Perisaccadic compression in two-saccade sequences

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Around the onset of a saccade toward a target, localization judgments are systematically biased toward the saccade endpoint. This perisaccadic compression is thought to be related to transsaccadic reorganization and due to interfering motor signals in visual maps. It has, however, only been investigated for saccades targeting a single target. Here, we examined whether saccade-sequence programming to stationary target(s) would affect the pattern of localization judgments of a briefly flashed stimulus. We presented saccade targets that could induce either a single saccade or two-saccade sequences and we flashed a bar around saccade onsets. For all two-saccade-sequence conditions, we showed that localization judgments of the stimulus flashed around the first saccade onset are biased toward an intermediate position between the two-saccade landing position, indicating the influence of the second saccade's parallel planning. This implies that motor-planning signals are most likely responsible for perisaccadic compression than motor execution feedback.

Keywords: saccade, mislocalization, compression, saccade-sequence, exploring saccade, targeting saccade

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Introduction

Around the onset of a saccade, localization judgments undergo a systematic bias toward the upcoming saccade endpoint. This well-described effect is known as "perisaccadic compression" (e.g., Lappe, Awater & Krekelberg, 2000; Morrone, Ross & Burr, 1997; Ross, Morrone & Burr, 1997). It has most commonly been linked to mechanisms that combine visual and extra-retinal signals in order to maintain visual stability across saccades and thus to transsaccadic reorganization. Indeed, motor factors are involved in compression (Awater & Lappe, 2004). For instance, saccade amplitude affects compression (Kaiser & Lappe, 2004; Lavergne, Vergilino-Perez, Lappe & Doré-Mazars, 2010), i.e., the greater the amplitude, the greater the compression. It has also been shown that the saccade endpoint, rather than the visual target position, determines the locus of compression (Awater, Burr,

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Lappe, Morrone, & Goldberg, 2005; Awater & Lappe, 2004), which suggests that the impending motor execution has a crucial role in this phenomenon. Recently, computational models proposed that compression is the result of the combination of a motor feedback signal with the flash related activity in visual maps (Hamker, Zirnsak, Calow & Lappe, 2008; Pola, 2011; VanRullen, 2004). Taken together, the variety of evidence tends to support the idea that motor planning or impeding execution is responsible for perisaccadic compression, though the discussion remains open (Ostendorf, Fischer, Gaymard & Ploner, 2006).

The classical paradigm used to reveal compression is to flash a stimulus, usually a bar, at different times around the onset of a saccade toward a target and then to ask the subject to localize the flashed bar. Until now, this phenomenon has mostly been studied for single saccades to small targets, most often a cross, yet saccades are more often executed in sequences in order to explore the visual environment. Besides, objects in our environment are more likely to be spatially extended than small isolated targets. For instance, the planning of a sequence of saccades is known to be different from that of a single saccade, in particular because it involves parallel processing (Becker & Jürgens, 1979; Zingale & Kowler, 1987), parallel attentional presaccadic shifts (Baldauf & Deubel, 2008; Godjin & Theeuwes, 2003), and additional cerebral activations (Hu & Walker, 2011). One might then expect a different pattern of compression for saccade sequences compared to single saccades. Moreover, it has been shown that "exploring saccades" executed within spatially extended objects are planned as fixed motor vectors that depend on object size and not on object position. These saccades are thus not planned in the same way as "targeting saccades" toward a small target or object as these depend upon the position of the stimulus (Lavergne, Vergilino-Perez, Collins, Orriols & Doré-Mazars, 2008; Vergilino-Perez & Findlay, 2006). Different patterns of compression for these two different kinds of saccades could then be expected if compression is linked to target selection.

Here we compare the pattern of compression for two-saccade sequences with the pattern of compression for a single saccade. We also compare saccade sequences in response to two small targets with saccade sequences in response to spatially extended targets. These spatially extended objects induced second saccades that could either explore the currently fixated object (when the object was long) or target a new object (when two small objects were presented). We used the classical paradigm for compression, that is, subjects localized a stimulus that was briefly flashed at various times around a saccadic onset. We expected different patterns of localization judgments for two-saccade sequences compared to single saccades, as well as different patterns depending on saccade type.

Methods

Subjects

Six subjects (three authors and three naïve subjects) participated in the experiment. All of them had normal or corrected-to-normal vision, were familiar with eye movement recording and 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 movements recording

The experiment was conducted in a dimly lit room (mean luminance: 0.06 cd.m^{-2}). Subjects were seated 57 cm away from the screen and their heads were stabilized with submaxillar dental prints and forehead rests. The stimuli were presented on an Iiyama HM240DT monitor with a refresh rate of 170 Hz and a resolution of 600 × 800 pixels. The border of the screen and its immediate surrounding were visible due to the luminosity of the screen. Eye movements were monitored by a Bouis oculomotor system (Bach et al., 1983) with an absolute resolution of 6 arc minutes and a linear output of more than 12° of visual angle. Viewing was binocular but only the movements of the right eye were monitored. The signal from the oculometer was sampled every 2 ms. Saccades were detected with an in-house program (based on Labview 7.1) using eye velocity ($>40°\cdot s^{-1}$), acceleration ($>3000°\cdot s^{-2}$), and minimal displacement (0.15°) thresholds. After saccade onset detection, offset was defined as the moment the velocity fell to less than $15°\cdot s^{-1}$.

Stimuli

Saccade targets (ST)

The fixation cross consisted of a 0.5° × 0.5° white cross (white color components: 255% red, 255% green, 255% blue; mean luminance: 12 cd·m^{-2}) presented 6° left from the screen center. Six different stimuli were used as Saccade Targets (ST). They consisted of 0.5° × 0.5° white cross(es) (mean luminance: 18 cd.m^{-2}) displayed on a dark grey background (grey color components: 128% red, 128% green, 128% blue; mean luminance: 5 cd·m^{-2}). They were composed of one, two, or a series of 0.5° × 0.5° cross(es) displayed at the right of the fixation cross (0.5° × 0.5°) which was displayed 6° left of the screen center. Crosses presented in this way (Figure 1) could induce either a single saccade or a two-saccade sequence.

