About the influence of post-saccadic mechanisms for visual stability on peri-saccadic compression of object location

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Peri-saccadic perception experiments have revealed a multitude of mislocalization phenomena. For instance, a briefly flashed stimulus is perceived closer to the saccade target, whereas a displacement of the saccade target goes usually unnoticeable. This latter saccadic suppression of displacement has been explained by a built-in characteristic of the perceptual system: the assumption that during a saccade, the environment remains stable. We explored whether the mislocalization of a briefly flashed stimulus toward the saccade target also grounds in the built-in assumption of a stable environment. If the mislocalization of a peri-saccadically flashed stimulus originates from a post-saccadic alignment process, an additional location marker at the position of the upcoming flash should counteract compression. Alternatively, compression might be the result of peri-saccadic attentional phenomena. In this case, mislocalization should occur even if the position of the flashed stimulus is marked. When subjects were asked about their perceived location, they mislocalized the stimulus toward the saccade target, even though they were fully aware of the correct stimulus location. Thus, our results suggest that the uncertainty about the location of a flashed stimulus is not inherently relevant for compression.

Keywords: attention, eye movements, space and scene perception

Introduction

Human observers are not aware of the repeated changes in the retinal image when they explore the environment and shift gaze from one location to another. The mechanisms the brain uses to create this constant percept of visual space have been explored by briefly flashing objects around saccade onset (Bischof & Kramer, 1968; Honda, 1993; Matin & Pearce, 1965; O'Regan, 1984). In a lit environment, the flashed object is perceived much closer toward the saccade target (Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). In total darkness, mislocalization predominantly shows a shift into the direction of the saccade and only little compression (Honda, 1989; Lappe et al., 2000; Schlag & Schlag-Rey, 2002). For near-threshold stimuli, however, at least relative compression occurs, i.e., the locations where the stimuli were flashed are perceived closer to each other, but not all flashes are necessarily perceived closer to the saccade target (Georg, Hamker, & Lappe, 2008). Mislocalization occurs when a stimulus is briefly presented but does not when it is visible for a longer period until saccade onset (Schlag & Schlag-Rey, 1995). It follows that the presence of post-saccadic information increases the amount of compression, presumably owing to a stability process that relies on visual information present immediately after the saccade (Lappe et al., 2000).

Post-saccadic mechanisms of stability have been explored in experiments in which the saccade target is displaced during the saccade. The perceived position of the pre-saccadic target stimulus critically depends on the size of the displacement and on whether the target is present immediately after the saccade (Bridgeman, Hendry, & Stark, 1975; Deubel, Bridgeman, & Schneider, 1998; Deubel, Schneider, & Bridgeman, 1996, 2002). In these experiments, a fixated target stimulus jumps and subjects have to saccade to the new position. Between saccade onset and saccade end, the target stimulus is displaced to the left or right. Small displacements are not noticed, a phenomenon now coined as saccadic suppression of displacement (SSD). In two recent studies, subjects were asked to report the pre-saccadic location of the displaced stimulus (Niemeier, Crawford, & Tweed, 2003, 2007). The pattern of mislocalization in those experiments shows similarities to experiments in which stimuli are briefly flashed. In trials with small displacements, the pre-saccadic saccade target stimulus was seen at the position of the post-saccadic stimulus, whereas in trials with larger displacements the subjects undershot the amplitude of the displacement. This mislocalization pattern looks like a compression toward the post-saccadic stimulus location, which could suggest a relation between these phenomena (Niemeier et al., 2007).

SSD has been explained by a post-saccadic process that spatially aligns the pre-saccadic representation to the post-saccadic one (Deubel, Bridgeman, & Schneider, 2004). Since saccadic suppression largely prohibits the perception of a motion cue (Burr, Holt, Johnstone, & Ross, 1982; Campbell & Wurtz, 1978), the displacement must be detected by comparing the pre-saccadic with the post-saccadic stimulus location. The Object Reference Theory (Deubel et al., 2004) proposes that the pre-saccadically attended references are searched for in the post-saccadic image, and if found, determine localization. According to this theory, a target jump is not detected since the object found after saccade serves as a reference, and the pre-saccadic target stimulus is aligned to the post-saccadic target stimulus. The failure to perceive the target jump does not result from a poor transsaccadic transfer of location information since displacement is easily seen in the so-called post-saccadic blanking paradigm, in which the saccade target stimulus is shown at its displaced position long after saccade ends (Deubel et al., 1996). Since the visual system searches for the pre-saccadic stimulus in the post-saccadic scene within a spatio-temporal "constancy window" (Bridgeman, 2007), no alignment occurs after the critical post-saccadic calibration period, and even small displacements are easily detectable.
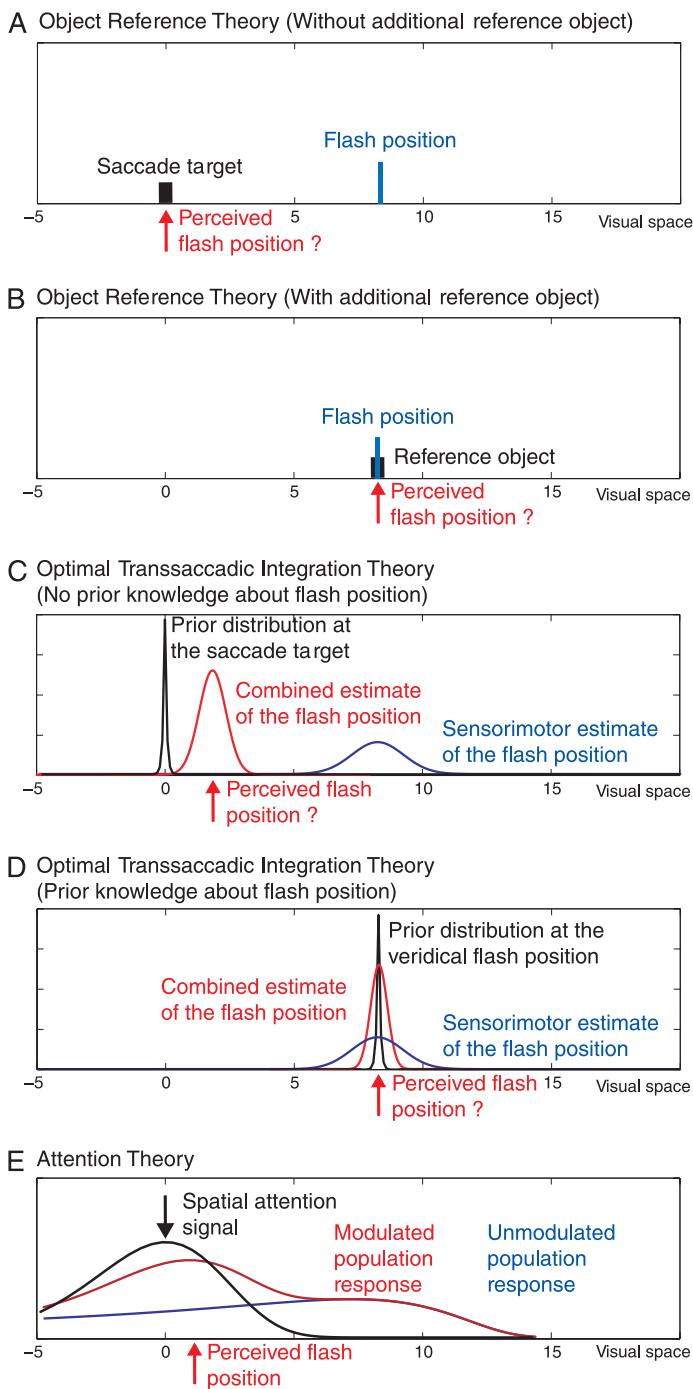
Optimal Transsaccadic Integration (Niemeier et al., 2003) suggests that the prior probability of a target jump is combined together with the sensorimotor estimate of the stimulus position to determine the optimal estimate of the stimulus location. Given a stimulus displacement, the probability density function of the sensory estimate for the displacement is determined from the joint probability of the saccade scatter, a hypometric internal eye position signal, and the retinal stimulus position. Since the hypometric eye position deviates peri-saccadically from the true eye position, the sensory estimate of the displacement is distorted. Under normal conditions of a stationary environment in which objects do not jump during saccades, the prior probability distribution of a target jump is sharply tuned. In this case, the prior knowledge dominates the final estimate so that the displacement is not perceived. Optimal Transsaccadic Integration explains the easy detection of small displacements (<1°) in the post-saccadic blanking paradigm by a change in the prior probability density distribution from a sharply tuned distribution to a more broadly tuned distribution. Thus, the model assumes that the blanking paradigm leads to more uncertainty about the object position. With this broadly tuned prior probability distribution, the model predicts that a target jump is likely being detected. The mechanisms determining the prior probability density distribution are not part of the model.

