5 plots absolute errors of localization, defined as the difference in degree between perceived positions when compression is maximal and when compression does not occur (i.e., baselines of perceived position outside the temporal window of compression). The error is minimal when the LT is close to the ST and gradually increases (considering LT side: before vs. beyond ST) with distance to the ST until a certain extent. Indeed, when LTs become too distant from ST (further than 5° for LTs before ST and further than 8° for LTs beyond), error size decreases again.

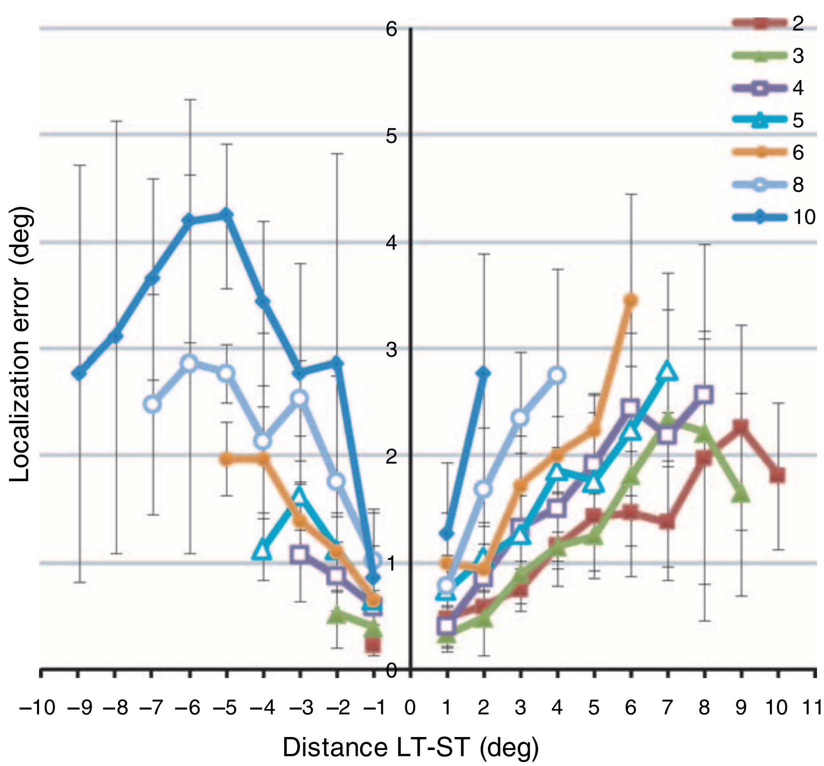


Figure 5. Mean maximal absolute errors of localization, over all subjects, as a function of LT–ST distance. Each curve corresponds to a single ST. Thin lines correspond to standard deviations.

Note also that the overall effect of ST position described in the Effect of saccade size section can be observed on the curves, as these are organized in a superimposed manner, from the smallest saccade size (ST = 2°) to the largest one (ST = 10°).

Relative errors

However, the absolute error pattern does not take into consideration how far the LT is initially perceived from the ST. To estimate the relative compression, we calculated, for each LT position, individual compression rates that express the absolute localization error (see previous section) as a percentage of the perceived distance between the LT and the saccade landing position when no compression occurs (i.e., distance between LT baseline and saccade landing position). Thus, greater compression rate represents greater strength of mislocalization. For example, a rate of 0% indicates no compression (the LT is perceived at its baseline position) whereas a rate of 100% indicates that the bar is perceived at the same location as the saccade landing position[1] and thus a maximal compression. We have chosen to relate distance to the saccade landing position rather than to the ST (as in Richard et al., 2009) because compression occurs toward the saccade endpoint (see Overall perceived position patterns section). Using the landing position is necessary for our analysis because of the very small distances involved in our experiment (compared to other studies). When we instead took the ST position as a reference, in some conditions nonsensical negative compression rates occurred. Mean values of compression rate calculated as percentages of the LT-landing point distance are presented in Figure 6. They are plotted as a function of the LT–ST distance since we wanted to see how the distance to the saccade target influences compression. Note that instead of plotting the rate as a function of the distance between LT and ST one could plot the rate as a function of the distance between the landing position and the LT. Doing this led to the same pattern of results (not shown). However, such a choice would have led to different distance LT-landing position between STs and would have prevented us from any possible analysis of variance.