There were three single-target conditions consisting of a single cross displayed at various eccentricities (3.5°,

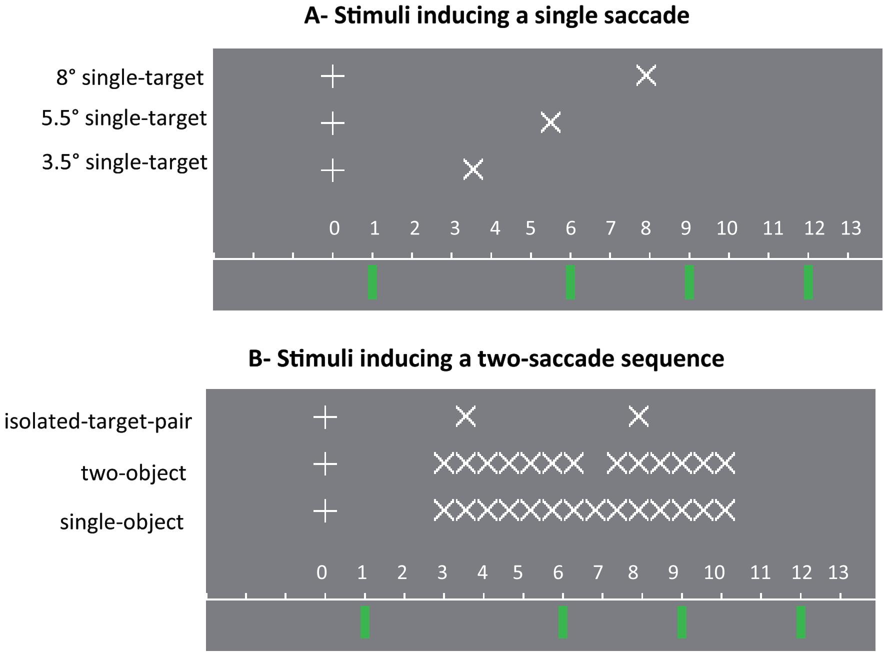


Figure 1. Spatial characteristics of stimuli and stimuli condition names. All stimuli were composed of one, two, or several 0.5° × 0.5° cross(es) and were always displayed in the sagittal plane to the right of the initial fixation cross. (a) Stimuli inducing a single saccade were single targets which could be displayed either at 3.5°, 5.5°, or 8° from the fixation cross. (b) Stimuli inducing a two-saccade sequence. Unlike as it appears on the figure, the ruler was always presented 1.8° below the stimuli. Green lines below the ruler represent the possible positions of the bar. Numbers from 0 to 13 indicate the position in degrees relative to the fixation cross and were not visible on the screen.

5.5°, or 8° right of fixation) which induced single saccades of various amplitudes and thus prevented the occurrence of stereotyped saccades. Three stimuli could induce a two-saccade sequence. Two of them were string conditions (the single-object and two-object conditions) with the strings displayed 2.3° to the right of the fixation cross. The single-object condition was formed by 12 adjacent crosses and was expected to evoke spontaneous two-saccade sequences, the first saccade landing on the left half of the string and the second on the right half (Lavergne et al., 2008; Vergilino-Perez & Findlay, 2006). The two-object condition was formed by 6 + 5 crosses separated by a 0.5° blank and was expected to evoke two saccades, one to each string. In addition to these string conditions, the isolated-target-pair condition consisted of two crosses, the first 3.5° and the second 8° to the right of the fixation cross (Figure 1).

Localization target (LT)

The Localization Target (LT) was a 0.3°-wide vertical green bar (green color components: 0% red, 128% green, 0% blue; mean luminance: 4 cd.m^{-2}) as high as the screen (27°) that could appear at four different positions: 1°, 6°, 9°, or 12° (Figure 1). A ruler, i.e., a white horizontal line with vertical tick marks at every degree (0.1°) was presented 1.8° degrees below the saccade target(s) and initial fixation cross during the whole trial.

Procedure

Each session began with a full calibration procedure during which subjects had to make a saccade to each of five bars presented successively from left to right in steps of 3°. Reference measures were taken for each of the five bars. If the variability of each measure was below a threshold (0.4 V) and if measures were linear, the calibration was considered successful and the experiment started.

Each experimental trial started with a calibration check. A bar appeared 6° left from the screen center, and subjects had to fixate upon 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. After a randomized time between 600 and 1100 milliseconds, the initial fixation cross disappeared and the saccade target appeared (go-signal for the saccade[s]) for 1000 milliseconds (Figure 2). The saccade target was one of the six stimuli in Figure 1, and as the subjects' task was to explore the stimulus, depending on the stimulus presented they could only execute either one saccade (for single targets; Figure 1a) or a sequence of two saccades (for two targets or a string of crosses; Figure 1b). The subjects were instructed to visually explore the entire stimulus. Note that subjects were never instructed to execute a sequence of two saccades for stimuli composed of one string of crosses. Indeed, saccades toward a spatially extended stimulus generally landed on the center of gravity of the stimulation (Coren & Hoenig, 1972) constituting a default landing position within the stimulus for the saccade (Findlay & Walker, 1999). Therefore we expected saccades to be directed to the center of gravity of each string of crosses in the two-object condition. However, the longer the targeted stimulus, the higher the probability that the saccade directed to it lands on a position close to the stimulus' beginning and is followed by a second within-object saccade. Such a saccadic behavior is well known in reading research (McConkie et al., 1989). Therefore we expected that, in most cases, the long string of crosses used in the single-object condition would be explored by a sequence of two saccades and, as expected, we observed a majority of two-saccade sequences with this type of stimulus; the first saccade landed on the left half of the string, and the second saccade landed on the right half.

At a randomized time around the onset of the first or second saccade (see following design), the bar was flashed for one video frame, around 5 milliseconds. An interstimuli interval window was calculated for each subject on the basis of their mean latency, as determined in a familiarization phase, in order for the bar to be flashed in a [–150; 150 ms] time window around saccade onset. We defined first saccade latency as the duration (in ms) between fixation cross offset and saccade onset, and second saccade latency as the duration between first saccade offset and second saccade onset. Seven-hundred milliseconds after the offset of the bar, a mouse pointer appeared 1° below the ruler, at one of four possible positions between 1°, 6°, 9°, or 12° right from the initial fixation cross position. Subjects were asked to report the perceived position of the bar by pointing the arrow of the mouse displayed on the screen at the position they thought the bar had been flashed and then clicking on the mouse button. When the bar was not perceived at all, the subject had to click on a predefined area at top left of the screen, and the trial was discarded from further analysis.

Design

In a given trial, only one of the six possible targets (Figure 1) was presented and only one bar was flashed at one of four possible positions around the onset of one. In trials where a single target was displayed–and therefore only one saccade was required–the bar was always flashed around the first saccade the system detected. For trials in which a two-saccade sequence was required (i.e., isolated-target-pair, or single-object or two-object conditions), the bar could be flashed randomly around the first or second saccade. Two designs have to be considered according to the number of saccades required. In both, all factors were within-subject factors: for trials where only one saccade was required (i.e., for single targets), the design was a 3*4 factorial design with the saccade target and bar positions as factors. For trials where a two-saccade sequence was required (i.e., isolated-target-pair or spatially extended stimuli), the design was a 3*4*2 factorial design with saccade target positions, bar positions, and saccade ranks around which the bar was flashed as factors. In a block, each trial was chosen randomly from these 36 possible conditions. Subjects performed 2,880 trials distributed into 20 blocks of 144 trials. In a block, each experimental condition was presented four times.

