Visual and non-visual factors in peri-saccadic compression of space

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Abstract

The perceptual stability of visual space becomes fragile in the wake of a saccadic eye movement. Objects flashed shortly before a saccade are mislocalized towards the saccade target. Traditional accounts for this effect have associated the mislocalizations with a sluggishness of the efference copy signal, which is important in space perception across eye movements. Recent theories of space perception, however, have emphasized a role of visual memory in the generation of trans-saccadic spatial stability. We have investigated the role of visual processes in the peri-saccadic compression of space. In our experiments, subjects performed saccades in front of a computer display while visual stimuli were briefly flashed on the screen just before or during the saccade. Subjects had to report the perceived location of the flash. When the saccade target's position was visibly available after the saccade, the perceived location of the flash was compressed towards the target's position. This compression occurred along the axis of the saccade, but for parts of visual space also along a direction orthogonal to the saccade. When the saccade target was not available after the saccade, the perceived location of the flash showed only a slight shift in saccade direction. In this condition, however, the perceived location of the saccade target itself was drawn towards the position of the flash. We propse a framework to explain these findings by a combination of pre- and post-saccadic processes.

Introduction

The overtly observable aspects of a saccade are very small. The saccade involves only a tiny motion of the eyeball. Yet, this tiny motion is orchestrated by the coordinated activity in a large network of interconnected brain areas. It spans all the way from the brain stem to mid-brain and cerebellar areas and several parts of the cortex. Moreover, the tiny eye movement of a saccade asserts massive influences on visual perception. On the one hand, because it provides necessary updates for vision to scan a scene and, on the other hand, because it causes dramatic changes to the visual input giving rise to problems of visual stability. In this paper, we will discuss effects that saccades induce in the localization of visual objects around the time that the saccade is initiated.

It has long been known that visual localization errors occur when a stimulus is briefly presented in the wake of a saccade (Matin & Pearce, 1965; Bischof & Kramer, 1968; Honda, 1989; Dassonville, Schlag & Schlag-Rey, 1995). In these experiments visual probe stimuli, usually small spots of light or luminous bars oriented orthogonal to saccade direction are presented for a few milliseconds as an observer prepares and executes a saccade. The observer is instructed to report the apparent position of the probe either using some pointing device that could be adjusted after the saccade or by relating the probe to reference stimuli such as a ruler or a previous or subsequent test stimulus. Localization is found to be close to veridical for probe stimuli presented more than 100 ms before or after a saccade. Stimuli presented from about 100 ms before to sometime during the saccade are mislocalized. The spatial and temporal pattern of localization errors obtained in such experiments gives rise to discussions about the origin of the mislocalization, and the brain processes that occur during the preparation and execution of saccades.

A number of studies have reported mislocalizations that consist of a spatially uniform shift of all apparent positions. This shift is in the direction of the saccade from up to 100 ms before saccade onset until about saccade onset (Honda, 1991; Dassonville, Schlag & Schlag-Rey, 1995). During the saccade, the shift is against saccade direction but still spatially uniform. This pattern of errors may be explained by a mismatch in time course between a presumed reference signal of eye position (von Helmholtz, 1896; von Holst & Mittelstaedt, 1950; Sperry, 1950), the true eye position, and the latency of the visual stimulus (Honda, 1991; Schlag & Schlag-Rey, 2002; Pola, 2004). Other studies have reported errors that are spatially non-uniform and consist of an apparent compression of spatial positions so that they cluster around the saccade target (Bischof & Kramer, 1968; Ross, Morrone, & Burr, 1997; Morrone, Ross, & Burr, 1997). These mislocalizations begin about 50 ms before saccade onset and peak close to saccade onset.

In the following we will discuss several experiments that looked into the role of visual and non-visual factors in peri-saccadic compression, present new data from an experiment investigating potential motor contributions from subsequent saccades, and propose a conceptual framework to explain the various findings.

Visual factors

Visual factors play an important role in distinguishing shift and compression. Studies that reported spatially uniform shift were typically conducted in darkened labs (Honda, 1989; Dassonville, Schlag & Schlag-Rey, 1995; Cai, Pouget, Schlag-Rey, & Schlag, 1997). At the onset of a saccade, only the probe stimulus was visible but no other visual object that could serve as a positional reference. Studies that found compression, on the other hand, involved stimulus presentation on a screen that contained, next to the brief probe flash, also reference objects such as a visual background or a ruler whereto the observer had to relate the probe position (Bischof & Kramer, 1968; Ross, Morrone, & Burr, 1997; Morrone, Ross, & Burr, 1997, see also Honda, 1993). Testing the same observers in both conditions we found that the presence or absence of a ruler on the stimulus screen strongly influenced the observed pattern of mislocalization (Lappe, Awater, & Krekelberg, 2000). In that experiment, observers performed a 12.8 deg visually guided saccade in front of a large dark projection screen in a dark experiment room. They initially fixated a bright fixation point that jumped 12.8deg to the right and was extinguished 50 ms later. Because the average latency of the saccade that followed the jump was around 200 ms no visual reference stimuli were available at the time of saccade onset or afterwards. The probe was a vertical bar that was flashed at one out of four locations around that saccade target. The observer reported the perceived probe position by adjusting a mouse pointer appearing 500 ms after the saccade. The apparent position of those probes was analyzed in relation to their presentation time relative to saccade onset. We found that the four probe positions were uniformly shifted first in and then against the direction of the saccade similar to the shift reported in earlier studies (Fig. 1A, left). However, when we introduced, in a second condition, a continuously visible ruler on the screen, which could serve as a visual reference for probe and target position, the spatial pattern of mislocalization changed and a strong compression of the apparent probe position towards the saccade target became visible (Fig. 1A, right). To assess the strength of compression quantitatively we calculated the standard deviation between the four apparent probe positions at each point in time for a measure of the average apparent separation of the probe positions. We then calculated the mean apparent separation in the 50 ms before saccade onset, i.e., when the eye was still fixating, and compared it to the mean separation 100 ms before and after the saccade. This resulted in a percentage measure of the compression immediately before the saccade. This procedure gave no compression in the darkness condition and strong compression in the ruler condition (Fig. 1B, dark bars). We concluded that the strength of compression was dependent on the presence of the ruler.