We asked whether compression might be caused by mechanisms of perceptual stability so that a correct alignment of the flash fails due to its brief presentation. We used location markers indicating the position of the central bar '-' of the flashed letter 'E' throughout the trial. The usage of the location marker has the advantage that it can serve two functions (depending on the theoretical viewpoint). First, it can establish a reference object. A post-saccadic reference object provides a spatial tag to which the pre-saccadic object is anchored, i.e., the spatial position of the pre-saccadic object is copied from the post-saccadic reference object. Second, the location marker indicates the exact location of the flash and thus should remove the uncertainty in location due to the brief presentation of the flash.

It is beyond the scope of the Object Reference Theory to make predictions about flashed objects. However, in order to develop a unifying account of peri-saccadic perception, we should consider that the Object Reference Theory might generalize from the post-saccadic detection of object displacements to the post-saccadic localization of a peri-saccadic flash. It might be possible that compression is the result of a post-saccadic misalignment (Figure 1A). If this is true, the additional reference object at the flash position should suppress a misalignment toward the saccade target. According to the theory, the pre-saccadic reference object is anchored to the post-saccadic reference object and the pre-saccadic target stimulus is anchored to the post-saccadic target stimulus. How is then the location of the flash determined in the presence of the reference object? Since the flash is presented directly on the location marker, it is reasonable to assume that the flash is seen at the same position (Figure 1B).

It has been suggested that Optimal Transsaccadic Integration describes general principles of transsaccadic perception which may also apply to other forms of distorted space perception (Niemeier et al., 2003). Assuming the model of Optimal Transsaccadic Integration (Niemeier et al., 2003) generalizes from a stimulus jump to a stimulus flash (which also includes the need to make prior assumptions about stimulus position rather than about displacement), it predicts that mislocalization is particularly strong if the position of the flash is subject to uncertainty. Thus, if no prior knowledge about the flash position is available, the saccade target stimulus might be

used as prior information (Figure 1C). A similar assumption has been made for explaining the error in spatial localization of a moving object at the time indicated by a brief flash (Brenner, van Beers, Rotman, & Smeets, 2006). It has been proposed that a high degree of uncertainty results in a target bias at the center of gaze which has been modeled as a Bayesian prior around the fovea. This would explain a compression toward the saccade target if the internal eye position is already mapped to the post-saccadic location. If this generalization holds, then compression could be linked to peri-saccadic spatial uncertainty. If there is no uncertainty of the flash position, no mislocalization should occur (Figure 1D).

The previous two models rely on judgements about the transsaccadic stability of space in order to explain mislocalization effects. No unifying theory of distorted spatial perception around eye movements exists at present. The compression of object location toward the saccade target has been suggested to result from peri-saccadic phenomena such as attention (Hamker, 2003; Hamker, Zirnsak, Calow, & Lappe, 2008) or remapping of receptive fields (Ross, Morrone, Goldberg, & Burr, 2001). In particular, Hamker et al. (2008) explained compression by a peri-saccadic shift of attention toward the saccade target (Figure 1E). This idea is build upon earlier models of attention which suggest that attention emerges from different sources of feedback (Hamker, 2005). Prior to an eye movement, activity increases at the location of the saccade target in the oculomotor areas such as the frontal eye field. The feedback of this activity distorts the population response of the flashed stimulus toward the saccade target. Since the flash is brief and the population response vanishes after some time, the brain must rely on the distorted population response to localize an object in space. According to this model, compression should still occur in the presence of spatial tags that

Figure 1. How is the location of a peri-saccadic flash determined? In all graphs, the saccade target is at 0 and the flash is at position 8. (A) In the Object Reference Theory, a briefly flashed stimulus could interfere with the alignment process and its location might be subject to a misalignment toward the saccade target. (B) A location marker at the flash location could be used as a reference object to which the flashed object is aligned. This should abolish mislocalization. (C) From the viewpoint of the Optimal Trans-saccadic Integration Theory, spatial uncertainty of the flash position paired with a bias of the prior toward the saccade target would result in a mislocalization toward the saccade target. (D) A location marker at the flash location could result in a prior at the veridical flash position and thus abolish mislocalization. (E) In the spatial attention account of peri-saccadic compression (Hamker et al., 2008), mislocalization is the result of a spatial attention signal directed toward the saccade target. As a result, the flash's population response gets distorted toward the saccade target. An additional reference object should not abolish mislocalization toward the saccade target, since any transient neural population response will be distorted by a neural gain enhancement.

remove uncertainty. Although subjects know exactly the position of the flash, their visual impression should be like seeing the stimulus closer to the saccade target. Thus, the additional location marker at the upcoming flash position allows us to disentangle post-saccadic influences and uncertainty from transient peri-saccadic effects.