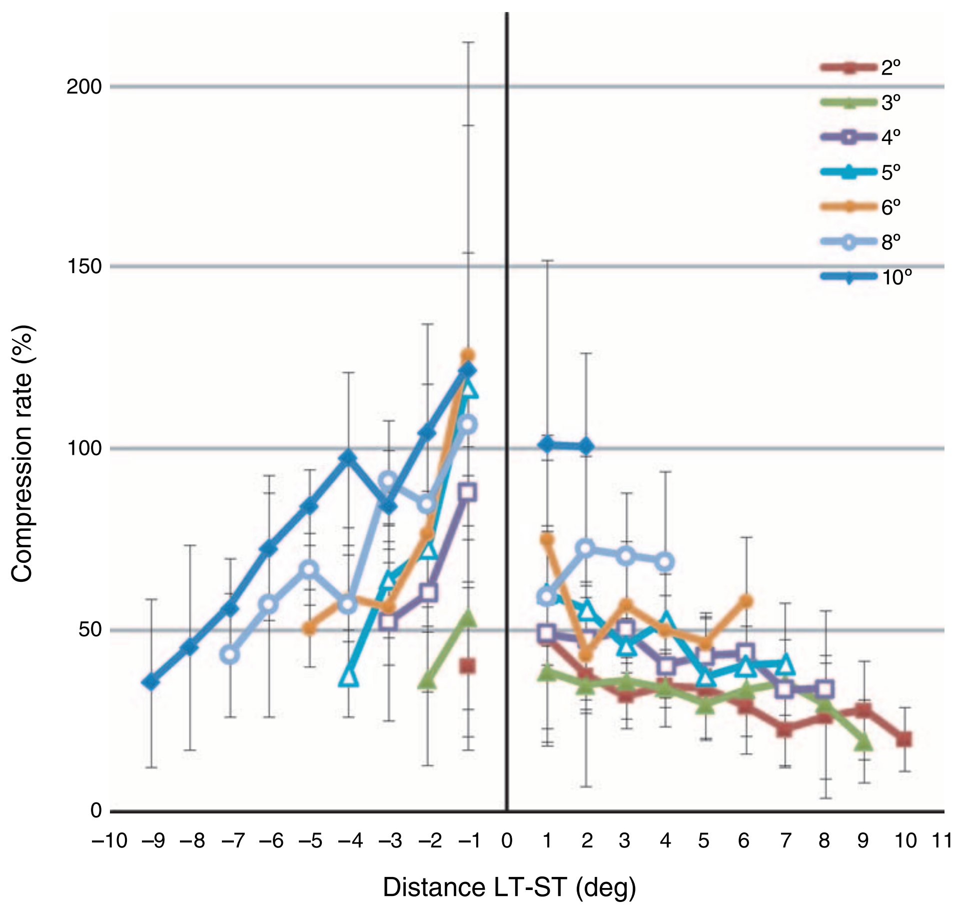


Figure 6. Mean compression rates (i.e., relative error rates) over all subjects, as a function of LT–ST distance. For LTs located beyond the ST, the rate is calculated as follows: (BL − *M*) / (BL − LP) with BL = baseline localization value; *M* = localization value when compression is maximal; LP = saccade landing position. Opposite values of numerator and denominator are taken for bars before ST. Each curve corresponds to a single ST position. Thin lines correspond to standard deviations.

ST position	LTs before ST	LTs beyond ST	Student's *t*-test
4°	17.9 (19.5)	−3.4 (2.3)	$t(4) = 2.83; p < 0.03$
5°	28.6 (20.7)	−4.4 (4.2)	$t(4) = 2.43; p < 0.04$
6°	16.7 (14.2)	−2.6 (3.4)	$t(4) = 2.08; p = 0.05$
8°	9.6 (5.4)	−4.3 (3.9)	$t(4) = 3.02; p < 0.02$

Table 2. Mean slopes resuming the linear alignment of compression rate on LT values by side (before vs. beyond) and ST position, and one-sided Student's *t*-test values (Student's *t*-tests were computed on absolute slope values). Values in brackets are standard deviations.

