

Does perisaccadic compression require foveal vision?

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Abstract. People make systematic errors when localizing a stimulus that is presented briefly near the time of a saccade. These errors have been interpreted as compression towards the position that is fixated after the saccade. Normally, fixating a position means that its image falls on the fovea. Macular degeneration (MD) damages the central retina, obliterating foveal vision. Many people with MD adopt a new retinal locus for fixation, called the preferred retinal locus (PRL). If the compression of space during the saccade is a special characteristic of the fovea, possibly due to the high density of cones that is found in the fovea, one might expect people lacking central vision to show no compression of space around the time of a saccade. If the compression of space during the saccade is related to the position that is fixated after the saccade, one would expect compression towards the PRL, despite the lack of a high density of cones in this area. We found that a person with MD showed a clear compression towards her PRL. We conclude that perisaccadic compression is related to the position that is fixated after the saccade rather than to the high density of receptors in the fovea.

Keywords: saccades, localization, macular degeneration, fixation, preferred retinal locus

1 Introduction

When a stimulus is presented briefly around the time of a saccade, it tends to be mislocalized. The systematic component of this perisaccadic mislocalization was originally interpreted as being a compression towards the saccade target location (Honda, 1993; Lappe, Awater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997), but it has recently been shown to be towards the position that is fixated after the saccade (Awater & Lappe, 2004; Maij, Brenner, & Smeets, 2011a; Matziridi, Brenner, & Smeets, 2013). Normally, the fixated position is the location that falls on the fovea, the part of the eye with the highest density of cones, located in the centre of the macula region of the retina (Iwasaki & Inomara, 1986).

The compression has traditionally been attributed to a mechanism for remapping a representation of the visual scene across saccades, in order to obtain a stable visual representation of the world across eye movements (Duhamel, Colby, & Goldberg, 1992; Melcher & Colby, 2008; Wurtz, 2008). Several models of such remapping include components that can be related to the variations in spatial resolution across the visual field on the retina and in early visual areas of the brain (the cortical magnification factor; Hamker, Zirnsak, Calow, & Lappe, 2008; Ross et al., 1997; VanRullen, 2004). An alternative explanation for perisaccadic compression is that it arises from uncertainty about the timing of the flash with respect to the saccade, together with a prior belief that objects that one has seen were near where one was looking (Maij et al., 2011a).

Macular degeneration (MD) is a medical condition in which the central retina is damaged, causing vision loss (a central visual field scotoma) through deterioration of photoreceptors (usually both rods and cones) in the centre of the visual field (the macula). The area of the macula comprises only a tiny part of the retina. The remaining part (the peripheral field) remains unaffected by the disease. Interestingly, even though the macula is devoted to such a small fraction of the visual field, almost half of the visual cortex is devoted to processing

macular information (Roberts, 2006). Faced with a loss of foveal vision, people with MD often adopt a new retinal locus for fixation, called the preferred retinal locus (PRL), which is not part of the scotoma and which operates as a 'pseudo-fovea' (Fletcher, Schuchard, & Watson, 1999; Timberlake et al., 1986; Timberlake, Peli, Essock, & Augliere, 1987; Whittaker, Budd, & Cummings, 1988). This provides a unique opportunity to distinguish between various origins of perisaccadic compression, because although the PRL in people with MD is similar to the fovea of people with normal vision in terms of defining where one is looking, it is quite different in terms of variations in retinal resolution. In particular, the decline in resolution is very different for different directions from the PRL, with a very extreme change towards the macula, and quite modest changes in the other directions.

If the compression around the time of a saccade is related to the high density of cones that is found in the fovea, one might expect people lacking foveal vision to show no systematic compression of space around the time of a saccade. If the compression is related to the position that is fixated after the saccade, one might expect people with MD to show similar compression as normally sighted participants, but towards their PRL, despite the lack of a high density of cones at that location.

To distinguish between these options, a MD participant (MH) with a clear PRL performed horizontal saccades while flashes were presented around the time of her saccades. She was asked to indicate where she saw the flash by touching the screen at that location. We examined whether she showed perisaccadic compression towards her gaze orientation after the saccade (ie towards the position that she fixates with her PRL). If not, we could conclude that such compression is a special characteristic of the fovea. If the compression is towards the part of the retina with the highest resolution, even in the absence of the fovea, MH may exhibit compression towards positions around the macula, but there should not be much preference for certain positions along the edge of the macula, because the density of cones is relatively constant.