Experiment I: Does compression occur in the presence of a location marker?

Methods

Subjects

Four female subjects S_1, S_2, S_3, and S_4 (between 22 and 28 years old, with normal or corrected to normal vision) participated in the experiment. All subjects were psychology students of the Westfälische Wilhelms-Universität Münster. They were familiar with the literature about peri-saccadic mislocalization and the design of the experiment, but they were naïve to the objective of the experiment. All subjects gave informed consent. All procedures were in accord with institutional guidelines and conformed to the Declaration of Helsinki.

General setup and eye movement recording

The experiments were conducted in a dimly lit room (luminance <0.05 cd/m^2). The head of the subjects was supported by a chin rest during the experimental session. Stimuli were presented on a 19″ monitor (Samsung Sync-Master 950 p) with a visible display size of 37 cm × 28 cm. The viewing distance of 59 cm to the screen resulted in a visual field of 34.8° × 26.7°. The display had a resolution of 800 × 600 pixels and a frame rate of 144 Hz. Movements of the eyes were recorded with a video-based eye tracker (EyeLink, SensoMotoric Instruments, Inc.) at a sampling rate of 250 Hz. The start of the eye movement was determined by a velocity threshold of 35°/s.

Stimuli

All stimuli were presented along the screen's horizontal midline. The fixation and the saccade target were indicated by a cross (0.5° × 0.5° in size). The fixation point (FP) was located 4° from the left side of the screen and the saccade target (ST) was placed 16° to the right of the FP. The location marker, a small horizontal line, had a size of 1.0° × 0.14°. It was shown throughout the trial at one of four possible positions ($P_1 = 8°$, $P_2 = 12°$, $P_3 = 20°$, $P_4 = 24°$) relative to the FP (Figure 2B). The test stimulus, whose perceived location had to be reported, formed together with the horizontal line the letter 'E' (1° × 2° in size) and was shown exactly on the location marker
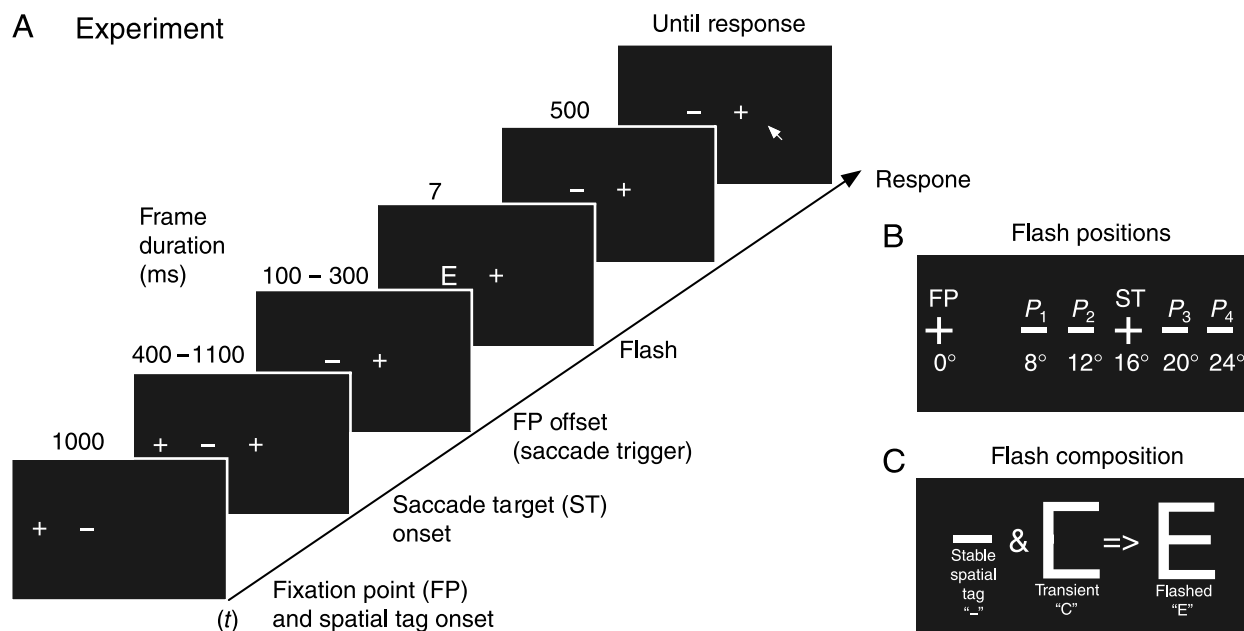

Figure 2. Experimental setup. (A) Presentation procedure. The trial began with the presentation of the fixation cross and the location marker (spatial tag). We used a visually guided delayed saccade task. The subject had to maintain fixation until the disappearance of the fixation cross and then saccade to the already visible target. Around the time of saccade onset, a test stimulus was briefly shown directly on the location marker. Five hundred milliseconds later, a mouse pointer appeared and the subject had to report the perceived location of the test stimulus by a mouse click. (B) Positions of the stimuli on the screen. The saccade target (ST) appeared 16° to the right of the fixation point (FP). The location marker as well as the flashed test stimuli was shown at one of four possible positions (8°, 12°, 20°, or 24°). (C) Composition of the flash. The location marker was visible throughout the trial. In addition, a transient, briefly presented bracket appeared for a single frame so that both together complement to the letter 'E'. Please note that all graphs are not drawn to scale.

(Figure 2C). All stimuli with a luminance of 48 cd/m^2 were shown on a background with a luminance of 7.2 cd/m^2. This results in a Michelson contrast of 0.74.

Instructions

The subjects were familiar with the design and knew that the test stimulus was shown in every trial exactly on the location marker. They were instructed to report the perceived position of the test stimulus.