Figure 6 shows that, for all STs, compression decreases with the increasing LT–ST distance. However, compression seems to decrease more strongly for bars located before the ST rather than for bars presented beyond the ST. We conducted statistical analyses in order to test this asymmetrical aspect of the distribution. We considered only data from saccade amplitudes of 4° to 8° so that we had at least 3 data points before and beyond each ST. We tested, for each side of each ST, the effect of LT–ST distance (as within-subject factor) and the linear adjustment of the compression rate along the LT–ST distance by specific comparisons. Linear trend significantly fitted the data for 4° and 5° STs for LTs beyond and before ($p \leq 0.05$ for all). Concerning 6° and 8° targets, the linear trend significantly fitted the data for LTs before ($p \leq 0.05$ for both) but only marginally for LTs beyond ($p < 0.09$ and $p < 0.07$, respectively). Slopes of linear regressions for compression rate values were determined for each side of each ST and statistical comparisons between LT sides were performed by one-sided Student's *t*-tests. Results plotted in Table 2 showed an effect of side for each ST, with greater slopes for LT presented before rather than beyond the ST.

Considering the increase of mislocalization with saccade size described in the Effect of saccade size section, we again observed that compression increases with saccade size since the upper curves correspond to largest ST positions and the lower ones to smallest ST. To replicate the effect of saccade size (ST position), we ran an ANOVA on compression rates, with LT side and ST position as within-subject factors, for STs between 4 and 8°. Note that due to the asymmetrical repartition of LT on both sides of each ST, compression rate was individually averaged over the 3 LTs immediately before and beyond ST. Results showed a significant effect of both factors (ST position: $F(3,12) = 6.56$; $p < 0.008$; LT side: $F(1,4) = 4.22$, $p = 0.05$), with no interaction ($F < 1$).

Discussion

We have presented a detailed analysis of peri-saccadic compression for saccades of small amplitude. We found that peri-saccadic compression occurs and can be measured even for very small saccades (2° amplitude) and that it increases in strength with saccade amplitude over the range of 2° to 10°. These results are in line with previous studies using larger amplitude saccades and a report by Morrone et al. (1997) for saccades of 2.5°. Furthermore, our results show that compression strength is modulated by the location of the stimulus with respect to the saccade target position. When considering the absolute localization error, compression increases with the distance to the ST in a symmetrical manner on either side of the ST, up to a maximum at a certain distance from the ST. When the stimulus is too far away from the ST, compression decreases again. When, alternatively, considering the relative compression as a percentage of the distance of the localization target from the ST, compression strength is highest for the closest stimuli and decreases with distance to the ST. Moreover, the relative compression rate differed depending on whether the stimulus was placed spatially before or beyond the ST. For a given saccade target, the increase in compression with shorter LT–ST distances was more pronounced for bars presented before compared to bars presented beyond the ST.

Effect of saccade amplitude on compression

The pattern of results observed in our study is coherent with Kaiser and Lappe (2004) who showed an overall greater amount of error for larger saccades, i.e., a greater strength of compression, and with Richard et al. (2009) who showed in their first experiment that when the index of compression is calculated over bars at the same relative position for each saccade target, its value decreases (mislocalization increases) with saccade amplitude. This was less pronounced in their second experiment, when the index is calculated over bars at the same absolute position.

Recent models have attributed the compression effect to the interaction between motor and visual signals. Hamker, Zirnsak, Calow, and Lappe (2008) have proposed a model in which they explained compression errors toward saccade endpoint by the motor feedback signal of the saccade that modulates processing in visual areas. In this model, the feedback of the upcoming saccade enhances the activity in visual maps at the upcoming saccade landing position, leading to a biased location judgment toward the saccade landing position as the saccade is about to start. The feedback signal acts in retinotopic visual maps and would be broader for smaller saccades thus leading to a weaker bias toward the saccade endpoint. A weaker bias for smaller saccades could also result if the feedback strength, rather than the feedback width, depends on saccade amplitude. Indeed, our results can also be linked to those of Ostendorf et al. (2007) who showed a positive correlation between compression strength and saccade peak velocity for 10° saccades. In our study, we could have expected such a covariation as peak velocity increases with saccade amplitude. Ostendorf et al. suggest that compression strength varies with the strength of the motor command. This is supported by neurophysiological findings. For instance, Anderson, Keller, Gandhi, and Das (1998) showed that firing rates of build-up neurons in the superior colliculus of monkeys increases with saccade amplitudes. An increase of the feedback signal could also be explained by the increase of average firing rates of burst-up neurons in the superior colliculus with saccadic peak velocities (Waitzman, Mas, Optican, & Wurtz, 1991).