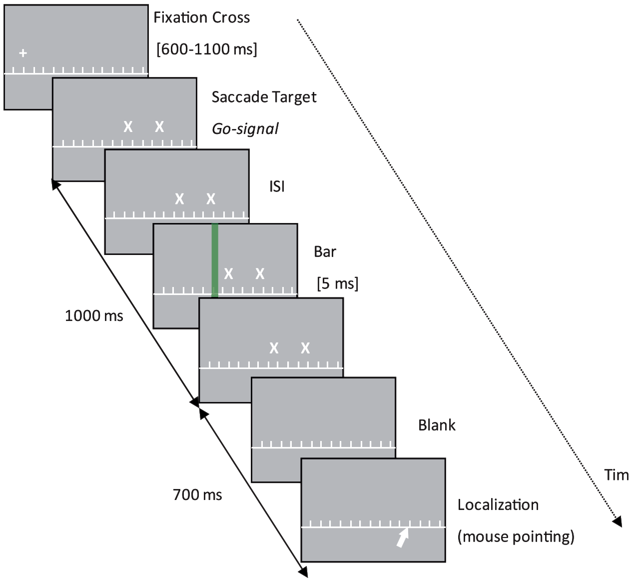


Figure 2. Temporal characteristics of a trial. At the beginning of each trial, the subject fixated a cross 6° left of the sagittal plane. After a randomized time between 600 and 1100 ms, the fixation cross disappeared (i.e., the go-signal for the saccade) and the saccade target appeared for 1100 ms to the right of the fixation cross. At a randomized time within in a temporal window of [–150, +150 ms] around the onset of the first or second saccade, a vertical bar appeared at one of four positions (1°, 6°, 9°, or 12°) for one video frame (5 ms). After 700 ms after the offset of the bar, a pointer appeared and the subject reported the position of the bar they perceived.

Data analysis

In the two-saccade conditions, the data for three of the subjects (two authors and one naïve subject) were not adequate for analysis. There were problems in the computation of the interstimuli intervals for the LT flash around the second saccade onset resulting in an insufficient amount of usable data associated with this saccade. These data were therefore not presented here. Thus, all analyses concerning two-saccade sequence stimuli presented in the following paragraphs describe data for three subjects only.

For trials in which the bar was flashed around the first or single saccade onset, 42% of data were excluded, corresponding to latencies shorter than 100 ms or longer than 500 ms (7%) and landing positions outside the object(s) boundaries or outside a 1° window around cross(es) in trials where isolated crosses were presented (18%). Trials in which a third saccade was executed within object(s) (6%), in which the bar was flashed outside a 300 ms time window centered on saccadic onset (10%), and in which the bar was not seen (1%) were also excluded. For trials in which the bar was flashed around the second saccade onset, 45% of data (computed on three subjects) were excluded following the same criteria, i.e., latencies shorter than 100 ms or longer than 500 ms (5%) and landing positions outside object(s) boundaries (18%). Trials in which the bar was flashed outside the chosen time window (20%) and trials in which the bar was not seen (2%) were also excluded.

Latencies and amplitudes of first and second saccades were analyzed using ANOVAS with stimulus condition and LT position as within-subjects factors. Data concerning single saccades were analyzed separately.

Results

Saccade latencies and landing positions

Single targets

As expected, saccade landing positions (Table 1) were affected by saccade target eccentricity ($F(2,10) = 4{,}569$, $p < 0.0001$), but not by LT position ($F\ (3,15) = 2.5$, ns.) with no interaction between these factors ($F\ (6,30) = 2.0$, ns.). Saccade latencies did not vary with target eccentricity ($F < 1$) or LT position ($F\ (3,15) = 1.9$, ns.), with no interaction between these two factors ($F < 1$).

Two-saccade sequences

Data concerning two-saccade sequence conditions were compared with each other and with that of the 3.5° single target which served as control condition.

Landing positions of first saccades were affected by stimulus condition ($F\ (3,15) = 5.7$, $p < 0.01$) due to larger landing positions in the two-object stimulus (3.8 ± 0.3°) compared to that observed for other stimuli ((3.5 ± 0.2°), $F\ (1,5) = 36.2$, $p < 0.003$). Landing positions, however, did not depend upon LT position ($F\ (3,15) = 1.4$, ns.), and there was no interaction between stimulus and LT position ($F\ (9,45) = 1.7$, ns.). As expected, first saccade latencies did not vary with stimulus condition ($F < 1$) nor LT position ($F\ (3,15) = 1.4$, ns.). The two factors did not interact ($F < 1$) (Table 1).

Landing positions of second saccades did not differ between stimuli ($F\ (2,10) = 1.7$, ns.) nor LT position ($F\ (3,15) = 2.5$, ns.) with no interaction between these factors ($F < 1$) (Table 1).

Compression in single saccade conditions

Figure 3a plots the mean perceived positions for each single-target position, averaged over subjects in 10-ms bins. For the three single-target conditions, LTs that were to the left of (i.e., spatially before) the target were perceived shifted in the direction of the saccade around saccade onset, whereas LTs that were presented to the right of (i.e., spatially beyond) the target were shifted in the opposite direction, indicating that compression occurred toward the saccade endpoint.

				Single-target		
	Single-object	Two-object	Isolated-target-pair	3.5°	5.5°	8°
First saccade						
Latency (ms)	188 (12)	187 (13)	192 (13)	189 (17)	193 (24)	202 (25)
Landing position (°)	3.7 (0.4)	3.8 (0.3)	3.4 (0.1)	3.4 (0.1)	5.3 (0.2)	7.8 (0.2)
Second saccade						
Latency (ms)	254 (24)	260 (25)	302 (46)			
Landing position (°)	8.4 (0.5)	8.1 (0.6)	8.0 (0.2)			

Table 1. Characteristics of saccades: Mean latencies (milliseconds) and landing positions (degrees) of first and second saccades as a function of the saccade target averaged over LT position and subjects. Values in parentheses are standard deviations.