The ruler in that experiment provided spatial references about probe and target positions but also retinal illumination that might have modified the contrast of the probe. In further experiments we found that both factors influence the strength of compression. The influence of contrast was measured in an experiment in which the contrast of the probe to the background was varied (Michels & Lappe, 2004). In this experiment, the screen background was dark grey (luminance 13.2cd/m^2) while the probes had luminance between 14.3cd/m^2 and 61.3cd/m^2. The strength of apparent compression varied with stimulus contrast such that strongest compression was observed at lowest contrast.

The influence of visual references we measured by varying the times at which the ruler was present on the screen (Lappe, Awater, & Krekelberg, 2000). We found that compression was weak when the ruler was present before, but not after, the flash of the probe (Fig. 1B, before and after probe conditions). Compression was strong when the ruler was present after the saccade, independent of whether it was visible at the time the probe was flashed, or not (Fig. 1B, ruler and after-saccade conditions). This suggests that the spatial reference information provided by the ruler is evaluated mainly after the saccade and that the apparent compression of stimuli presented before the saccade is at least partly dependent on signal processing that occurs after the saccade. To further determine the time course over which the ruler influences localization errors we varied the onset time and duration of the ruler presentation after the saccade. When the ruler was turned off when the probe flashed and switched on only 250 ms later the apparent compression was diminished (Fig. 1B, 250ms-gap condition). When the ruler was present only from saccade offset up to 100 ms later, compression strength was also diminished (Fig. 1B, 100ms-duration condition). These results suggest that there is a temporal window immediately after the saccade when the presence of visual references influences the strength of compression.

To further compare the contribution of retinal stimulation and contrast reduction provided by the ruler with that of visual references also provided by the ruler we introduced a further condition. In this condition, the ruler was replaced by a horizontal white line, visually identical to the ruler but with no tick marks or numbers present (Awater & Lappe, 2005). This line provides retinal stimulation and contrast reduction but no visual references along the saccade direction. Consistent with the prediction that both factors contribute to compression strength the compression was about half of that observed with the tick marks (Fig 1B, line condition compared to ruler condition). But a second perceptual effect became very much apparent in this experiment: although the saccade target was always presented at the same spatial location it appeared to be at different locations for the different probe positions. Asking observers to report the apparent location of the saccade target rather than of the probe quantitatively confirmed this observation (Awater & Lappe, 2005). Depending on the probe position the saccade target could be mislocalized by several degrees of visual angle. This mislocalization was such that the distance between the apparent target position and the apparent bar position was compressed. When we calculated a compression index for the apparent bar-target distance, a sizable compression also became visible in the darkness condition and the compression in the line condition became equal to the compression in the ruler condition (Fig. 1B, gray bars). Although perceived target locations were influenced by the flash of the probe, saccadic amplitudes remained veridical when the probe was flashed within 100 ms before saccade onset. Thus, the saccade target's apparent position, which was visually indicated only for 50 ms after fixation point onset, could be decoupled from the motor command that drives the saccade. Moreover, the mislocalization of the saccade target occurred also without a saccade (Awater & Lappe, 2005). When the sequence of fixation point offset, target on- and offset, and probe presentation was run with the explicit instruction to keep fixation throughout the trial (i.e. not make a saccade to the target) the perceived location of the target was shifted towards the probe position very much like in the saccade condition. Compression of the probe positions did not occur in this situation.

The apparent position shift of the target in saccade and fixation conditions suggests that the target shift results from visual factors unrelated to the saccade, or possibly from covert saccade planning that might have occurred in the fixation condition. We will now turn to the role of motor parameters in peri-saccadic compression and return to the target mislocalization in the presentation of the proposed framework for peri-saccadic mislocalization.

Motor factors

The necessity of saccade execution for the compression effect has been investigated by comparing perception during executed saccades with perception during 'simulated' saccades, in which the visual stimulation during the saccade is mimicked as closely as possible by moving the visual image at saccadic speeds while the observer fixates. Apparent position shifts of probe stimuli occur also in such experiments, but the pattern of mislocalization differs from that observed during real saccades (Morrone, Ross, & Burr, 1997). Thus, the execution of the saccade contributes to the compression. Because peri-saccadic mislocalization during real saccades begins already for stimuli presented 50-100 ms before the saccade, i.e., when the eye is still directed towards the fixation point the role of the actual movement of the eye is not clear. Motor signals that drive the eye movement - or colloraries of these signals - are likely involved. Two experimental paradigms, the anti-saccade task and saccadic adaptation, have been used to differentiate between motor execution and motor planning (and visual stimulation factors).

In the anti-saccade task, when the fixation point jumps in a certain direction, observers are instructed to withhold the saccade in the direction of the jump, and to perform a saccade in the opposite direction of the jump. In this case, the peripheral visual stimulus, i.e., the saccade target in regular or pro-saccade trials, is decoupled from the motor planning and execution of the saccade. Thus, one may ask whether peri-saccadic compression is directed towards the visual image of the saccade target, or towards the motor signal of the saccade. In these experiments, peri-saccadic localization errors were directed in the direction of the actual saccade, not towards the visual target stimulus (Awater & Lappe, 2004). Strength of compression was identical in anti- and pro-saccade trials. This suggests that the actual motor plan underlies the compression.