Procedure

Each trial began with the appearance of the fixation cross and the location marker (Figure 2A). The position of the location marker was randomly chosen from one of the four possible positions. After 1000 ms the saccade target appeared. The trigger to execute the saccade was the removal of the fixation cross, which occurred 400–1100 ms after the appearance of the saccade goal. Immediately after the removal of the fixation cross, the stimulation software controlled for correct fixation to ensure that subjects do not inadvertently fixate the location marker. If subjects did not fixate around ±4° of the fixation cross, the trial was aborted. In order to flash the test stimulus around the time of saccade onset, the time of the flash was between 100 and 300 ms after fixation offset. The test stimulus was presented for a single video frame (7 ms) on the position of the location marker. After the flash, the saccade target and location marker were visible for the remaining time of the trial. Five hundred milliseconds after the flash, the mouse pointer appeared and the subject had to report the perceived position of the test stimulus by a mouse click at the corresponding horizontal position. The next trial automatically began after the response of the last event and a blank screen of 500 ms. Subjects completed multiple experimental sessions over several weeks. Each session consisted of 100 trials.

Data analysis

Data were analyzed in Mathematica 5.2 (Wolfram Research). Trials in which the latency was not between 100 and 400 ms or in which the eye landed more than 3° away from the saccade target were omitted from further analysis. For statistical analysis, we compared the average indicated position in a peri-saccadic time window with the one in a post-saccadic time window, the latter serving as baseline. Note that the post-saccadic time window can extend into the saccade period. Thus, it rather refers to the localization effects outside the critical period around saccade onset. This was done for all four flash positions where all measurements are assumed to be statistically independent. Due to the central limit theorem of statistics, mean values of independent samples of arbitrary distributions with finite variance are approximately normal distributed if the sample size n is sufficiently large.

Usually n is assumed to be large if $n \geq 30$. Thus, the width w of the peri-saccadic time window was chosen to contain at least 30 data points and to lie in the region were the effect is strong according to visual inspection ($\bar{n}$ = 38.38, SD_n = 4.33, $\min_n$ = 33, $\max_n$ = 45, $\bar{w}$ = 38.44, SD_w = 17.67, $\min_w$ = 20, $\max_n$ = 70). To assess the significance of the differences between both time windows, we used Welch's generalization of the independent two-sample t-test for unequal variances. All tests were conducted one sided. The test-wise α'-level was adjusted due to Bonferoni correction ($\alpha' = \alpha/m$, where m is the number of comparisons), since for compression we expect that stimuli at all positions are peri-saccadically mislocalized toward the saccade target. The probability of a Type I error for a given subject is $\alpha = 0.05$. The total numbers of trials that were included in the analysis are listed for each subject and condition in the result figures.

As a control, we performed the same tests after the exclusion of outliers. A measurement was treated as an outlier if it fell outside the region of ±2.5 standard deviations (SDs) around the respective mean. Again at least 30 data points were in the peri-saccadic time window.

We also repeated the analysis (including the removal of outliers) for larger bins ($\bar{w}$ = 64.69, SD_w = 13.84, $\min_w$ = 40, $\max_w$ = 100) covering more data points ($\bar{n}$ = 76.94, SD_n = 28.14, $\min_n$ = 34, $\max_n$ = 126).

To visualize the combined mislocalization effect for each subject across all flash positions, we used the compression index of Lappe et al. (2000) and Michels and Lappe (2004), which is the standard deviation of the mean indicated position over time. A value of 0 indicates no relative compression and a value of 100 indicates maximal compression, i.e., the indicated position of all flash positions would be the same. Mean values were obtained by a sliding mean procedure. Initially, the left and right bin borders were set to the earliest measurement with respect to saccade onset for a given data set. The right border was then moved forward in time until the bin contained 20 data points. The mean indicated position for the bin was computed and assigned to the mean time of that bin serving as a node. After this, the left border was moved forward in time in steps of 1 ms and the above calculations were repeated. If the last bin contained less than 20 data points, it was combined with the preceding one. Finally, the set of all nodes for a given flash position was interpolated linearly.

Results

All four subjects show a clear compression of stimulus location, even though the true location of the flashed test stimulus was provided as a continuously visible reference (Figure 3A). The compression is comparable to that of previous experiments in which the flash position was not
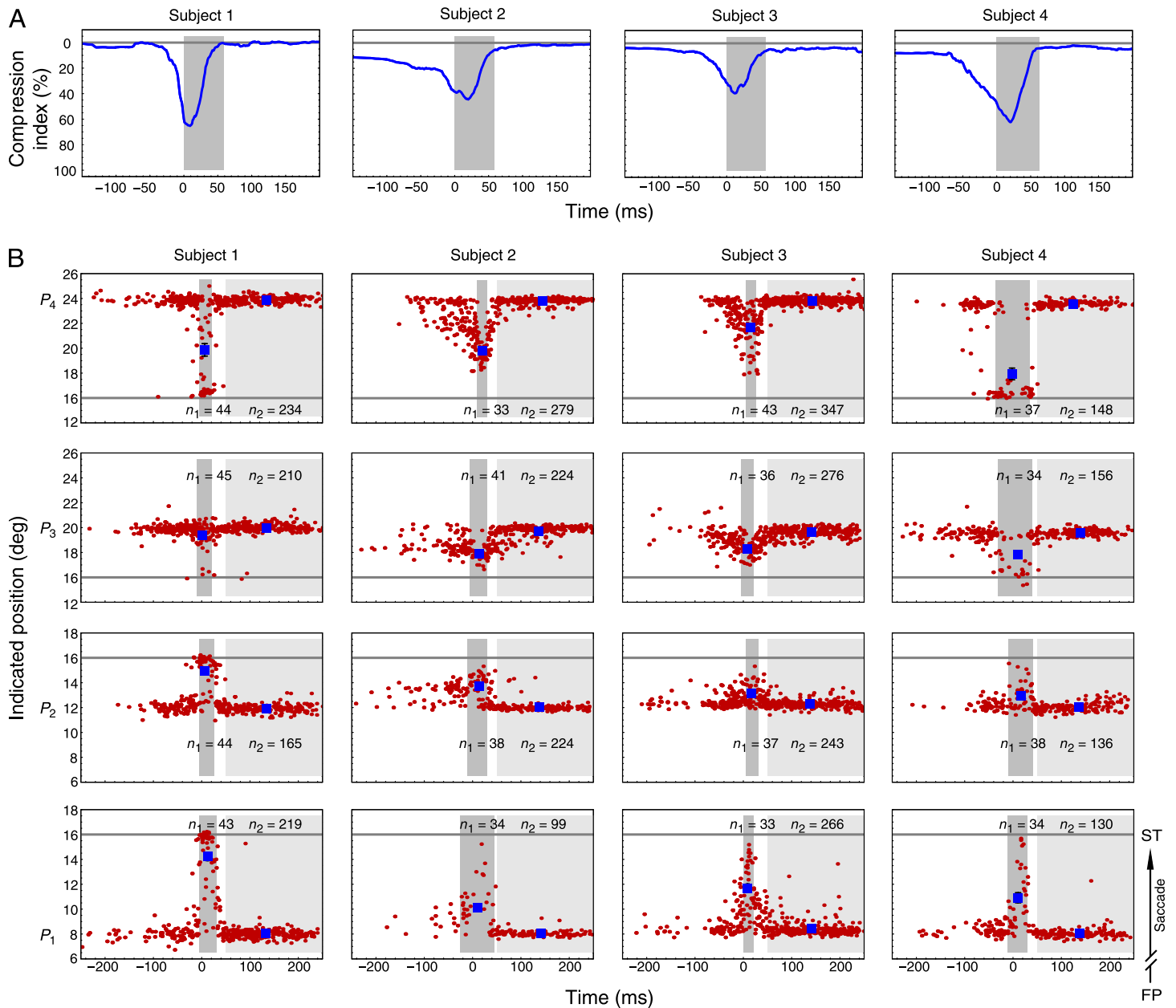
Figure 3. Results of the main experiment for four different subjects. (A) Compression strength as determined by the relative separation. This index indicates the apparent mean separation of the flashed stimuli by calculating the standard deviation across the four perceived locations as a function of time. An index of 0 indicates no compression and an index of 100 indicates maximal compression. The gray area denotes the mean saccade duration of the respective subject. (B) Each panel shows the perceived location of the test stimulus with the time of the flash plotted relative to saccade onset (0 ms). Each column depicts the results at the four different locations ($P_1 - P_4$) where the location marker and the test object have been shown. Each red dot represents the result of a single trial. The position of the saccade target is depicted by the horizontal gray line. The two gray shaded areas in each panel show the parts of the data that were used for further statistical analysis and the numbers report the number of trials that fell in the selected period. The blue square shows the mean perceived location within the selected period and the error bars reflect the standard error of the mean. If no error bars are shown, they are smaller than the squares. All subjects show compression. At each of the four possible positions, within a critical period around saccade onset, the flash is mislocalized in the direction of the saccade target. All mean perceived locations of the trials around saccade onset (dark gray shaded area) are significantly different from the post-saccadic means (light gray shaded area).