2 Methods

2.1 Participant

One of the authors (MH; age 30; female) volunteered to participate in this study. At the age of 13, MH was diagnosed with Stargard's disease, a type of juvenile macular degeneration. On the basis of the results of a visual field test and scanning laser ophthalmoscope measurements, her PRL eccentricity was determined at 15.5 deg and her PRL stability was 1.2 deg (standard deviation of fixation; for more details see case 1 in Van der Stigchel et al., 2013). In addition to the main experiment, we measured MH's localization of moving targets during fixation and the location of her scotoma relative to her PRL. At the time of the experiment she was naive with respect to the aim of the study. She was later informed of the theory and participated in the interpretation of the data. The current study is part of a research program that has been approved by the ethics committee of the Faculty of Human Movement Sciences (ECB 2006-02).

2.2 Apparatus and experimental setup

For the main experiment the participant sat in front of a touch screen (Elo Touch CRT 19", 800 × 600 pixels, 36 × 27 cm, 100 Hz) on which visual stimuli were presented using the Psychophysics Toolbox (Brainard, 1997). A chin-rest was placed in front of the touch screen to keep MH's head fixed at a viewing distance of 57.3 cm. At this viewing distance one centimeter equals one degree of visual angle. The eye movements were recorded with an Eyelink II eye-tracker (SR Research Ltd) using the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002). This system records eye orientation with a spatial resolution of 0.2 deg and a temporal resolution of 500 Hz. Two additional experiments were performed. For an experiment

that examined whether MH also showed compression without saccades (similar to Brenner, van Beers, Rotman, & Smeets, 2006) the same setup was used, but eye movements were not recorded. For mapping the participant's flash detection near her PRL, stimuli were presented on a Sony GDM-FW900 Trinitron CRT screen (1024×768 pixels, 40×30 cm, 120 Hz). All experiments were conducted in a normally illuminated room (fluorescent lamps).

2.3 Main experiment

2.3.1 Perisaccadic stimuli. The stimuli for each trial consisted of one black fixation dot (0.5 deg diameter; 9 cd m^{-2}), a similar black target dot, and a flashed vertical green bar (0.6×4.4 deg, 94 cd m^{-2} ; $\text{CIE}_{xy} = 0.30, 0.56$), all on a white background (125 cd m^{-2} ; $\text{CIE}_{xy} = 0.28, 0.32$; figure 1). The fixation dot was presented randomly at one of 20 possible locations on the screen. The target dot was always presented 7 deg to the right of the fixation dot. The green bar was flashed 3.5, 4.9, 6.3, 7.7, or 9.1 deg to the right of the fixation dot, which means that it was presented at 50%, 70%, 90%, 110%, or 130% of the distance between the fixation and the target dot. The bar's centre was always at the same height as the fixation and target dots.

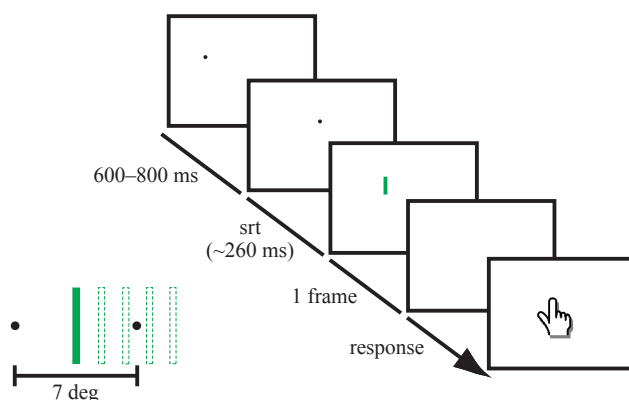


Figure 1. [In colour online, see <http://dx.doi.org/10.1068/p7666>] Perisaccadic mislocalization task: schematic overview of an example trial. A black fixation dot appears on the screen. After a random interval of 600–800 ms, it is replaced by a black target dot 7 deg to the right of the fixation dot that remains visible for the average saccadic reaction time (srt) on previous trials, which is about until MH makes a saccade to the target dot. At that moment a vertical green bar is presented at one of five possible locations for one frame (see inset, with a bar at 3.5 deg and dashed outlines indicating the other four possible locations). MH had to touch the screen with her index finger at the location at which she had seen the green bar.