Strength of compression depends on localization target position

In absolute coordinates, an LT that is close to the ST is less compressed than an LT that is further away, but only up to a certain extent: when the LT is too far from the ST, compression decreases again. These results are in line with Awater and Lappe (2004) who found weak absolute compression for LTs close to the saccade target for a 7° saccade. This weak compression would be expected since closer bars have less chance to be subject to absolute errors.

However, the relative errors pattern described in the Relative errors section shows that the mislocalization is more coherent when expressed in relative terms. In this section, we have shown that when the mislocalization is related to the perceived distance of the LT from the ST, compression is larger for the closest ones and systematically decreases with the LT–ST distance. Our results also showed an effect of LT side in relative coordinates, suggesting an asymmetric pattern of error depending on whether the stimulus is flashed before or beyond the target. The increase of compression with the decrease of the LT–ST distance seems sharper for bars located spatially before the target in relative coordinates. These results are in line with those of Richard et al. (2009) calculated with an index very similar to our compression rate. If we consider their smallest saccade amplitude condition (14°), the LTs in that study could be flashed at different distances from their ST (approximatively −14°/−8°/−7°/−6°/+7°/+14°/+20°/+26°). Richard et al. found a larger compression for bars flashed before the ST than beyond the ST and largest compression for smallest LT–ST distances.

Our asymmetric mislocalization pattern could result from the combination of two processes: a compression of localization toward saccade endpoint (Lappe et al., 2000; Ross et al., 1997) and a uniform shift in the direction of the saccade (e.g., Cai, Pouget, Schlag-Rey, & Schlag, 1997; Honda, 1989). Whereas the mislocalization of LTs flashed beyond the target clearly reflects the effect of compression, the mislocalization of LTs presented spatially before the ST could be the result of a combination of both mechanisms. However, our calculation of the shift index in the time around saccade onset revealed only a rather small shift in our experiment, suggesting that its contribution to the asymmetry may be only minor.

The asymmetry may, alternatively, be related to the interaction between the properties of the retinotopic maps in which the stimuli are encoded and the oculomotor feedback that biases the visual representations in these maps, as proposed by recent modeling studies. According to these studies, the spatial distribution of mislocalization in compression experiments depends on the cortical magnification in retinotopic maps (Hamker et al., 2008; Richard et al., 2009; Zirnsak, Lappe, & Hamker, 2010). The LT–ST distances encoded in these maps become smaller as the LT becomes more peripheral, i.e., as the LTs moves from before to beyond the ST. Moreover, the oculomotor feedback signal of the upcoming saccade modulates the activity on these maps by boosting the activity of the cells coding for the future saccade landing position. These models assume that the feedback signal gradually decreases with distance from the saccade target. Cells from visual space that are located closer to the saccade target are subject to stronger modulations than cells that are located further from the feedback center. Space compression is then caused by this local gain increase that acts on retinotopic maps that are themselves subject to the cortical magnification. Considering these mechanisms, we can explain our pattern of compression as follows: the cortical magnification can be responsible for the greater compression obtained for LTs flashed before than beyond the saccade target; the stronger gain increase of activity linked to the feedback signal can explain the greater compression for LTs close to the ST. Then, the asymmetrical pattern found in our study would be induced by the combination of these two mechanisms.

Compression and small saccades

Our study clarifies what can be expected for the compression effect on small saccades. We confirm that compression does exist for such small saccades but is much weaker than for larger ones. The best way to apprehend compression for such saccades is to flash stimuli that are not too distant from the target, as both absolute and relative errors decrease for farthest LT in our results. Regarding the absolute error, which is very often considered in studies, bars should be at least 4° beyond the target for smallest saccades (2–4°), in order to get an effect of at least 1°. The maximal effect would be for stimuli around 7°. Moreover, our study shows that when working with small saccades, relative errors should be considered, i.e., errors that take into account the distance between the LT and the saccade landing position. Indeed, an asymmetric pattern of compression depending on the LT side and distance relative to the saccade target emerges with relative but not with absolute errors.

Acknowledgments

The authors wish to thank Sylvain Haupert and Eric Orriols for their assistance in developing the experimental software and the two anonymous reviewers for their helpful comments.

Commercial relationships: none.
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Footnote

[1]Compression rates higher than 100% correspond to an error of localization that overpass the landing position of the eye, i.e., that is even closer to fixation cross for bars beyond the target and that is further from the target for bars spatially before the target.

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