predictive. Compression starts about 50 ms before saccade onset, peaks in the early phase of the eye movement and varies between subjects from 40% to 65%. Particularly, the time course of compression fits well to the data obtained by Michels and Lappe (2004) who investigated the change of compression dependent on contrast for a 20° saccade without a location marker and used the same eye tracker. For high contrasts, comparable to those of our study, the peak compression occurred shortly after the eyes start to move and began around 50 ms before saccade onset. The strength of peak compression observed was also around 50%.

All trials for all subjects are shown in Figure 3B. We can observe that in the critical period around saccade onset the stimuli at all flash positions are mislocalized toward the saccade target. For statistical analysis, we compared the average indicated position in the peri-saccadic and post-saccadic time windows. We define compression if, at all four positions, stimuli are peri-saccadically mislocalized toward the saccade target. For all subjects, all deviations are highly significant. A summary of the statistics is given in Table 1. We ran additional tests (see Data analysis section) to test the robustness of the effects (test results are not shown): When removing outliers, all differences remain significant. Further, the obtained result is not dependent on a particular time window for the peri-saccadic case. All differences remained significant also for a broader peri-saccadic time window. Since subject S_2 seems to have an elevated baseline in the pre-saccadic case, we used post-saccadic baselines for all subjects. However, we also obtain significant results for subject S_2 when using a pre-saccadic baseline.

We conclude that neither prior knowledge about the flashed object's location nor the post-saccadic reference object prevent peri-saccadic compression. Even when the subjects knew the exact position and a spatial tag was visible throughout the trial, they nevertheless saw the flashed object closer to the saccade target. This observation argues against the idea that the compression of objects toward the ST inherently depends on an uncertain location of the flashed object. It also suggests that the flashed object is not anchored to the reference object.

Nevertheless, subjects could have used the cross indicating the saccade target as a reference. Although the subjects knew that the flash occurred on the dash, they might have used the saccade target as a reference object because it is particularly emphasized by spatial attention. To exclude this possibility, we ran a control experiment with a memory guided saccade.

Control experiment I: Memory guided saccade condition

In the first control experiment, the saccade target was presented only briefly and extinguished well before the saccade was initiated. Thus, at the time of the saccade and thereafter the reference object was the only visible stimulus in addition to the flash. This rules out the possibility that the visibility of the saccade target diminishes the influence of the reference object.

Subject	Flash position	$\bar{x}_1$	$\sigma_1^{\bar{x}}$	$\bar{x}_2$	$\sigma_2^{\bar{x}}$	t	df	p
S_1	P_1	14.22	0.35	8.02	0.04	17.43	43	2.05×10^{-10}
	P_2	14.93	0.21	11.92	0.03	14.01	44	3.44×10^{-10}
	P_3	19.41	0.15	19.98	0.03	-3.78	48	2.16×10^{-4}
	P_4	19.87	0.50	23.88	0.02	-8.00	43	2.33×10^{-10}
S_2	P_1	10.12	0.31	8.05	0.03	6.71	33	5.75×10^{-8}
	P_2	13.69	0.16	12.05	0.03	9.91	40	1.13×10^{-12}
	P_3	17.91	0.09	19.72	0.04	-18.94	53	1.24×10^{-25}
	P_4	19.84	0.18	23.80	0.02	-21.56	32	3.43×10^{-21}
S_3	P_1	11.69	0.37	8.43	0.04	8.91	32	1.47×10^{-10}
	P_2	13.12	0.14	12.30	0.02	5.78	37	5.78×10^{-7}
	P_3	18.31	0.13	19.63	0.02	-9.80	37	3.86×10^{-12}
	P_4	21.67	0.21	23.83	0.01	-10.11	42	3.61×10^{-13}
S_4	P_1	10.92	0.41	8.05	0.04	7.02	33	2.22×10^{-8}
	P_2	12.97	0.17	12.06	0.03	5.24	39	2.81×10^{-6}
	P_3	17.81	0.25	19.59	0.03	-6.87	33	3.34×10^{-8}
	P_4	17.95	0.47	23.55	0.04	-11.92	36	1.72×10^{-14}

Table 1. Statistics of the main experiment. Mean values and standard errors of the mean are shown for the peri-saccadic time window ($\bar{x}_1$, $\sigma_1^{\bar{x}}$) and the post-saccadic baseline ($\bar{x}_2$, $\sigma_2^{\bar{x}}$) together with the corresponding t statistic, the degrees of freedom (df), and the p values. The critical p value is $p = 0.0125$.