	1° LT		6° LT		9° LT		12° LT	
	3.5° Single-target	Target-pair	3.5° Single-target	Target-pair	3.5° Single-target	Target-pair	3.5° Single target	Target-pair
100%	**NS**	**NS**	**0.04**	**0.002**	**0.002**	**0.002**	**0.004**	**0.00**
	1.3	*2.1*	*2.1*	*5.2*	*5.1*	*5.3*	*4.4*	*8.1*
50%	**0.005**	**0.0002**	**NS**	**0.01**	**NS**	**NS**	**NS**	**NS**
	4.1	*8.6*	*1.0*	*3.7*	*0.1*	*1.5*	*<1*	*1.6*
0%	**0.0001**	**0.00001**	**0.005**	**0.03**	**0.002**	**0.03**	**0.003**	**0.002**
	9.4	*15.2*	*4.1*	*2.3*	*5.2*	*2.4*	*4.5*	*4.9*
−50%	**0.00001**	**0.00001**	**0.0004**	**NS**	**0.0001**	**0.0008**	**0.0002**	**0.00005**
	14.7	*21.8*	*7.2*	*<1*	*10.4*	*6.2*	*9.0*	*11.4*
−100%	**0.00001**	**0.00001**	**0.0001**	**NS**	**0.00001**	**0.0001**	**0.00001**	**0.00001**
	20.0	*28.4*	*10.3*	*<1*	*15.5*	*10.0*	*13.4*	*17.9*

Table 2. One-tailed student-test significance thresholds (in bold, liberty degrees = 5) for comparison of compression ratios to five different standard values (100, 50, 0, −50, and −100%) for each LT of 3.5° single-target and isolated-target-pair conditions. NS stands for "non significant." Values in italics are the student t-test values.

Compression around first saccade onset in two-saccade sequence conditions

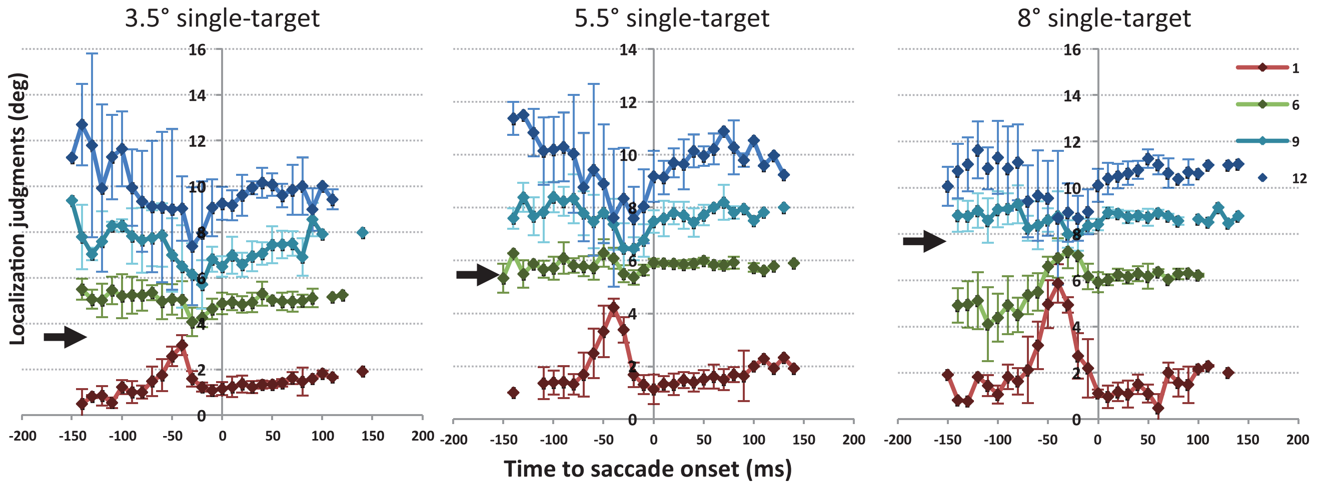
Mean perceived positions for stimuli inducing a two-saccade sequence as function of time are plotted in Figure 3b. In order to test the impact of a second saccade on perisaccadic compression around the first saccade of the sequence, we compared the isolated-target-pair condition to the 3.5° single-target condition. To test the effects of the various second saccades, we compared the results of the three two-saccade conditions.

Impact of a second saccade: 3.5° single-target vs. isolated-pair conditions

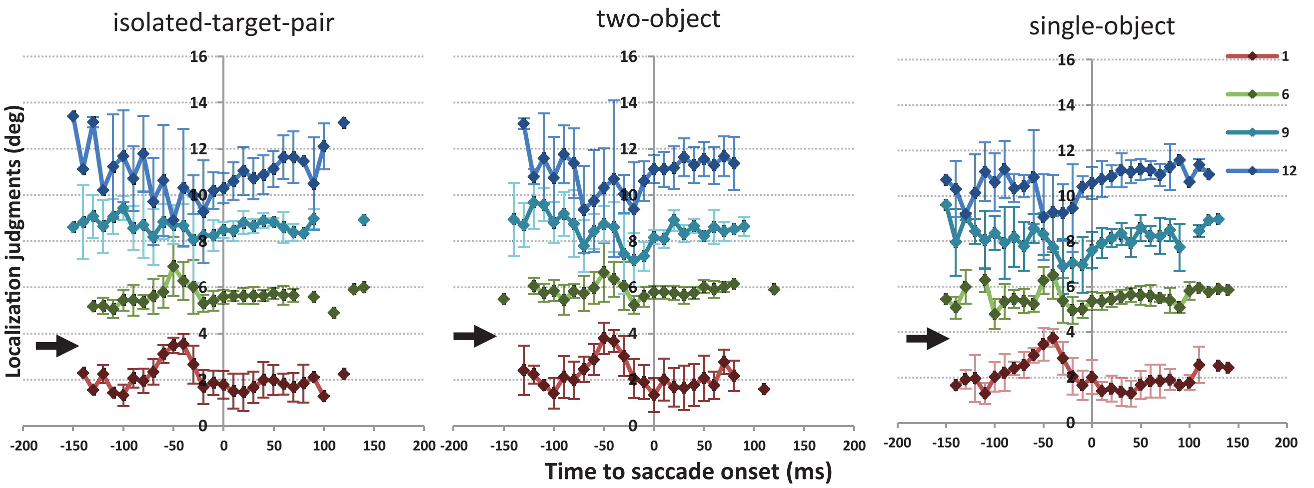
The pattern of localization judgments in the isolated-pair condition (Figure 3b, left) show a compressive pattern before saccade onset, but this pattern seems quite different from that observed for the 3.5° single target (Figure 3a, left). Indeed, whereas in the 3.5° single-target condition compression clearly occurs towards the saccade landing position (i.e., 3.4 ± 0.1°), it is not the case in the isolated-target-pair condition. Compression locus doesn't seem to be the first saccade landing position (i.e., 3.4 ± 0.1°) but a shifted position toward the second saccade landing position.