2.3.2 Procedure. A trial started with a fixation dot appearing on the screen (figure 1). MH had to fixate the dot. After a random interval of 600–800 ms the fixation dot disappeared and the target dot appeared on the screen for about 260 ms (see below). MH was asked to make a saccade from the fixation dot to the target dot as soon as the target dot appeared on the screen. To be able to present the bar near the moment of the saccade, we predicted the saccade onset for each new trial on the basis of the average saccadic latency (the time between the presentation of the target dot and the start of the saccade) on previous trials (Maij, Brenner, & Smeets, 2009). The green bar was presented for one frame near the predicted time of the saccade onset at one of the five possible locations. MH was asked to touch the screen with the index finger of her dominant (left) hand at the location at which she saw the green bar. By the time she touched the screen, all stimuli had disappeared. If she did not see the bar for some reason, she could indicate having missed it by touching the bottom of the screen. Once the screen had been touched, a new trial started with a new fixation dot appearing at a new position on the screen.

Each session consisted of 400 trials: 80 for each of the 5 bar locations (conditions). The trials were presented in random order within a session, with the restriction that the same condition was never presented on successive trials. The fixation dot was also never presented at the same location on successive trials. There were short breaks during the session. MH performed six sessions in total.

2.3.3 Calibration and synchronization. At the beginning of each session the touch screen was calibrated using the standard nine-point calibration provided by Elo Touch. The recording of the eye movements was calibrated using the standard nine-point calibration procedure of the Eyelink II. The validity of the measured eye movements was ascertained with the Eyelink's validation procedure, whereby the same points are fixated again and the calibration is considered to have been successful if the calibrated gaze during this validation was within 1 deg of the corresponding point for all of the calibration points. MH's eye movement calibration passed this standard validation procedure (that is usually used with normally sighted participants).

To determine the precise timing of stimulus presentation on the screen in relation to the recorded eye movement, a 2 deg white dot was presented on a black square (2×2 deg) in the lower right corner of the screen, at the same time as the flashed green bar. This dot was not visible to the participant, but a photodiode attached to the lower right corner of the screen measured the light from this dot and sent a signal to the parallel port of the Eyelink computer as soon as the dot appeared. This signal was recorded in the data file of the Eyelink computer, which allowed us to later know precisely when the green bar occurred in relation to the eye movement (Maij, Brenner, Li, Cornelissen, & Smeets, 2010). No corrections were made for the timing differences between green bars presented at different places on the screen, so the real timing of the green bar was known only to within a few milliseconds.

2.3.4 Data analysis. The Eyelink's gaze position data of the participant's dominant (left) eye were used to determine characteristics of the primary saccades (the first saccades occurring after the target dot appeared on the screen). The first of two consecutive sampling intervals for which the tangential velocity of the eye movement exceeded 35 deg s^{-1} was considered to be the saccade onset, and the first sample after that at which the velocity returned below this value was considered to be the saccade end. The first position at which the finger touched the screen was considered to be the perceived position of the green bar, or, if the bottom of the screen was touched, an indication that the participant had not seen the green bar.

Trials were discarded if there was no saccade between 100 ms before and 100 ms after the time of the presentation of the green bar (wrong timing; $\sim 7\%$ of the trials), if the length of the saccade was less than 50% or more than 150% of the 7 deg distance between the fixation and the target dot (wrong amplitude; $\sim 7\%$ of the trials), if the direction of the saccade deviated by more than 22.5 deg from a movement to the right (wrong direction; $\sim 3\%$ of the trials), if the saccadic reaction time was less than 85 ms or more than 350 ms (wrong latency; $\sim 3\%$ of the trials), or if the bottom of the screen was touched as an indication that MH had not seen the green bar (no localization; $\sim 18\%$ of the trials).

We were mainly interested in localization in the direction of the target dot. We therefore defined the perceived position as the horizontal distance from the fixation dot to the touched location. We also determined the moment of the presentation of the green bar relative to the saccade onset. As the saccade latency varied from trial to trial, the bar occurred at various times relative to saccade onset. We determined the average perceived position for each moment at which the bar was presented with respect to saccade onset by calculating a moving weighted average of the perceived positions around that moment with weights based on a Gaussian window ($\sigma = 7 \text{ ms}$). We did so for each condition. We will refer to the resulting curves as mislocalization curves.