In the saccade adaptation paradigm, the visual target location and the motor execution of the saccade become decoupled through an adaptation process. As the observer executes a saccade induced by a target jump of a defined size the target is slightly displaced during the saccade. Therefore, at the end of the saccade there is an error between the landing position of the eye and the post-saccadic target position. When this procedure is repeated for a number of trials the amplitude of the induced saccade gradually adapts such that the saccade will end closer to the post-saccadic target position. After the adaptation procedure, a target jump of the defined size induces a saccade of the adapted amplitude. Thus, target location and motor execution are decoupled. Awater, Burr, Lappe, Morrone, and Goldberg (2004) measured peri-saccadic compression after saccadic adaptation. They presented probe flashes around the occurrence of adapted saccades. Adaptation changed the pattern of compression such that probe positions at saccade onset were seen closer to the landing point of the eye rather than the initial target location. Like the results of the anti-saccade study, the results of the adaptation experiment, therefore, suggest that the motor plan of the actually executed saccade is the driving force behind the compression. There is, however, a caveat to this conclusion because the experiments showed that also probes outside the temporal range of peri-saccadic compression, i.e., probes presented more than 100 ms before saccade onset were mislocalized. This early pre-saccadic mislocalization shifted apparent probe positions in the direction of adaptation. For instance, when the saccadic amplitude was reduced by back-stepping the target during the saccade perceived pre-saccadic probe positions similarly shifted backwards in parts of the visual field. Thus, the clustering of apparent probe positions near the actual saccade landing position at saccade onset may result partly from a combination of adaption-induced position shifts and peri-saccadic compression towards the initial target position.

The above studies show that the saccadic motor plan, or a corollary of it, is involved in generating the compression. An oculomotor feedback signal of the saccadic motor plan may originate from a number of brain structures that are involved in saccade planning or execution. Depending on where the signal originates in the brain it might be encoded as direction and amplitude or as a two dimensional map of saccade goal position. The second, but not the first, case predicts that mislocalizations should occur in a two-dimensional manner around the saccade goal position. We have tested this in an experiment in which probes of small light dots were used that were arranged in a grid around the saccade target position. The peri-saccadic mislocalization of these probe positions showed a clear two-dimensional pattern such that positions at high eccentricities were mislocalized in oblique directions towards the saccade goal (Kaiser & Lappe, 2004). Thus, the saccade-related signal that drives the mislocalization is a signal of goal position rather than saccade amplitude.

If the compression is induced by an oculomotor feedback signal then one may also ask how compression is related to the planning and execution of subsequent saccades. It is known that perceptual and motor processes in single tasks can be decoupled. Specifically for saccadic compression, it has been reported that pointing movements towards the apparent position of the peri-saccadic probe do not exhibit compression although perceptual judgments of probe position do (Burr, Morrone, & Ross, 2001). We were therefore, interested in the question of whether targeting saccades to the apparent probe position conducted after the primary saccade to the target show evidence of compression. In these experiments, subjects were seated in front of a monitor that displayed an initial fixation point 10 deg left of the center and a gray visual background containing a black ruler. When the fixation point jumped 20 deg to the right (towards position 10 deg) subjects performed a saccade towards that position. A vertical bar was flashed as the probe for 8 ms at a random time around saccade onset at one of seven possible locations (-22.4 deg., -14.9 deg., -7.6 deg., 0 deg., 7.6 deg., 14.9 deg., 22.4 deg.). Subjects were instructed to direct their gaze after the primary saccade to the apparent position of the probe stimulus and to keep fixating that position. Gaze direction was measured with an SMI EyeLink video-based eye tracker at a temporal resolution of 250Hz. Final gaze positions after the secondary saccade were taken as measurements of the targeting saccade to the apparent probe positions. These measurements were compared to perceptual ratings taken in separate trials in which subjects had to indicate the apparent probe position with a mouse pointer. Fig. 2A,B shows results of this experiment for one subject. The lines give running averages of apparent probe positions for the seven true probe positions in the 300 ms around the saccade. Saccade onset is at 0 ms. A comparison of the plots for mouse pointing (Fig. 2A) and gaze direction reveals that compression is very similar in the two conditions. The percentage of compression in the 50 ms before the saccade was the same in both conditions. This shows that perceptual and saccade targeting mislocalizations are identical. Thus, the compression observed in the perceptual judgments is reflected also in the positions of targeting saccades. Similar results have been reported in investigations of the peri-saccadic shift of apparent positions in the dark using the double-step saccade paradigm (Dassonville, Schlag & Schlag-Rey, 1995; Honda, 1997).

Since mislocalizations in perceptual judgments and targeting saccades are so similar, one must ask whether perceptual judgments rely on the execution of subsequent saccades. This would seem possible if subjects, after the primary saccade, conduct first a saccade to the apparent probe position before they report the probe position verbally or with a pointer. We therefore, tested a further condition in which subjects had to give perceptual judgments with a mouse pointer but were required to keep fixation at the target position after the primary saccade (Fig. 2C). Compression in this condition was of equal strength to the compression observed under free eye movements after the primary saccade and under conditions of targeting saccades after the primary saccade. Thus, we conclude that secondary targeting saccades are unnecessary for compression to occur and that the compression observed in the targeting saccades likely results from the use of the compressed perceptual signal for planning these eye movements.