Methods

Subjects

Two subjects (S_3 and S_4) that participated in the main experiment took part in the control experiment.

Procedure

The control experiment was identical to the main experiment with the exception that subjects had to execute a memory guided saccade and stimuli were only presented at positions $P_1 = 8°$ and $P_4 = 24°$. The saccade target was only shown for 200 ms and remained invisible for the rest of the trial (Figure 4). The signal to saccade was the removal of the fixation cross 300–700 ms after saccade target offset. The remaining procedure was identical to the main experiment with the visually guided saccade.

Data analysis

The general procedure was identical to the analysis of the main experiment. First, a peri-saccadic time window containing at least 30 measurements was compared to a post-saccadic baseline. The peri-saccadic window size for S_3 was $w = 40$ with $n = 34$ for both P_1 and P_4. The window size for S_4 was $w = 95$ with $n = 31$ for P_1 and $w = 70$ with $n = 36$ for P_4. The same analysis was run after the removal of outliers. We also repeated the analysis for larger bins covering more data points. The window size for S_3 was $w = 75$ with $n = 73$ for P_1 and $w = 85$ with $n = 79$ for P_4. The window size for S_4 was $w = 120$ with $n = 77$ for P_4. The time window for P_1 was
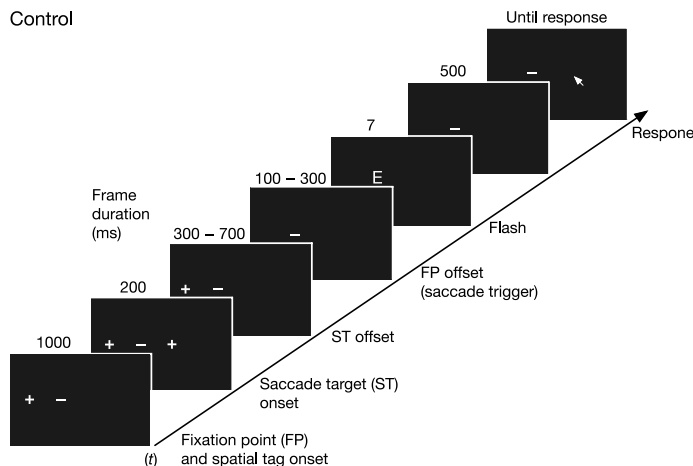

Figure 4. Control experiment. In order to ensure that the results are not biased by the presence of the saccade target, we performed a control experiment with a memory guided delayed saccade task. The saccade target was only visible for 200 ms and then disappeared for the rest of the trial. The trigger for the saccade was given 300–700 ms after the disappearance of the saccade target. The location marker as well as the flashed test stimuli was shown at one of two possible positions (8° or 24°). Please note that all graphs are not drawn to scale.
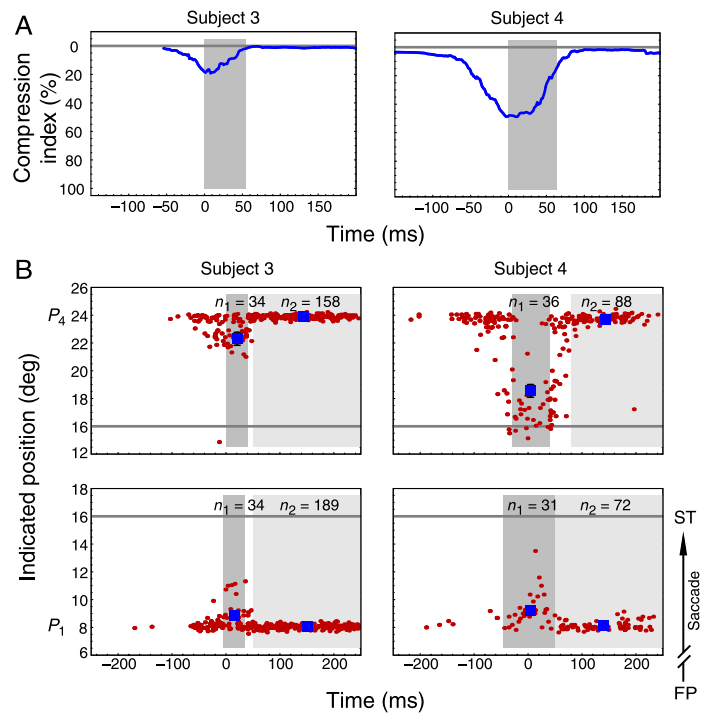

Figure 5. Results of the control experiment for the two participating subjects S_3 and S_4. (A) Compression strength in the control experiment with the reference object as the only reference available. Same notation as in Figure 3A. (B) For the composition of each panel, refer to Figure 3B. Similar to the condition where the saccade is visible, the two tested subjects show a mislocalization in the direction of the saccade target. All mean perceived locations of the trials around saccade onset (dark gray shaded area) are significantly different from the post-saccadic means (light gray shaded areas).

identical to the one used in the initial analysis since it contained already all measurements where the effect was apparently visible.

Results

Both subjects show compression (Figure 5A). The systematic mislocalization toward the saccade target in the critical time period (Figure 2B) is statistically significant (Table 2). Thus, even when the dash was the only visual reference available, subjects perceived the flashed stimulus closer to the saccade target.

Control experiment II: Peri-saccadic object perception

When we asked the subjects about their peri-saccadic percept, they reported having seen the entire letter 'E', not

Subject	Flash position	$\bar{x}_1$	$\sigma_1^{\bar{x}}$	$\bar{x}_2$	$\sigma_2^{\bar{x}}$	t	df	p
S_3	P_1	8.84	0.19	8.05	0.01	4.24	33	8.34×10^{-5}
	P_4	22.30	0.46	23.88	0.01	-3.41	33	8.77×10^{-4}
S_4	P_1	9.24	0.22	8.11	0.04	5.14	31	6.70×10^{-6}
	P_4	18.55	0.46	23.69	0.08	-11.09	37	1.18×10^{-13}