2.4 Localization during fixation

A similar dissociation to the one described above for perisaccadic compression can also be examined for a previously reported localization bias during fixation (Brenner et al., 2006). The compression of perceived positions towards the fovea (along the moving target's path) that was found in that study arose when subjects had to localize moving targets at the time that the fixation point flashed (or at the time of a tone). Here too, the compression could be towards the location that corresponds with the highest retinal resolution, or towards the location that is fixated, which normally coincide. By presenting motion more or less parallel to the border of the macula, we can isolate fixation, with the PRL, from large changes in resolution. We therefore also investigated the pattern of localization without eye movements in an additional experiment.

2.4.1 Stimuli. The stimuli for each trial consisted of one bright green fixation dot (0.5 deg diameter; 198 cd m^{-2} ; $\text{CIE}_{xy} = 0.28, 0.42$), a flashed black dot (0.5 deg diameter; 9 cd m^{-2}), and a moving black dot (0.5 deg diameter), all on a grey background (91 cd m^{-2} ; $\text{CIE}_{xy} = 0.28, 0.32$; figure 2a). The fixation dot was presented at the centre of the screen. The black dot could move horizontally from left to right across the screen at one of two different velocities: about 7.5 deg s^{-1} or 30 deg s^{-1} . It could move along one of two paths, passing either about 1 deg or 2.5 deg below the fixation dot.

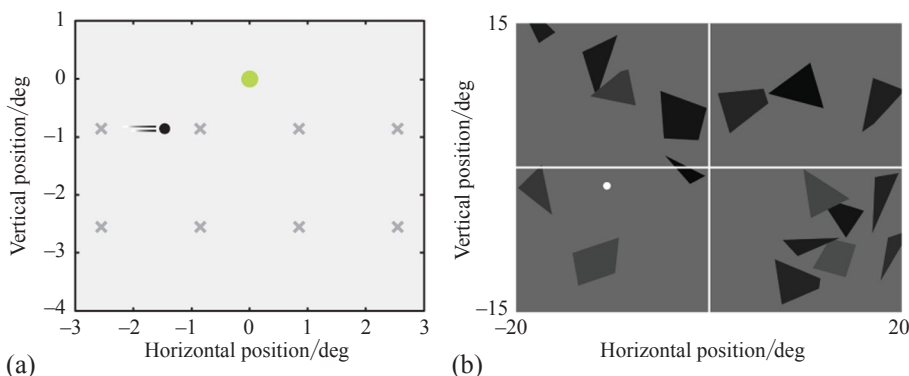


Figure 2. [In colour online.] Methods of additional experiments. (a) Localization task during fixation. A fixation dot (bright green dot) appeared on the screen. After a random interval, a black dot appeared moving along one of two paths below the fixation dot from the left to the right of the screen. Some time after the black dot appeared, the green fixation dot was replaced by a black dot for one frame (flash), while the original black dot continued moving. The flash always occurred when the moving dot was at one of four horizontal positions on the paths (positions indicated by crosses). MH had to indicate the moving dot's position at the moment of the flash. (b) Flash detection map. MH had to fixate the centre of the screen, while triangular and quadrilateral objects moved in random directions at random velocities across the screen. At random moments (intervals between 1200 and 1700 ms) a white dot was flashed on the screen for one frame. The flash could appear at any location on the screen except on the fixation cross. Whenever MH perceived a flash, she had to indicate whether it was to the right or to the left of the vertical line at the screen centre (by clicking the right or the left arrow key of the keyboard, respectively). If she did not perceive a flash, no key was pressed.

2.4.2 Procedure. A trial started with the bright green dot appearing on the screen (figure 2a). MH had to fixate the dot. After a random interval, the black dot started moving along one of the two paths. Between 500 and 1000 ms after the black dot started moving to the right, another black dot was flashed for one frame 'covering' the fixation dot. The original black dot continued moving for about 250–500 ms after the flash occurred (so the moving dot was visible for between 500 and 1000 ms before the flash and between 250 and 500 ms after the flash).

The flash always occurred when the moving dot was at one of four horizontal positions on the paths (about 1 deg or 2.5 deg to the left or the right of the fixation dot; positions indicated by crosses in figure 2a). MH was not aware of this. She had to fixate the bright green dot while the black dot was moving, but she was free to move her eyes after the moving dot disappeared. She had to indicate the moving dot's position at the moment of the flash by touching the screen at that location with the index finger of her dominant hand. If she could not indicate the moving dot's position at the moment of the flash for some reason (eg because she was not fixating correctly and therefore missed the flash), she could go to the next trial by touching the bottom of the screen.