A conceptual framework for peri-saccadic mislocalization

The studies described above revealed different types of perceptual mislocalization at the time of saccadic eye movements. In some conditions, a uniform mislocalization in the direction of the saccade occurred. In other conditions, mislocalizations resembled a compression of visual space around the saccade target. The uniform shift occurred when no visual references were available immediately after the saccade and when probe stimuli were of high contrast. Compression occurred when probe stimuli were of low contrast and visual references were present immediately after the saccade. Thus, the visual parameters of the stimuli as well as the presence or absence of visual references immediately after the saccade are important for the compression of the apparent position of peri-saccadically flashed objects.

An explanation for the described properties of the compression requires the combination of pre- and post-saccadic processes, both involving visual and non-visual factors (Fig. 3). Visual information about the target position and the probe position is registered before the saccade and encoded in memory. After the saccade, the memory representation has to be accessed and has to be combined with new visual or non-visual information about the current eye position. Because neither the target nor the probe is visible after the saccade, both positions have to be reconstructed from memory signals and the available post-saccadic information. Our proposal rests on two assumptions. The first assumption is that the apparent distance between the saccade target, and the probe is compressed in the encoding of the pre-saccadic scene. The second assumption is that the reconstruction of the scene after the saccade prefers post-saccadic visual reference information over non-visual eye position signals. Below, we will discuss the support for these assumptions provided by the studies presented above.

The role of post-saccadic visual references can be understood in comparison with studies of trans-saccadic visual stability. Current ideas on visual stability across saccades hold that most of the visual information before the saccade is discarded, and a new representation of the visual world is generated from newly incoming information after the saccade (Bridgeman, van der Heijden, & Velichkovsky, 1994; Hamker, 2005a). Deubel et al. (1996; 1998) as well as McConkie et al. (McConkie & Currie, 1996; Currie & McConkie, 2000) argue that visual stability is realized by a store and compare mechanism. The basic assumption in this theory is that the perceptual world remains stable if nothing changes during the saccade. Thus, the store and compare mechanism uses pre-saccadic information from only a small number of objects, most importantly the saccade goal itself. This information is stored in a non-retinotopic memory across the saccade. Immediately after the saccade the visual system searches the saccade target in a restricted spatiotemporal window and compares the stored representation with the new visual information after the saccade. If the 'new' saccade target is identified as the 'old' saccade target it will be used for the re-calibration of the visual scene. In our experiments, the saccade target was never present after the saccade but visual reference information from the ruler was available to indicate the position of the saccade target. This reference information might be used instead of the image of the saccade target to localize the saccade's goal position, allowing the reconstruction of visual space from pre-saccadic memory with respect to the saccade target's ruler location.

The store and compare mechanisms, thus, could be involved in generating peri-saccadic compression. Post-saccadic visual space is constructed from visual information in the post-saccadic scene together with limited memory information from the pre-saccadic scene. This post-saccadic reconstruction is centered at the post-saccadic position of the saccade target. The probes in our experiment are only presented in the pre-saccadic scene. Therefore, their position has to be reconstructed from visual memory after the saccade. If pre-saccadic memory is mainly preserving information from the saccade target then it is conceivable that information about other objects is distorted towards the saccade target position. We may speculate, therefore, that the observed compression is due to memory distortions induced by the pre-saccadic concentration of resources on the saccade target, or due to distortions within the pre-saccadic scene.

The observed mislocalization of the saccade target in the white-line and darkness conditions supports this view. An apparent shift of the target position towards the probe position occurred both in the presence and in the absence of a saccade. This suggests that the registered and encoded distance between target and probe is compressed independently of the occurrence of a saccade. However, the position of the probe was mislocalized only when the subject performed a saccade, not when the subject kept fixation. Within the store and compare mechanism the difference between those conditions can be explained since the post-saccadic reconstruction of the scene obviously only becomes necessary when a saccade has occurred. In this case, the probe and target positions would be retrieved from the encoded compressed distance between target and probe position. If the target position is indicated by visual references then it can be localized veridically, but the retrieved probe position will appear compressed. If, on the other hand, the target position is not indicated by visual references and the probe location is perceived correctly then the perceived target position would appear compressed towards the probe.

Why is the target position not derived correctly from extra-retinal eye position signals after the saccade in darkness and in the white line condition? If the saccade target position is not visually indicated after the saccade then, both the target's and the probe's position ultimately must be determined from a combination of visual memory with extra-retinal eye position information. If the task is to indicate the probe then, the probe's position should be determined from its pre-saccadic retinal location and the eye-position signal as proposed earlier (Honda, 1991; Schlag & Schlag-Rey, 2002; Pola, 2004). This is consistent with our results in the darkness condition. The same procedure may in principle be used to locate the target position as well. However, our results on the apparent target position show that this is not the case. Because the target is mislocalized towards the probe, its position must be derived from the use of the probe's position (inculding extra-retinal information) and the memory of the compressed distance between the probe and the target in the pre-saccadic scene.