Compression strength was measured by computing compression ratios (Lavergne et al., 2010; Richard, Churan, Guitton & Pack, 2009) for each LT of each ST, which express the *maximal observed error* of localization of the LT as a percentage of its *maximal possible error*. For a given LT, the *maximal observed error* was defined as the highest deviated value of localization recorded within the critical period when compression is known to occur ([−50; 0 ms] to saccade onset) relative to its baseline value (i.e., its mean localization value within the period when compression does not occur). This baseline value was defined as the individual trial-weighted mean value of localization within periods when compression is known not to occur ([−150; −75 ms] and [50; 150 ms] to saccade onset). Following the same rationale, the *maximal possible error* was defined as the difference between the localization baseline value and the saccade landing position, which corresponds to the location where compression usually occurs. Thus, a greater compression ratio represents a greater strength of compression: 0% indicates no compression (the LT is perceived at its baseline position), and 100% indicates a maximal compression (the LT is perceived at the same location as the saccade landing position[1]). Compression ratios were computed for each LT and saccade target, taking the first saccade landing position as a reference landing position in the denominator[2] (Figure 4a). In accordance with the global localization pattern (Figure 3b, left), the 6° LT ratio in the isolated-target-pair condition is negative, indicating that the LT appeared to be shifted away from the first saccade position, as opposed to what would be expected. Other LT ratios were positive (Figure 4a). Two-tailed student t-tests were used to compare each of these ratios between the isolated-target-pair and the 3.5° single-target condition. Differences for LTs at 1° ($t(5) = 3.4$, $p < 0.02$), 6° ($t(5) = 4.0$, $p < 0.01$), and 9° ($t(5) = 2.6$, $p < 0.05$) emerged, indicating that these LTs were not compressed in the same manner in 3.5° single-target and isolated-target-pair conditions. In contrast, ratios for the 12° LT were similar in the two conditions ($t < 1$) indicating that this LT was similarly compressed in both cases. In order to quantify these ratios, we compared them to 0% (indicating no compression), 100% (indicating maximal compression toward the saccade landing position), −100% (indicating an equivalent displacement shifted in saccade direction), and the respective halfway values of 50% and −50%. Results are presented in Table 2. In the isolated-target-pair, the 6% ratio was found to be

A- Stimuli inducing a single saccade



B- Stimuli inducing a two-saccade sequence: around 1st saccade onset



C- Stimuli inducing a two-saccade sequence: around 2nd saccade onset

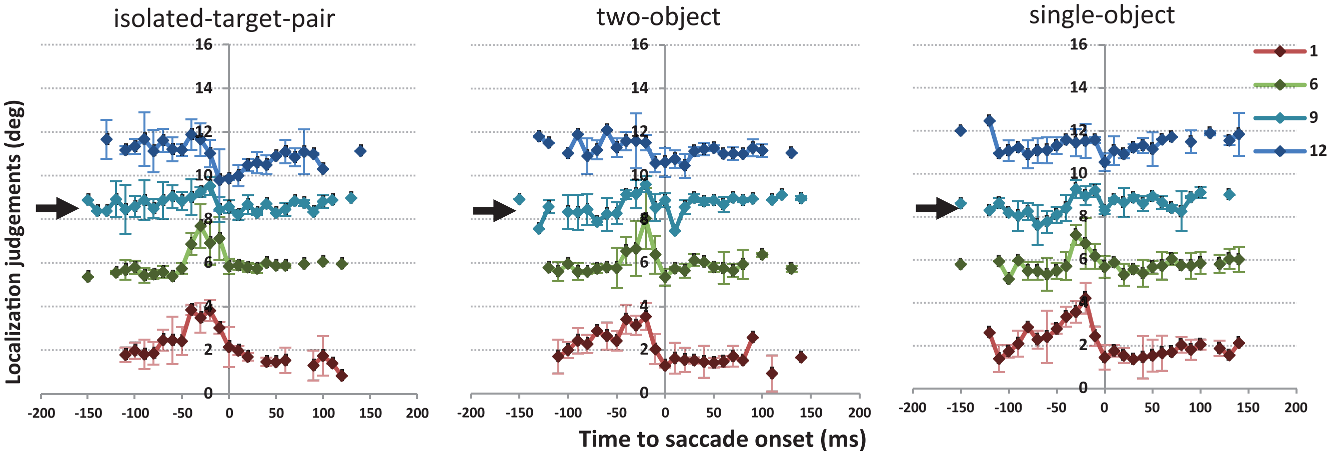


Figure 3. Mean LT localization judgments as a function of time relative to saccade onset. Data are presented in 10-ms bins. (a) Data corresponding to single-target conditions. (b) Data corresponding to two-saccade sequence conditions for which the LT was flashed around the first saccade onset. (c) Data corresponding to two-saccade sequence conditions for which the LT was flashed around the second saccade onset. Each curve corresponds to one LT position. Horizontal black arrows correspond to the landing position of the upcoming saccade.

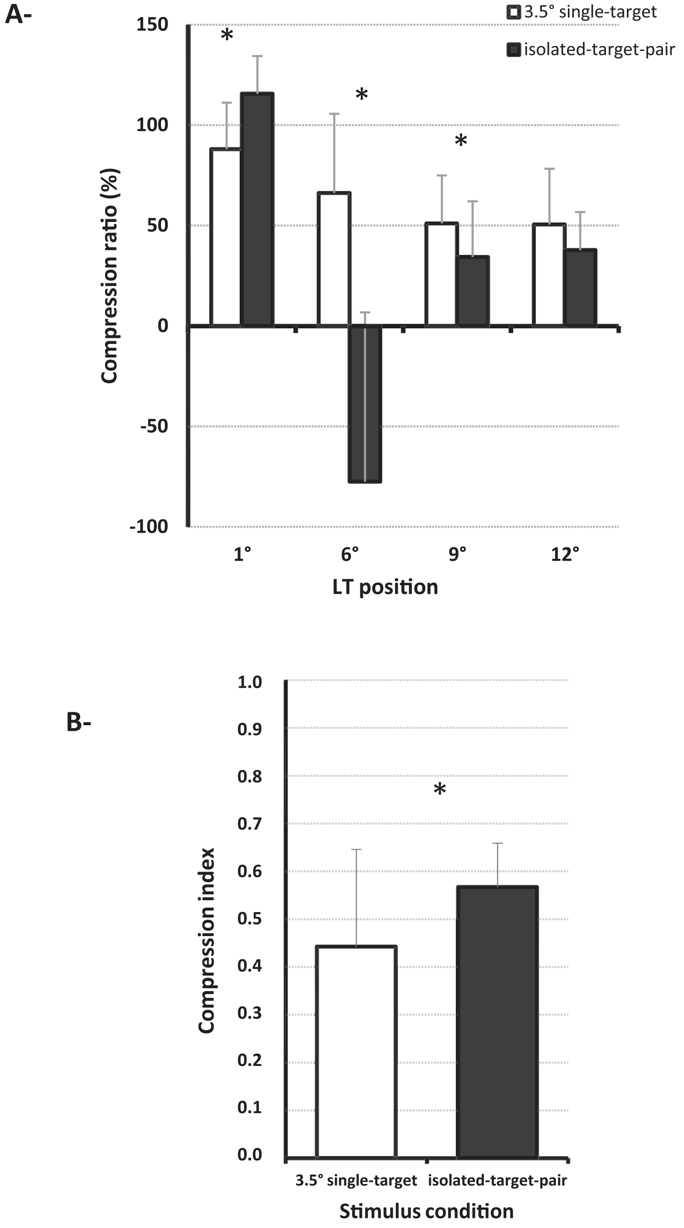


Figure 4. Mean compression ratios computed as a function of the first saccade landing position per LT condition (a) and mean compression indexes (b), averaged over subjects for the 3.5° single-target and the isolated-target-pair, when the LT was flashed around the first saccade onset. Thin lines correspond to standard deviations.