Each session consisted of 320 trials. There were short breaks during the session. MH performed two sessions.

2.4.3 Data analysis. The first position at which the finger touched the screen was considered to be the moving dot's perceived position at the moment of the flash, or, if the bottom of the screen was touched, an indication that MH could not make the judgment (20% of the trials). We determined the average touched horizontal and vertical positions for each of the real locations of the moving dot at the moment of the flash, for each of the moving dot's two velocities.

2.5 Flash detection map

To map MH's visual field in relation to her PRL (and thereby confirm an earlier report of the position of her PRL; Van der Stigchel et al., 2013), we performed a simple test in which she fixated the centre of a white cross that covered the whole screen. On the screen, triangular and quadrilateral objects moved in random directions and at random velocities on a grey background (figure 2b). At random intervals, brief flashes (bright discs) were presented at random locations on the screen. The moving dark objects were intended to encourage MH to respond to the flashes rather than to any change in the scene, because that was also her task in the other experiments. Whenever MH perceived a flash, she indicated whether it was on the right or the left side of the screen by clicking the right or the left arrow key of the keyboard, respectively. If MH did not see the flash, no button on the keyboard was pressed and the next flash was presented on the screen after the random interval. This is a very efficient method to map the extent of the scotoma near the PRL.

3 Results

3.1 Main experiment

3.1.1 Eye movements. After excluding trials for various reasons (see data analysis section), 1487 useful localization judgments remained (about 62% of the 2400 trials). This is quite a normal percentage of successful trials (Maij et al., 2009; Maij, Matziridi, Smeets, & Brenner, 2012), which means that MH made reliable saccades and that she reliably detected the quite tall flashed bars (4.4 deg). As one may expect on the basis of the location of her PRL (see flash detection map section), MH mainly touched the screen where the lower half of the bar had been (0.95 ± 0.96 deg lower than the centre of the bar; mean and standard deviation). The mean amplitude of the primary saccades was about 5.67 ± 1.14 deg (ie MH undershot the target by about 20%). The mean saccadic latency was about 270 ± 32 ms, and the mean saccade duration was about 37 ± 11 ms. In 65% of the trials she performed a secondary saccade (about 360 ms after the primary saccade) with a mean amplitude of 1.56 deg to the right.

3.1.2 Mislocalization pattern. The pattern of mislocalization (figure 3) is similar to the one found in previous studies with normally sighted participants (figure 4; data from part of experiment 2 of Matziridi, Brenner, & Smeets, submitted), with a compression of perceived positions during the saccade and a hint that peaks in the mislocalization occurred slightly earlier with respect to the saccade for flashes that are closer to the fixation dot than for ones

that are further away in the direction of the saccade target (Awater & Lappe, 2006; Lappe et al., 2000; Maij et al., 2011a; Maij, Brenner, & Smeets, 2011b; Matziridi et al., 2013; Ostendorf, Fischer, Finke, & Ploner, 2007). The most important aspect of figure 3 is that perisaccadic compression was towards the position that was fixated after the saccade: the PRL for MH (the fovea for the normally sighted).

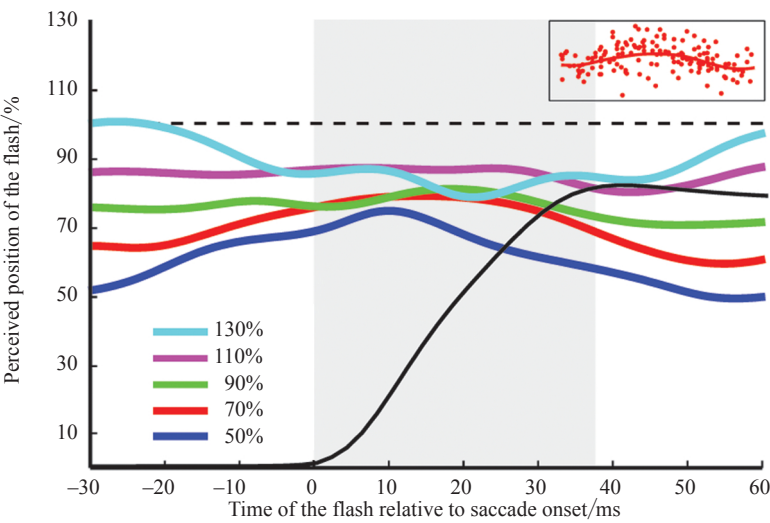


Figure 3. [In colour online.] Result of main experiment: MH’s mislocalization curves for each location of the green bar. The bar locations are indicated by differently coloured curves. Each curve is a smoothed average of the perceived locations of bars presented at various times relative to saccade onset. MH was instructed to make a saccade from the fixation dot (0%) to the black target dot (horizontal dashed black line at 100%). The grey area shows MH’s average saccade duration. The black solid curve represents MH’s average saccade. The inset shows the raw data that were used to obtain the red, 70% curve.