The above considerations may explain why, if we assume a compression of distance between target and probe in the pre-saccadic encoding, probe positions in the post-saccadic judgment appear compressed towards the target in the presence of visual references but not without visual references. They also explain why the target may appear shifted towards the probe without visual references both after saccades and during fixation. They do not explain, however, why the distance between the probe and the target is compressed in the first place. The observations described above point to a pre-saccadic origin of this compression. The anti-saccade and the saccade adaptation results show that a motor command signal must be involved that may be dissociated from the visual target position. Thus, an oculomotor feedback signal is most likely responsible for the pre-saccadic induction of compression. This signal would originate from motor command structures and be fed back to visual areas. Such signals have been described (Sommer & Wurtz, 2002; Moore & Armstrong, 2003) and linked to the boosting of the sensitivity of visual neurons surrounding the target position in order to enhance spatial processing in that area (Hamker, 2005b). Such a modulatory influence on neural activities may distort the representation of stimulus locations in the map surrounding the saccade target leading to changes in position signals (Hamker, Zirnsak, & Lappe, 2004). This view is consistent with the two-dimensional mislocalizations (Kaiser & Lappe, 2004) and their similarity to cortical magnification factors (Hamker, Zirnsak, & Lappe, 2004; VanRullen, 2004). It is also consistent with the finding that low contrast stimuli lead to stronger compression than high contrast stimuli (Michels & Lappe, 2004) because the gain modulation is most effective for visual stimuli that yield non-saturated responses.

Conclusion

The framework we propose has a pre-sacccadic and a post-saccadic component (Fig. 3). Before the saccade, the visual signals of the target and the probe are registered and encoded in memory. Either the registration or the encoding in memory is subject to a compression of the distance between the target and the probe, presumably by the action of a modulatory oculomotor feedback signal. Thus, the compression is induced by pre-saccadic processes. After the saccade, the spatial locations of the pre-saccadic objects have to be reconstucted from the pre-saccadic memory in combination with visual reference information about target position and non-visual information about eye position. The system prefers to use visual reference information when available, locating the saccade target in the visually indicated position and mislocating the probe according to the compressed pre-saccadic memory representation. If visual reference information about the target position is not available after the saccade the system must use non-visual information about eye position for the reconstuction of the pre-saccadic locations. In this case, the apparent probe location is uniformly shifted due to errors in the eye position signal but residues of compression in the pre-saccadic encoding can be seen in the mislocalization of the target position.

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References

Awater, H., Burr, D., Lappe, M., Morrone, M. C., & Goldberg, M. E. (2004). The effect of saccadic adaptation on the localization of visual targets. *J Neurophysiol*,

Awater, H., & Lappe, M. (2004). Perception of visual space at the time of pro-and anti-saccades. *J.Neurophysiol*, 91, 2457-64.

Awater, H., & Lappe, M. (2005) Mislocalization of perceived saccade target position induced by perisaccadic visual stimulation. *J.Neurosci*, in revision,

Bischof, N., & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychologische Forschung*, 32, 185-218.

Bridgeman, B., van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behav.Brain Sci*, 17, 247-92.

Burr, D. C., Morrone, M. C., & Ross, J. (2001). Seperate visual representations for perception and action revealed by saccadic eye movements. *Curr.Biol*, 11, 798-802.

Cai, R. H., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature*, 386, 601-04.

Currie, C. B., & McConkie, G. W. (2000). The role of the saccade target object in the perception of a visually stable world. *Perc. Psychophys*, 62, 673-83.

Dassonville, P., Schlag, J., & Schlag-Rey, M. (1995). The use of egocentric and exocentric location cues in saccadic programming. *Vision Res*, 35, 2191-99.

Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Res*, 38, 3147-59.

Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Res*, 36, 985-96.

Hamker, F. H. (2005a). A computational model of visual stability and change detection during eye movements in real world scenes. *Vis. Cogn*, 12, 1161-76.

Hamker, F. H. (2005b). The reentry hypothesis: The putative interaction of the frontal eye field, ventrolateral prefrontal cortex, and areas V4, IT for attention and eye movement. *Cerebral Cortex*, 15, 431-47.

Hamker, F. H., Zirnsak, M., & Lappe, M. (2004). A computational model of saccadic mislocalization of briefly flashed stimuli based on spatial reentry. *J.Vision*, 4(8), 736a.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Percep.Psychophys*, 45, 162-74.

Honda, H. (1991). The time course of visual mislocalization and of extraretinal eye position signals at the time of vertical saccades. *Vision Res*, 31, 1915-21.

Honda, H. (1993). Saccade-contingent displacement of apparent position of visual stimuli flashed on a dimly illuminated structure background. *Vision Res*, 33, 709-16.

Honda, H. (1997). Interaction of extraretinal eye position signals in a double-step saccade task: Psychophysical estimation. *Exp.Brain Res*, 113, 327-36.

Kaiser, M., & Lappe, M. (2004). Perisaccadic mislocalization orthogonal to saccade direction. *Neuron*, 41, 293-300.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature*, 403, 892-95.

Matin, L., & Pearce, D. G. (1965). Visual perception of direction for stimuli during voluntary saccadic eye movements. *Science*, 148, 1485-88.

McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *J.Exp.Psychol.: Hum.Percept.Perform*, 22, 563-81.

Michels, L., & Lappe, M. (2004). Dependence of saccadic compression and suppression on contrast. *Vision Res*, 44, 2327-36.

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of fronal cortex. *Nature*, 42, 370-73.

Morrone, M. C., Ross, J., & Burr, D. C. (1997). Apparent position of visual targets during real and simulated saccadic eye movements. *J.Neurosci*, 17, 7941-53.

Pola, J. (2004). Models of the mechanism underlying perceived location of a perisaccadic flash. *Vision Res*, 44(24), 2799-813.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature*, 386, 598-601.

Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Res*, 35, 2347-57.

Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly: delays and localization errors in the visual system. *Nature Rev. Neurosci*, 3, 191-200.

Sommer, M. A., & Wurtz, R. H. (2002). A pathway in primate brain for internal monitoring of movements. *Science*, 296, 1480-82.

Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *J.Comp.Physiol.Psychol*, 43, 482-89.