significantly lower from 0 and positive standard values (one-tailed student t-tests from 0: $t(5) = 2.3$, $p < 0.03$; from 50: $t(5) = 3.7$, $p < 0.05$; from 100: $t(5) = 5.2$, $p < 0.002$) except -50% and 100% (one-tailed student t-test, $t(5) = 5.2$, $p < 0.004$) and also from 0% ($t(5) = 2.3$, $p < 0.04$), whereas it did not differ from -100% ($t < 1$). As a comparison, the 6° LT ratio for the 3.5° single target was significantly greater than -100% ($t(5) = 10.3$, $p < 0.00005$) and 0% ($t(5) = 4.1$, $p < 0.005$) so that it did not differ from 100% ($t(5) = 1.9$, ns.). These results confirm that, whereas the 6° LT is maximally compressed toward the saccade landing position in the 3.5° single-target condition, this same LT is shifted away from the first saccade landing position in the isolated-target-pair condition. Comparison of other LTs to these same values showed that ratios for others LTs are in the same positive range for 3.5° single-target and isolated-target-pair conditions, indicating that other LTs are compressed in both conditions.

In order to test the overall variation of compression strength between stimuli conditions, we computed the compression index (Lappe et al., 2000) for each condition, which shows the relative perceived separation between LT positions. This index is defined as the standard deviation across all mean perceived LT positions at a given time (i.e., when compression is maximal), normalized to the standard deviation across LTs when no compression occurs (i.e., baselines of perceived positions outside the temporal window of compression). At the time compression is thought to be maximal, the strongest effect of compression, which corresponds to the fact that positions of all LTs are seen as one position, would lead to an index close to 0. On the opposite, a minimal effect of compression, which corresponds to the fact that LTs are perceived with the same separation as for baseline values, is expressed by an index close to 1. Mean compression indexes computed in the time window when the maximal mislocalization occurred are plotted in Figure 4b. The index was greater for the isolated-target-pair condition compared to that for the 3.5° single target (0.6 ± 0.1 vs. 0.4 ± 0.2, two-tailed student t-test: $t(5) = 2.7$, $p = 0.04$) indicating a lower compression when two targets are presented rather than only one.

Comparison between different saccade sequence conditions

Overall, patterns of localization were quite similar in the three two-saccade sequence conditions (Figure 3b). Indeed, as in the isolated-target-pair condition, the locus of compression appeared shifted beyond the first saccade endpoint in other two-saccade sequence conditions: the 6° LT was not perceived closer to the first saccade landing position, but in saccade direction instead. However, 9° and 12° LT were perceived closer to the saccade landing position, indicating that compression occurred for these bars. Thus, compression occurred for these three two-saccade sequence conditions, but not toward the first saccade landing position. Analyses of variance conducted on compression ratios for each LT (Figure 5a) with stimulus condition (isolated-target-pair, two-object, and single-object) as a within-subjects factor confirmed that both single-object and two-object conditions were similar to that observed in the isolated-target-

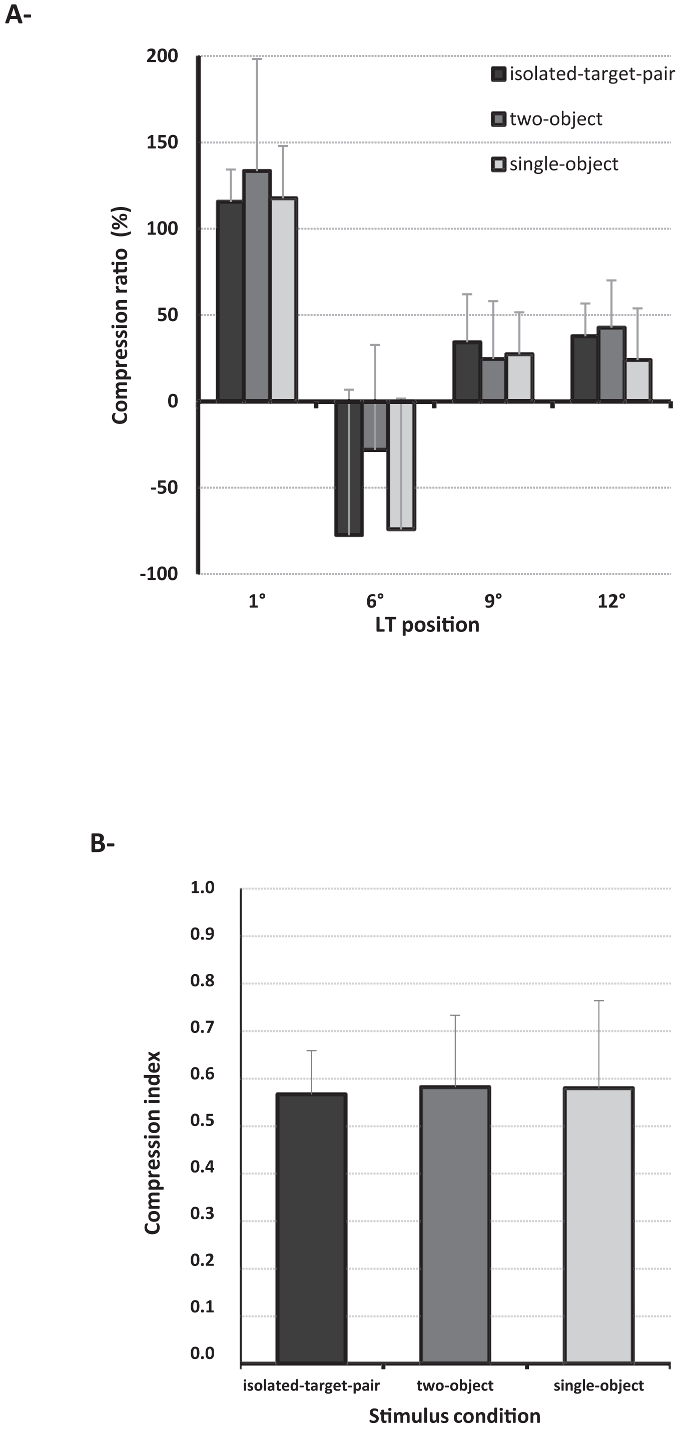


Figure 5. Mean compression ratios computed as a function of the first saccade landing position per LT condition (a) and mean compression indexes (b), averaged over subjects for the three stimulus conditions inducing a two-saccade sequence when the LT was flashed around the first saccade onset. Thin lines correspond to standard deviations.

pair condition as no effect was found for either LT (all *F*s ns., or $F < 1$). This suggests that, whatever the second saccade type, compression occurred in the same way in a two-saccade sequence.