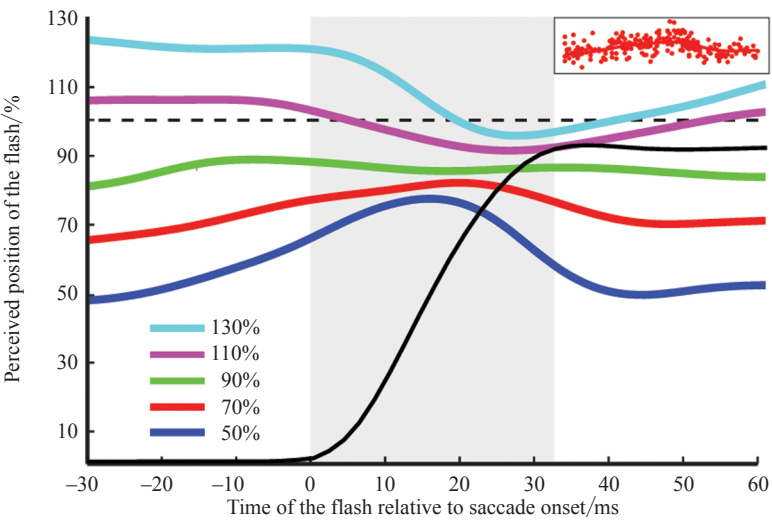


Figure 4. [In colour online.] Normally sighted participants’ mislocalization curves for each location of the green bar. Average of five normally sighted participants. Data from part of experiment 2 of Matziridi et al. (submitted). The task was similar to the one performed by MH in the current study (figure 3). The only difference is that the interval between the presentation of the fixation and the target dot was 500 ms longer, and the saccadic reaction time was 150 ms shorter for these participants than for MH. Details are as in figure 3.

MH also had an overall compression towards the position that she fixated after the saccade for flashes presented well before and after the saccade, whereas for normally sighted participants the compression was observed for only flashes presented close to the saccade. We propose that this difference is consistent with compression being related to uncertainty. To relate this difference to precision, we determined the variability of MH's localization judgments before and after the saccade, and compared it with the variability of the five above-mentioned controls (from part of experiment 2 of Matziridi et al., submitted) during the same times. For each person, we determined the standard deviation of responses to all flashes that took place more than 50 ms before saccade onset for every flash location, and averaged these standard deviations across flash locations. We did the same for the flashes that took place more than 50 ms after saccade onset. We then averaged the resulting mean standard deviations for each person and found that MH's value (0.92 deg) falls outside the 95% confidence interval of the controls (0.21–0.67 deg).

3.2 Localization during fixation

Figures 5a and 5b show the localization pattern during fixation for the two different velocities of the moving dot. The results show small or no compression when the dot moved slowly (figure 5a) and clear compression towards the position at which the dot's path came closest to the fixation dot when the dot moved fast (figure 5b).