VanRullen, R. (2004). A simple translation in cortical log-coordinates may account for the pattern of saccadic localization errors. *Biol.Cybern*, 91, 131-37.

von Helmholtz, H. (1896). *Handbuch der Physiologischen Optik*. Hamburg: Leopold Voss.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip (Wechselwirkung zwischen Zentralnervensystem und Peripherie). *Naturwissenschaften*, 37, 464-76.

Figure captions

Figure 1

The dependence of perisaccadic comrpession on visual references.

A: Different patterns of perisaccadic mislocalization observed in the same subject in darkness condition (left) and in a condition with a ruler identifying the target position after the saccade (right). Probes (flashed bars) were presented randomly at one out of four locations (arrows). Apparent positions at various times relative to saccade onset are shown by individual dots in the lower panels. Lines give running averages through the data from the four true locations. Around saccade onset, apparent positions are shifted in saccade direction in the dark condition and compressed onto the saccade target location (at 6.4 deg) in the ruler condition.

B: Strength of perisaccadic compression (dark bars) measured as the ratio of the mean apparent separation of bars within 50 ms before saccade onset and the mean apparent separation 100 ms before and after the saccade (6 subjects). Apparent separation was assessed by taking the standard deviation over the four bar positions. The three dark bars on the left give the apparent compression in darkness, and with a horizontal line or a ruler continuously present. Darkness and ruler data are from Lappe, Awater, & Krekelberg (2000), data of the line condition are from Awater & Lappe (2005). The bars on the right show strength of compression for various presentation times of the ruler: only before the flash of the probe, only after the flash of the probe, immediately after the saccade until response, immediately after the saccade but only for 100ms, only before the probe and 250 ms later. In this last condition, the ruler was blanked from probe onset until 250 ms later, i.e., it re-appeared about 150 ms after the saccade. Compression is strong when the ruler is present immediately after the saccade (ruler, after-probe, and after saccade conditions).

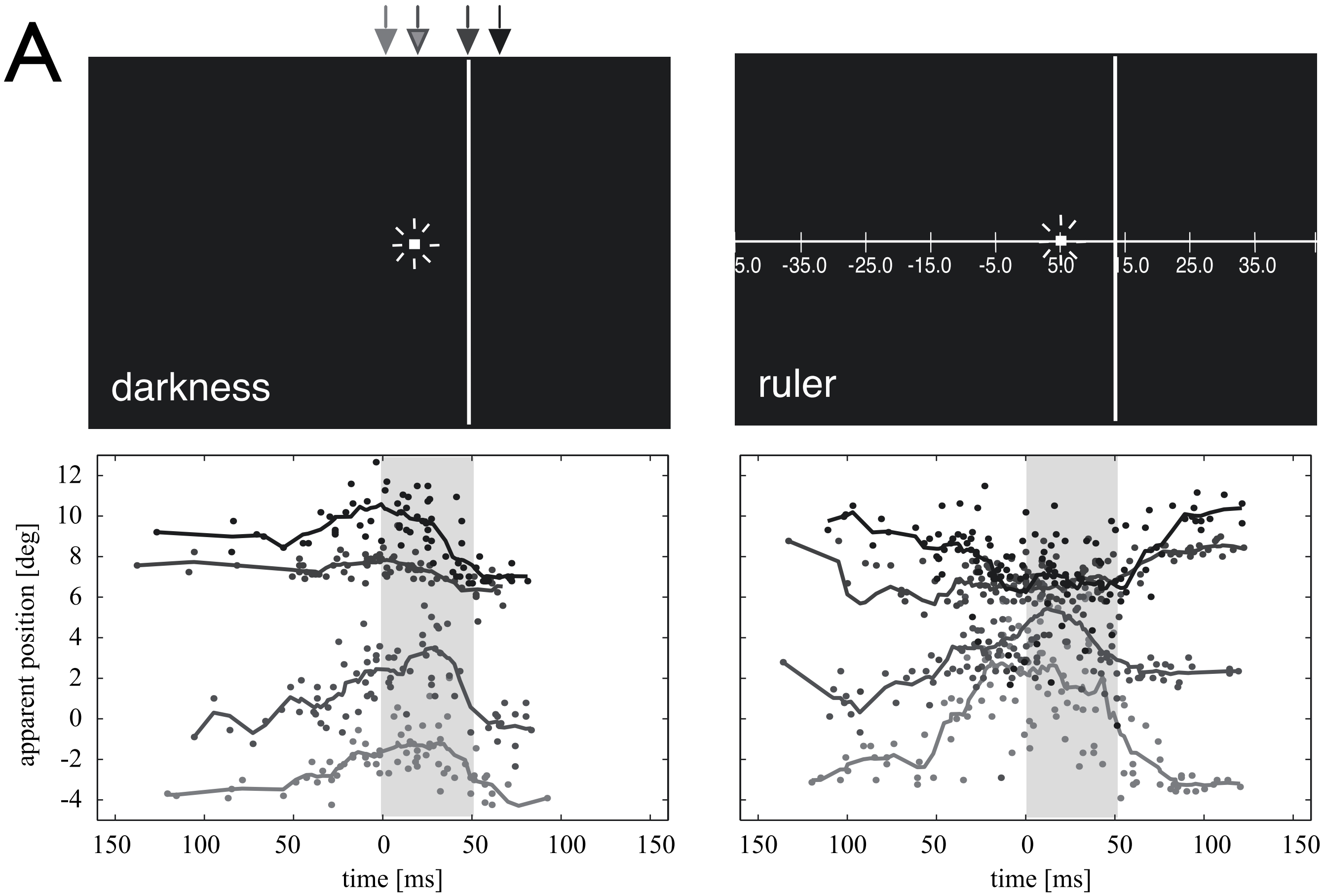
The light bars in the dark and line conditions show the strength of compression when instead of the apparent probe positions the apparent distance between the probe and the saccade target was calculated. These values differ because in the dark and line conditions the saccade target is mislocalized towards the location of the probe (Awater & Lappe,2005). The combined effect of both mislocalizations leads to increased compression.