Table 2. Statistics of the Control experiment I. Mean values and standard errors of the mean are shown for the peri-saccadic time window $(\bar{x}_1, \sigma_1^{\bar{x}})$ and the post-saccadic baseline $(\bar{x}_2, \sigma_2^{\bar{x}})$ together with the corresponding t statistic, the degrees of freedom (df), and the p values. The critical p value is $p = 0.025$.
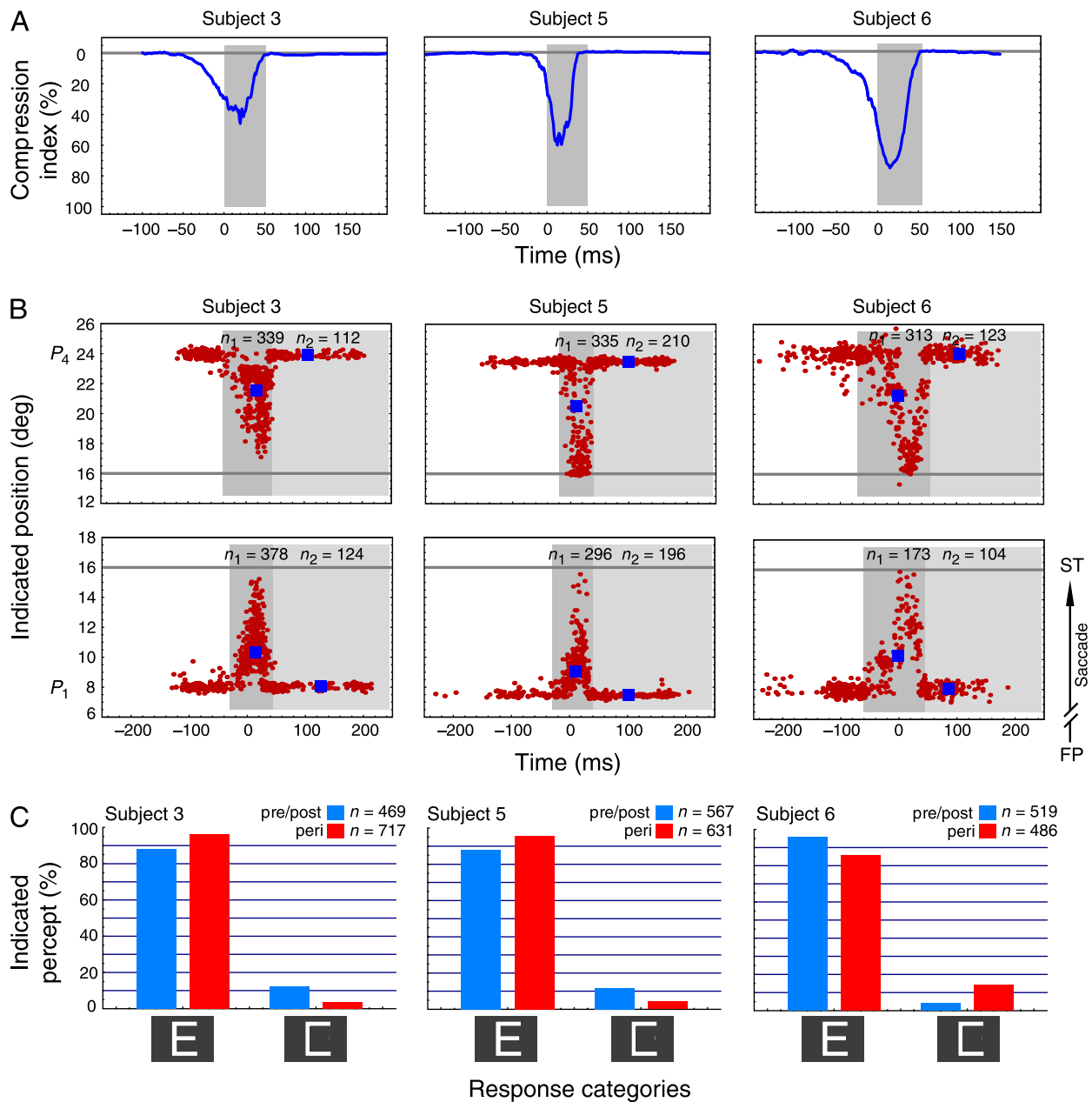

Figure 6. Results of the control experiment for three subjects S_3, S_5, and S_6. Same notation as in Figure 3. (A) Compression strength. (B) Perceived stimulus location in each trial. (C) Indicated percept. The data have been assigned into a pre/post- and peri-saccadic condition depending on the intervals used for data analysis in (B). The number of trials in each condition is given at the top right of each panel. Subjects were asked to indicate whether they have perceived the letter 'E' or the bracket. In the majority of trials, all subjects reported to see the letter 'E'.

merely the transient bracket, closer to the saccade target (Figure 2C). To quantitatively estimate the perceived object shape, we ran a further experiment in which subjects reported their percept after each trial.

Methods

Subjects

Three subjects (S_3, S_5, and S_6) participated in the control experiment. S_5 and S_6 are Ph.D. students of the West-fälische Wilhelms-Universität Münster. S_5 (female) was naïve to the objective of the experiment. S_6 (male) is an author of the manuscript.

Procedure

The control experiment was identical to the main experiment with one exception: after the subject reported the perceived location of the flashed object, a choice display appeared asking the subject for the percept in the trial. The subject had to decide between two categories: the perception of the letter 'E' or the bracket. The report choices had to be made by a mouse click on one of the category icons. Furthermore, the subjects had to indicate if the dash was perceived in addition to the E or the bracket. This latter question was included in order to see whether, in case of a mislocalized flash, the dash was perceived at its veridical location concurrently with the flash, or whether it was only visible as part of a bound object.

Data analysis

The general procedure was identical to the analysis of the main experiment. We classified the trials into pre/post- and peri-saccadic cases to evaluate if the percept in the critical period around saccade onset differed from the percept long before or after saccade.

Results

All subjects showed compression (Figures 6A and 6B). The systematic mislocalization toward the saccade target in the critical time period (Figure 3B) is statistically significant ($p < 0.025$). All three subjects reported to perceive the letter 'E' in more than 80% of the trials in the peri-saccadic case as well as in the pre/post case. When mislocalization occurred, the subjects perceived the flash ('E' or bracket) concurrently with the dash (S_3: 100%, S_5: 91.44%, and S_6: 99.59%). Thus, in the case of mislocalization, subjects most often perceived the letter 'E' and simultaneously a dash. This suggests that the bound object rather than the transient is subject to mislocalization.