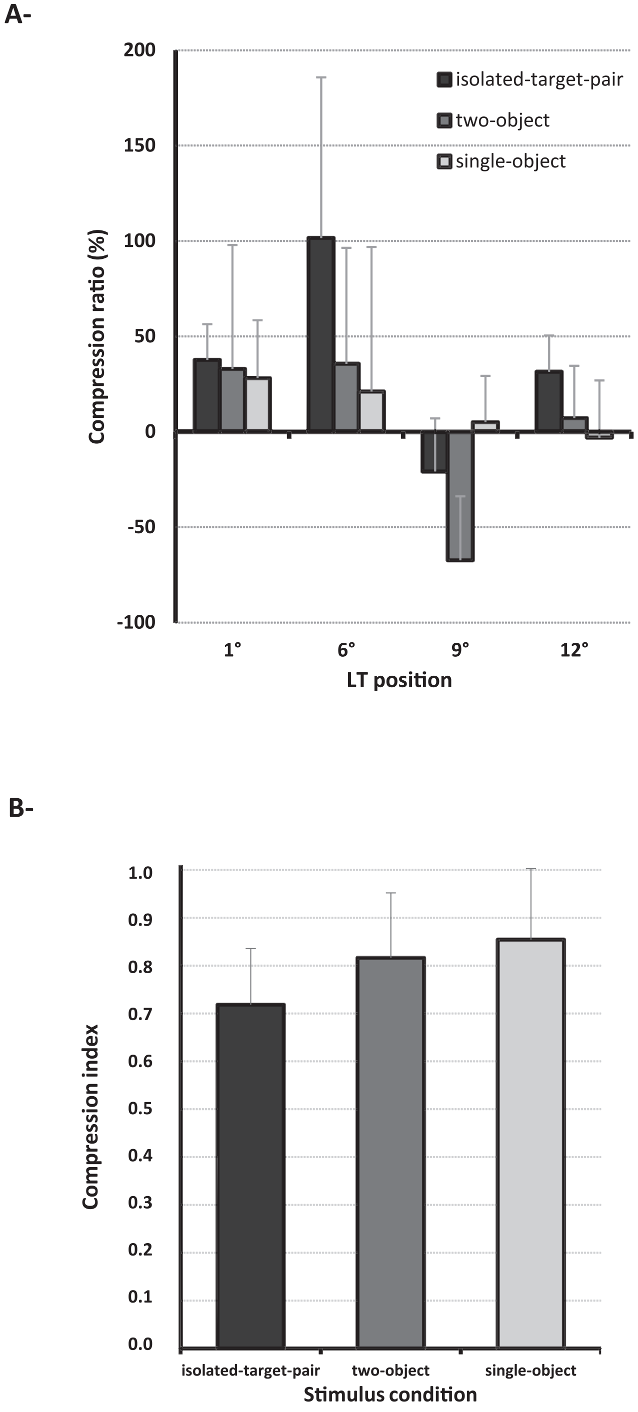


Figure 6. Mean compression ratios computed as a function of the second saccade landing position per LT condition (a) and mean compression indexes (b), averaged over subjects for the three stimulus conditions inducing a two-saccade sequence,when the LT was flashed around the second saccade onset. Thin lines correspond to standard deviations.

In accordance with these results, the same analysis computed on compression indexes (Figure 5b) did not differ between stimulus conditions ($F(2,10) = 0.7$, ns.).

Compression around second saccade onset in two-saccade sequence conditions

Overall patterns are depicted in Figure 3c and are quite similar for the three conditions with a slightly greater compression in the isolated-target-pair condition compared to others. As for mislocalization around the first saccade onset, we computed compression ratios for each LT. Second saccade landing positions were used to compute the denominator. Data are plotted in Figure 6a. Each LT is compressed toward the second saccade endpoint except for the 9° LT, as it remains unclear whether it is compressed or shifted in the saccade direction. Unfortunately, due to the small amount of data, no statistical analysis could be computed to decide between these two possibilities. Compression indexes were overall larger than those observed around the first saccade onset, indicating that compression was lower around second saccade onset. Comparison between stimuli conditions suggests an increasing compression from isolated-target-pair to two objects, indicating that compression decreases when the second saccade is toward an object that is more spatially extended.

Discussion

In our experiment, we flashed a stimulus around the onset of a single saccade toward a target of various eccentricities or around saccade onsets in a two-saccade sequence. We replicated both well known saccade amplitude and stimulus relative distance effects on perisaccadic compression. By comparing the 3.5° single-target condition to the isolated-target-pair condition, we found that the occurrence of a second saccade had an effect on the pattern compression found around the first saccade onset. Finally, by contrasting different two-saccade sequences in which the second saccades were of different types (exploring a long object, targeting a short object, or targeting an isolated target), we found that compression around the first saccade onset was affected in the same way whatever the second saccade type.

Saccade sequence planning and shift of compression locus

In the saccade-sequence conditions, we found a compressive pattern around the first saccade onset, but the compression locus appeared shifted in a saccade direction at an intermediate position between the first and the second saccade landing positions. Analyses showed differences between the 3.5° single-target and the isolated-target-pair conditions for three LTs (1°, 6°, and 9°) and not for the 12° LT. Notably, the 6° LT was shifted in a saccade direction in the isolated-target-pair condition instead of being compressed toward the first saccade landing position as observed with a single target, leading to a saccade of the same amplitude. Both 1° and 9° LTs were compressed, but in a different manner, suggesting again that the compression locus was different for the single saccade and the two-saccade sequence conditions. As compression decreases with LT distance from the feedback center, it is probable that the 12° LT was too far from this center in both cases for a differential compression to emerge between the 3.5° single-target and the isolated-target-pair conditions.