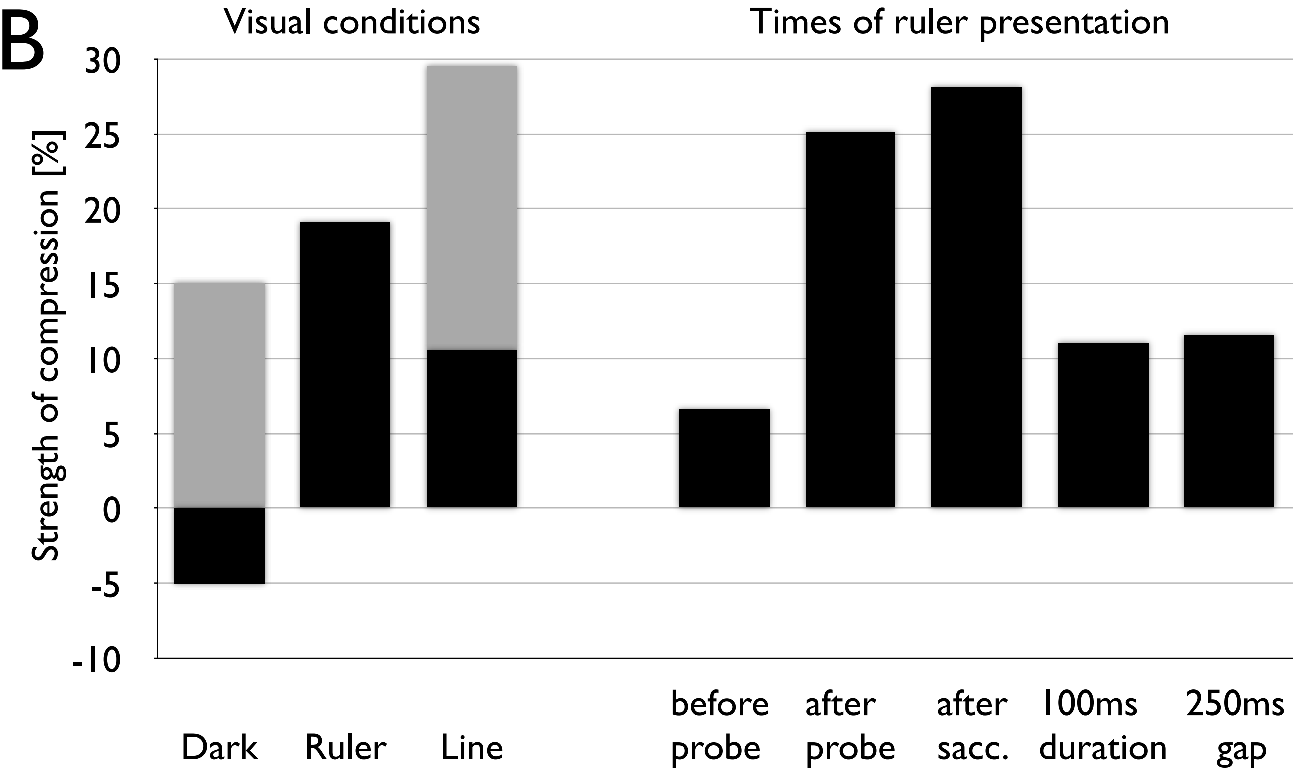
Figure 2

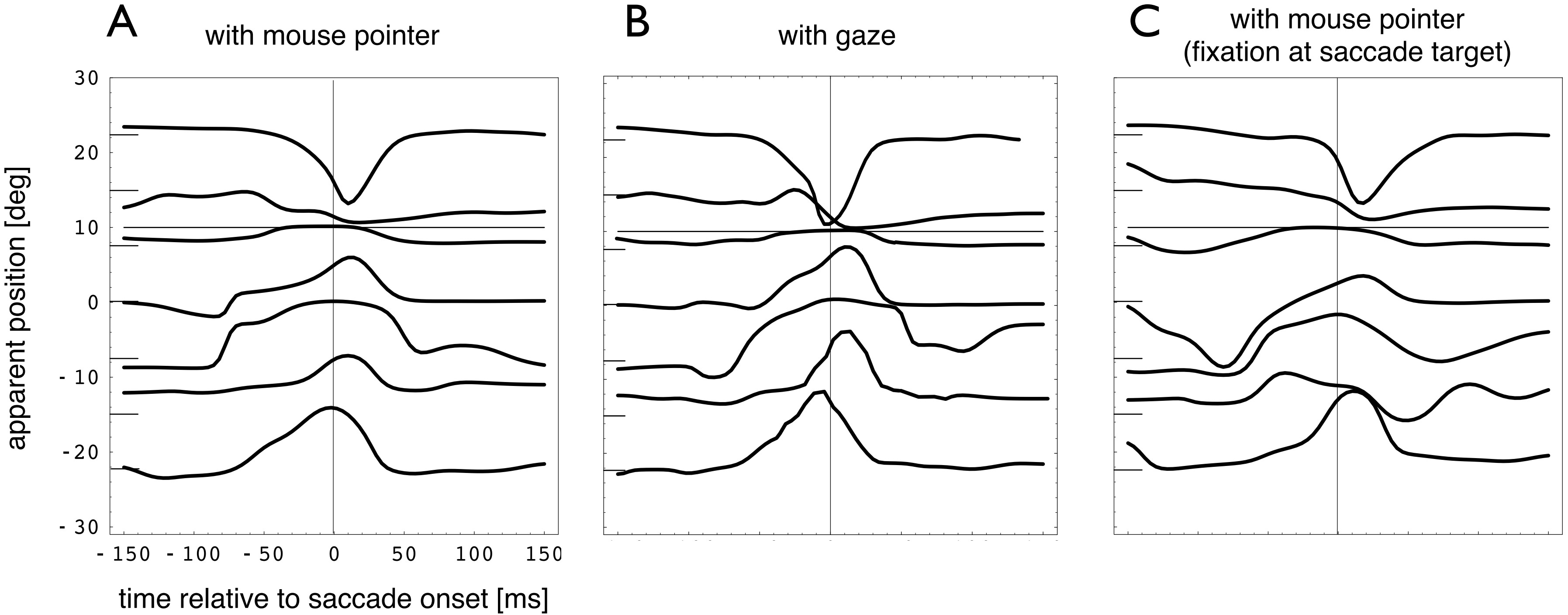
Perisaccadic localization quantified by different reporting procedures in a single subject. The saccade was from position –10 deg to position 10 deg with respect to straight ahead. Probes were flashed at 7 positions (-22.4 deg., -14.9 deg., -7.6 deg., 0 deg., 7.6 deg., 14.9 deg., 22.4 deg.) in randomized order. A: Apparent positions (running averages, individual data points not shown for clarity) indicated by a mouse pointer that appeared 500 ms after the saccade and had to be moved to the perceived probe location by the subject. The subject was free move his eyes at this time. B: The subject was instructed first to make a saccade to the target and then a saccade to the probe which was flashed around the occurrence of the first saccade. Apparent probe positions were computed from the landing position of the second saccade. C: Apparent probe positions indicated by mouse pointing as in A. However, in this condition the subject was required to keep fixation at the saccade target after the first saccade and adjust the mouse pointer using peripheral vision. The compression was very similar in all three conditions. Same results were obtained from two further subjects.

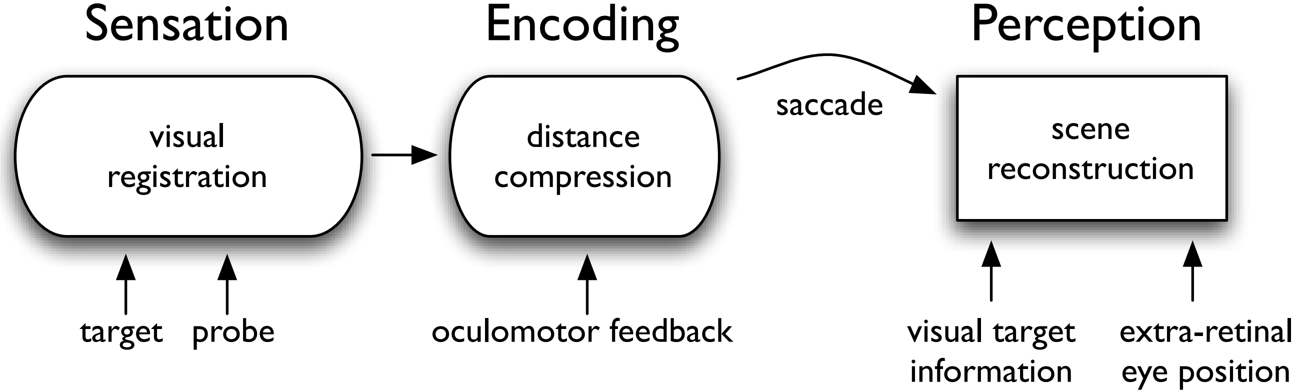
Figure 3

Schematic illustration of the steps involved in peri-saccadic compression. First, the visual signals of the target and the probe have to be registered. The locations of target and probe and the distance between the two is then encoded for trans-saccadic memory. Either the registration or the encoding in memory is subject to a compression of