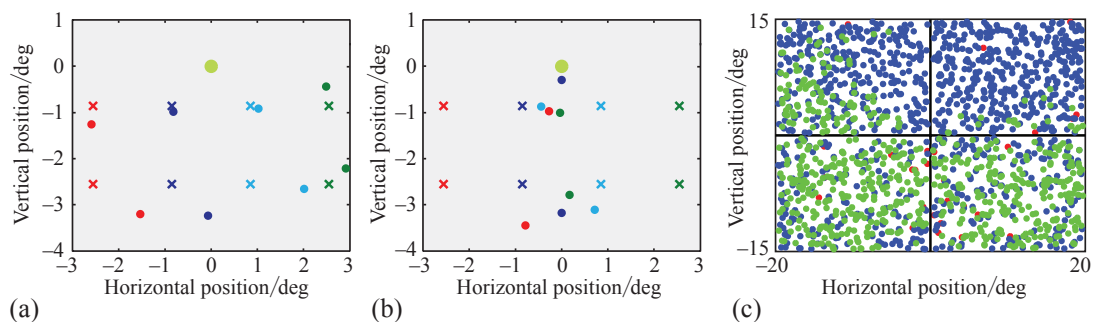


Figure 5. [In colour online.] Results of additional experiments. (a, b) Localization task during fixation. (a) MH's judgments of the moving dot's position for the slower velocity (7.5 deg s^{-1}). The filled circles represent the average perceived positions when the moving dot was at one of the eight positions indicated by a cross at the time of the flash (identified by the colour). (b) MH's judgments of the moving dot's position for the faster velocity (30 deg s^{-1}). Details are as in (a). (c) Flash detection map. The green dots represent correct answers, the red dots represent incorrect answers, and the blue dots represent flashes for which no response was given (presumably because MH did not perceive the flash).

3.3 Flash detection map

The aim of this experiment was to confirm the position of MH's blind region with respect to her PRL. This allowed us to identify the visible areas on the screen. The green dots in figure 5c represent locations for which MH perceived the flash and indicated the correct side of the screen. The red dots represent locations for which MH indicated the wrong side of the screen. The blue dots represent locations for which MH did not detect the flash. Figure 5c shows that MH's PRL leads her to fixate in such a manner that the region to the right and above her fixation is not visible. Consequently, positions slightly to the left and right of the PRL should have a similar receptor density to the PRL itself. Our findings look consistent with the visual field test reported in Van der Stigchel et al. (2013).

4 Discussion

In the present study we examined whether the phenomenon of perisaccadic compression is a special characteristic of the fovea, possibly due to the high density of cones in this area, or whether it is related to the position that is fixated after the saccade. We did so by having MH (who has a loss of central vision due to MD) localize a briefly presented bar around the time of a saccade. If perisaccadic compression is a special characteristic of the fovea, we would expect MH, who lacks foveal vision, to show no compression of space around the time of the saccade, in contrast to normally sighted participants. If perisaccadic compression is related to the position that is fixated after the saccade, we would expect MH to show compression towards her new retinal locus for fixation (PRL).

The results showed a compression of space during the saccade (figure 3). The compression was towards MH's saccade endpoint and not towards the physical saccade target (end of solid black line rather than dashed line in figure 3). This is in line with the findings of Awater and Lappe (2004), Maij et al. (2011a), and Matziridi et al. (2013). The reason that compression is also observed before and after the saccade in MH (and not in controls) might be related to MH's larger variability than the controls before and after the saccade. This increased variability is in line with our suggestion that MH has considerable uncertainty about the flashed bar's position even when her eyes are not moving. Such spatial uncertainty might lead to a compression towards the position that is fixated after the saccade (Maij et al., 2011a).

Another remarkable difference between the data of MH and that of controls is in their eye movements. MH's saccades undershot the target by about 20%, whereas the controls undershot the target by only about 10%. Why does MH undershoot more? It has been argued that undershooting is a strategy for maximizing the time with clear vision by minimizing saccadic flight time (Harris, 1995). According to this reasoning, a larger variability in endpoints means that it is optimal to undershoot more (followed by a correction saccade). As MH's standard deviation is twice as large as that of controls, this reasoning might explain why she undershoots the target more than controls.

Brenner et al. (2006) found that the fixation position was also important when spatial uncertainty was caused by motion on the retina rather than by the eyes moving. In that study participants had to judge the position of a moving dot at the moment of a flash, during fixation. We had MH perform a similar experiment (figure 2a). The results (figures 5a and 5b) show a similar pattern to the ones of normally sighted participants (data in figure 6 of Brenner et al., 2006): small or no compression when the dot moved at a slow velocity and clear compression towards the position at which the dot's path came closest to the fixation dot when the dot moved at a faster velocity. Brenner et al. (2006) claimed that uncertainty about the moment of interest affected judgments of the position of the moving dot at the moment of the flash. They proposed that people are biased toward believing that they are looking at what they see. These results support the interpretation of our perisaccadic mislocalization experiment in showing a bias towards the fixation position when confronted with uncertainty (also see Brenner, Mamassian, & Smeets, 2008). Because MH, who has a loss of foveal vision, showed compression towards her PRL, we conclude that compression is towards the position that is fixated after the saccade rather than being related to the high density of cones in the fovea.

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