One possible explanation for this difference is linked to the availability of two reference points in the isolated-target-pair condition compared to the 3.5° isolated target. Indeed, the locus of compression has been shown to be determined by the saccade target position when it is available (Awater & Lappe, 2006), but when it is missing, the saccade target landing position and surrounding visual references are used. In our experiment, saccade targets remained available during the execution of the two saccades, thus one could argue that the visual processing of each target could be sufficient to shift the compression locus. Therefore, the shift of the compression locus would be the consequence of the processing of two reference points when two targets are present instead of when only one target is present. However, this explanation may not be sufficient to explain our data, as we have shown that compression is equally shifted in all two-saccade-sequence conditions, including that toward a spatially extended object(s) for which the saccade target is visually different from that in the isolated-target-pair condition. Note also that in the single-object condition, the saccade that is executed within the object is not directed toward any particular position in the object (Beauvillain, Vergilino-Perez & Dükic, 2005; Doré-Mazars, Vergilino-Perez, Collins, Bohacova, & Beauvillain, 2006) and thus no visual selection is used to compute this saccade, which is known to be coded as a function of object size only (Collins, Vergilino-Perez, Beauvillain & Doré-Mazars, 2007; Lavergne, Vergilino-Perez, Collins & Doré-Mazars, 2010; Lavergne, Vergilino-Perez, Lemoine, Collins & Doré-Mazars, 2011). Thus, for this particular kind of saccade-sequence, the argument of shift of compression being due to the selection of a spatial position is less likely. Following the same rationale, we can also deduce that the interaction between motor signals and visual persistence of the flash that is known to play a role in perisaccadic mislocalization of flashes (Pola, 2011) cannot totally account for our results. Indeed, if it were the case, one might have expected different patterns for visually different stimuli. In particular, stimuli made of 14 crosses (single-object) and therefore more luminous than the one made of two crosses (isolated-target-pair) should have led to greater compression. It was not the case.

An alternative explanation for our results could be that a parallel processing of the two saccades of the sequence is being processed during the preparation of the first saccade. Hence, oculomotor signals susceptible to the influence of visual processing and involved in perisaccadic compression would therefore be related to the planning of the first as well as the second saccade. The parallel processing of two saccades during the first saccade latency would imply that both saccades influence compression and therefore deviate the compression locus. This hypothesis would also explain the lesser amount of compression for two-saccade sequence conditions compared to single saccades. Indeed, parallel saccade planning would create two peaks of activities in oculomotor maps, leading to a broader activity in these maps than the activity induced by a single target. Hamker et al. (2008) propose that compression emerges from oculomotor regions like the superior colliculus or the frontal eye field. This broader activity would create a weaker modulation on visual maps and therefore lead to a weaker compression. In analyses not presented here, we computed compression ratios by replacing the first saccade landing position by an average of both saccade-landing positions as a denominator. We compared the pattern to that of the 5.5° single-target condition, and both patterns statistically differed, probably because the 5.5° single-target landing position was smaller than the average of first and second saccade landing positions. Neurophysical findings (McPeek & Keller, 2002) showed that, for short intersaccadic intervals, the activity of neurons in motor layers of the superior colliculus is related to the second saccade landing position during the preparation and the execution of the first saccade of a saccade-sequence. Such activity would be good candidate for modulating visual maps, as computational models suggest that the motor feedback (or a corollary discharge for it) responsible for compression originates in the superior colliculus or the frontal eye field (Hamker et al., 2008). Such signals, which are thought to be related to spatial remapping and presaccadic orienting of attention (Wurtz, 2008) can also be linked to studies that showed a parallel allocation of presaccadic attention at all saccade goals of saccade sequences (Baldauf & Deubel, 2008; Godjin & Theeuwes, 2003). However, short intersaccadic intervals are usually observed for corrective saccades, which is not the case in our study. In a recent communication by Zimmermann, Burr & Morrone (2011), the use of a double-step paradigm led to a pattern of results similar to ours using a double-step paradigm with horizontal saccades, which suggests that parallel saccade planning is responsible for the observed effects on compression in saccade sequences. In our experiment, the parallel planning of saccades consists of processing a representation of the plan of each saccade as proposed by Zingale & Kowler (1987). This representation is stored in advance in order to facilitate the sensorimotor transformation during the execution of the sequence. Therefore, such a representation would be involved in compression. Note however that Zimmermann et al. (2011) also demonstrated that, in a double-step paradigm where a first vertical and a second horizontal saccade had to be executed, two compression foci emerged at the time of the first saccade. LTs closer to the first target were mislocalized to the first target, whereas LTs closer to the second saccade target were directed to the second target and not to an intermediate position of the two targets. The compression toward an intermediate position observed in our results could thus be due to the averaging of a simultaneous attraction to the first and the second target, i.e., of simultaneous orienting of attention to these targets. Such a parallel allocation might play a role in the deviation of the compression locus, however it cannot alone explain the whole pattern of results of our study, and notably it does not explain why the compression is weaker around the second saccade onset.

Another explanation would be that this shift of compression occurs toward the second saccade landing position, because the judgment of the LT localization occurs after the second saccade execution. The compression pattern would then reflect transsaccadic reorganization at the final postsaccadic position. No statistical analysis presented here can refute this hypothesis[2]. However, in a recent study, Lappe, Awater & Michels (2009) have asked subjects to localize a flashed bar around a saccade toward an isolated target, asking them not to move their eyes after they had executed their saccade. They compared their compressive patterns to that under free gaze condition and observed no difference. This strongly suggests that compression is linked to oculomotor signals of the saccade around which the bar was flashed, independently of the saccades that can be made afterward.

Compression for targeting vs. exploring saccades

The comparison of compression patterns between the three two-saccade sequence conditions showed that, around first saccade onset, perisaccadic compression affected each LT in the same way regardless of the nature of the second saccade of the sequence. However, in the single-object condition, one could have expected a different pattern than in the two other saccade-sequence conditions, as these involved a second targeting saccade. Indeed, as previously mentioned, unlike targeting saccades, exploring saccades planning is a function of object size and does not aim for a particular position inside the object within which they are executed (Beauvillain et al., 2005; Doré-Mazars et al., 2006). One could have expected different reference points in the compressive pattern of these two types of saccades. It was not the case, and this suggests that saccade target selection is not the signal driving compression and/or that different motor plan signals can be involved in compression.

Conclusion

Overall, our results support the hypothesis that motor signals are involved in perisaccadic compression. These motor signals seem to be more linked to saccade planning than execution. Indeed, we propose that the shift of compression locus observed in saccade-sequences is due to parallel saccade planning, indicating an anticipated reorganization at each of the successive saccade endpoints.

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Footnotes

[1] Compression ratios higher than 100% correspond to an error of localization that overpasses the landing position of the eye, i.e., it is even closer to the fixation cross for bars beyond the target and further from the target for bars spatially before the target. Negative compression ratios correspond to an error in the opposite direction of what's expected (i.e., saccadic landing position), i.e., away from the fixation cross for bars veridically presented beyond the saccade landing position and closer from the fixation cross for bars veridically spatially before the saccade landing position.

[2] Compression ratios were also computed by taking the second saccade landing position as the reference landing position in the denominator. Unfortunately such ratios could not be calculated for the 9° LT because baseline values for this LT were too close to second saccade landing positions, leading to nonsensical high ratios because of too small values at the denominator.

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