the distance between the target and the probe. Presumably this compression reflects the action of a non-visual modulatory oculomotor feedback signal. This is assumed to happen before the saccade. After the saccade, the layout of the pre-saccadic scene has to be reconstructed from the pre-saccadic encoding and the available post-sacccadic information about target position (visual) and eye position (non-visual). Since the system prefers to use visual reference information, the saccade target is localized in the visually indicated position, and the probe appears compressed according to the compressed pre-saccadic memory representation. In the absence of visual target information non-visual information about eye position is used for the reconstruction of the pre-saccadic probe locations. In this case, the apparent probe location is shifted along saccade direction because of errors in the eye position signal.


A
darkness
ruler
5.0 -35.0 -25.0 -15.0 -5.0 5.0 15.0 25.0 35.0
apparent position [deg]
12 10 8 6 4 2 0 -2 -4
150 100 50 0 50 100 150
time [ms]
150 100 50 0 50 100 150
time [ms]


B
Visual conditions
Times of ruler presentation
Strength of compression [%]
30 25 20 15 10 5 0 -5 -10
Dark
Ruler
Line
before probe
after probe
after sacc.
100ms duration
250ms gap


A
with mouse pointer
B
with gaze
C
with mouse pointer
(fixation at saccade target)
apparent position [deg]
30
20
10
0
- 10
- 20
- 30
- 150
- 100
- 50
0
50
100
150
time relative to saccade onset [ms]


Sensation
Encoding
Perception
visual registration
distance compression
saccade
scene reconstruction
target
probe
oculomotor feedback
visual target information
extra-retinal eye position