Discussion

We investigated the relationship between peri-saccadic compression and mechanisms of visual stability. Theories of visual stability have been primarily developed to explain why we do not perceive a displacement of a stimulus (Bridgeman et al., 1975; Deubel et al., 1996, 1998, 2002; Niemeier et al., 2003, 2007). Another line of experiments used briefly flashed stimuli to reveal the mechanisms that lead to the subjective experience of a stable world (Bischof & Kramer, 1968; Lappe et al., 2000; Matin & Pearce, 1965; Morrone et al., 1997; Ross et al., 1997; Schlag & Schlag-Rey, 2002). In these experiments, a strong dissociation occurred between trials performed in total darkness, without reference stimuli available, and trials ran under illuminated conditions in which other stimuli than the flashed ones were available. In total darkness, the mislocalization shows a shift in saccade direction, whereas under illuminated conditions a mislocalization toward saccade target, known as compression, occurs. The shift in direction to the saccade vector even occurs in the presence of pre-saccadic references (Cai, Pouget, Schlag-Rey, & Schlag, 1997). To shed light on the different observations made under complete darkness and illuminated conditions, Lappe et al. (2000) investigated the influence of (post-saccadic) references, compared to a no reference condition, and observed compression primarily in the reference condition. The simplest interpretation of this result is that (post-saccadic) references are causally relevant for compression. Hamker et al. (2008) instead suggested that compression occurs pre-saccadically because of spatial attention directed to the saccade target. This model is supported by the recent observation that compression (at least in the sense that the distance between the indicated perceived positions shrinks) occurs for near-threshold stimuli in total darkness (Georg et al., 2008). Moreover, compression of verbally reported relative stimulus distances has also been observed without visual references when the subject was stimulated with uniform bright light after saccade onset (Morrone, Ma-Wyatt, & Ross, 2005); a finding that is equally consistent with the model. To shed more light on the different mechanisms involved in localizing a flashed stimulus, the present study investigated how post-saccadic mechanisms for visual stability could possibly affect compression. The study is in several ways distinct from the one of Lappe et al. (2000), where the reference was given in form of a horizontal ruler. This ruler did not unambiguously mark the location of the flash in any given trial, since the flash randomly appeared at one of four potential ruler locations. Moreover, the ruler was effective in eliciting compression even when presented only after the saccade and not at the time of the flash. Therefore, references provided by the ruler in Lappe et al. (2000) were not so much informative about the flash location but

rather provided post-saccadic information about the location of the saccade target. In the present study, we used spatial tags to make the flash location fully predictive. The usage of a spatial tag has the advantage that it can serve two functions (depending on the theoretical viewpoint). First, it indicates the exact location of the flash, and thus, it potentially removes the uncertainty in location due to the brief test stimulus presentation. Second, it can establish a spatial reference. Deubel et al. (2002) demonstrated that a spatial reference is established, even if the post-saccadic stimulus is dissimilar to the pre-saccadic one.

According to our results, peri-saccadic compression does not crucially depend on the uncertainty of the stimulus location. Around saccade onset, the briefly flashed stimuli were perceived closer to the saccade target, even when the saccade target was not visible and the spatial tag was the only visible reference. Theories of post-saccadic stimulus localization (originally designed to explain Saccadic Suppression of Displacement) cannot be easily expanded to account for the compression of visual space. Our results argue against Optimal Integration as compression occurred although there was no uncertainty about the stimulus position. However, we made the specific assumption that a spatial tag for the flashed stimulus location translates into a prior for the flash position. Our results also argue against the Object Reference Theory as a cause for compression. A continuously visible reference was not used as a spatial tag to post-saccadically align the peri-saccadic flash to the reference. We want to emphasize that the authors of these theories did not claim that their theories are applicable in the experimental condition using brief flashes. However, the search for a unifying account of peri-saccadic perception requires to test the generalizability of the existing theories. These generalized Optimal Integration and Object Reference theories would predict no mislocalization in our experimental condition. We observed a similar range of compression as in previous experiments (Michels & Lappe, 2004) with similar contrast but different subjects, yet we cannot rule out less strict versions of these theories which might still predict compression in such conditions.

Our findings support the recent computational model explaining peri-saccadic compression by directing spatial attention to the planned saccade endpoint (Hamker et al., 2008). The simulations demonstrate that attention, implemented as a neural gain control, leads to a distortion of the neural stimulus representation. When this distorted population response is decoded for stimulus position, the model replicates the typical pattern of compression. In the vast majority of trials, subjects perceived the letter 'E' concurrently with a dash, even when the letter was perceived to be mislocalized. Thus, the dash was at the same time part of the mislocalized object and was visible in its veridical location. This suggests that the transient bracket stimulus was bound with the dash into a single

object which was then shifted in spatial position. Such a late distortion of spatial position has been predicted by the model (Hamker et al., 2008). The processes of how the brain transfers a retinocentric representation into an eye movement invariant representation by using references or eye position signals is beyond the scope of the model, which uses an ideal transformation to localize a stimulus in a world-centered coordinate system.

Thus, a complete model of peri-saccadic perception relies presumably on at least two steps (Awater & Lappe, 2006), i) a peri-saccadic mechanism that distorts the population response resulting in compression in retino-centric coordinates and ii) a post-saccadic scene construction that takes additional information, such as the distance to other objects into account. Our data, in particular the memory guided saccade condition, speaks against a simple alignment procedure in the second stage. Some additional knowledge must be used by the visual system to prevent the peri-saccadically distorted population from being post-saccadically anchored to the reference. Probably, only the reference object is used for the alignment procedure which would still require that the visual system can differentiate between the neural population response of the flash and the reference object. Under this assumption, the whole post-saccadic scene, including the stimulus trace from the peri-saccadic flash, could be transformed by the same parameters.

The combination of a peri-saccadic distortion for compression with an optimal inference account as the second stage could also be flexible enough to be consistent with our data. In this case, the flash position is peri-saccadically distorted toward the saccade target and post-saccadically aligned to the reference depending on the prior assumption about its location. The problem with this explanation, however, is that a strong stability assumption should counteract the distortion from the early stage. In contrast, we observe a clear mislocalization in the direction to the saccade target (Figure 3). Therefore, a combined model requires that the flash is not localized by using a prior. Binda, Bruno, Burr, and Morrone (2007) also used an optimal inference approach between corollary discharge and the retinal signal to simulate the displacement of flashes into the direction of the saccade vector. They applied a cue integration approach and did not use a prior. A prior should only be used to connect the pre-saccadic scene with the post-saccadic scene via the reference object and the already distorted flash should be localized relative to the reference object. Again, this would require that the brain has a neural mechanism available that allows to generate a prior and selectively apply this prior only to the static stimulus. Future models that aim to combine both stages require independent measures of the prior. Thus, our observations challenge existing theories of space perception. A combination of the theories into a two-step account demands a more detailed description of the usage of prior knowledge and of post-saccadic mechanisms for visual stability, but it

appears feasible that a future unifying account of peri-saccadic perception should consider both early attentional effects and late post-saccadic mechanisms of scene construction.

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