Perifoveal spatial compression

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We report a strong compression of space around a visual anchor presented in the near visual periphery (<5°). While subjects kept fixation, a salient visual stimulus (from now on referred to as "anchor") was presented, followed by a brief whole-field mask. At various times around mask onset a probe dot was flashed. Subjects estimated the position of the probe dot in relation to a subsequently presented comparison bar. The probe dot location was perceived nearly veridically when presented long before or after mask onset. However, when the probe dot was presented simultaneously with the mask it appeared shifted toward the anchor by as much as 50% of their separation. The anchor had to appear briefly before mask onset to attract the probe dot. No compression occurred when the anchor was presented long before or after the mask. When the probe dot and anchor were presented with similar brief duration, the more peripheral stimulus always shifted toward the more foveal stimulus independently of their temporal order. We hypothesize that the attraction might be explained by the summation of the neural activity distributions of probe and anchor.

Introduction

How the visual system retrieves the position of objects in space is a matter of ongoing research. A number of studies report shifts of the perceived location of a target away from the location that corresponds to its retinal position and these results challenge the "labeled line" theories for coding of spatial position (Fischer, Spotswood, & Whitney, 2011): First, the perceived position of briefly presented objects is modulated by motion (Whitney, 2002). Visual objects presented close to a moving pattern are mislocalized towards the direction of motion (Whitney, Westwood, & Goodale, 2003; Whitney & Cavanagh, 2000). Strong mislocalization effects are seen when the visual objects are shown on top of a moving stimulus (Tse, Whitney, Anstis, & Cavanagh, 2011). Second, shifts of visual attention modulate the perceived space by repelling visual objects away from the cued position (Suzuki & Cavanagh, 1997). Third, adaptation methods have been used to change perceived position. Visual adaptation to a prolonged exposed stimulus alters the perceived offset of a probe stimulus in a vernier alignment task (McGraw, Roach, Badcock, & Whitaker, 2012; Whitaker, McGraw, & Levi, 1997). Also saccade adaptation, an experimental modification of saccade amplitude, changes the apparent position of stimuli presented at the saccade target position (Schnier, Zimmermann, & Lappe, 2010; Zimmermann & Lappe, 2010, 2011). The strongest mislocalization effects occur when probe stimuli are presented at the time of saccade eye movements (Ross, Morrone, Goldberg, & Burr, 2001). The mislocalization starts 70 ms before and peaks at saccade onset. Stimuli presented in complete darkness will appear shifted in saccade direction homogeneously across the visual field when shown in the perisaccadic temporal range. Under dim light conditions with a saccade target, perisaccadic test
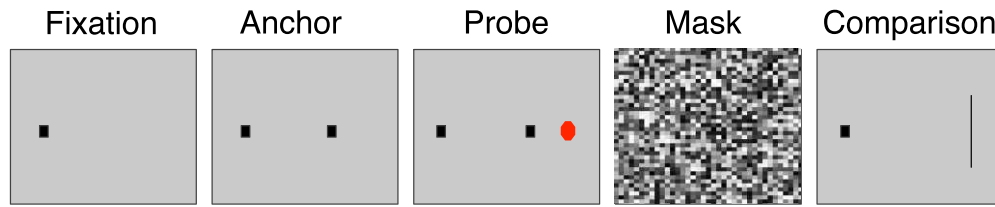
Figure 1. Probe localization trial. To begin, the subject fixated on a point 10° to the left of the screen center for a duration ranging from 940–1440 ms. Then an anchor dot appeared 5° to the right of screen center. At various times around onset of a random dot mask, a colored probe dot was presented at −2.5°, 1°, 9°, or 12° from fixation for one frame (17 ms). Long after the mask offset a comparison bar was shown and the subject had to indicate the perceived position of the probe relative to the bar.

stimuli appear compressed toward the saccade target. Probe stimuli presented on the foveal side of the saccade target appear shifted in saccade direction whereas probe stimuli presented beyond the saccade target appear shifted against saccade direction (Lappe, Awater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997). Also stimuli presented orthogonally to the saccades path appear compressed (Kaiser & Lappe, 2004).

Perisaccadic mislocalization is modulated by visual anchors (Cicchini et al., 2013): A visual stimulus presented −150 ms to 100 ms relative to saccade onset will shift the compression focus to its position. If no saccade target is shown at all and saccades are performed into a featureless region, perisaccadic localization is almost veridical (Zimmermann, Burr, & Morrone, 2012).

Here we investigated whether compression of space toward an anchor is a general phenomenon that can even be observed when tested with a brief probe having high spatial uncertainty while the eye is steadily fixating. We decreased the spatial certainty of the probe dot by presenting a whole-field random texture. This mask also mimics the effects of the high-speed motion produced by the saccadic displacement of the retinal image, which leads to a drastic reduction of visual sensitivity (Ross, Burr, & Morrone, 1996). We show that in the presence of this mask, spatial locations, as measured by briefly flashed probes, are attracted toward an anchor that is either more stable or closer to the fovea, effectively demonstrating a compression of space around the anchor.

Experiment 1

Methods

Apparatus

Subjects were seated 57 cm from a Samsung Sync-Master 2233 (Seoul, South Korea) with head stabilized by a chin- and headrest. The visible screen diagonal was 20 inches, resulting in a visual field of 40° × 30°. Stimuli were presented on the monitor with a vertical frequency of 60 Hz at a resolution of 800 × 600 pixels. The stimuli were presented on a homogeneously gray background (41.8 cd/m^2).

Participants

Human subjects (five participants, three females and two males, including one author, mean age: 37 years), with normal or corrected-to-normal vision participated in all experiments with informed consent. The experiments were carried out in the Institute of Neuroscience and Medicine (INM-3), Research Center Juelich, Germany, following the principles laid down in the declaration of Helsinki.

Procedure

A trial started with the presentation of a fixation point 10° to the left of the screen center on the vertical midline (see Figure 1). Subjects were required to keep gaze on the fixation point throughout the trial. After 1000 ms plus a random delay between 0 and 500 ms an anchor stimulus (black rectangle, size: 0.75° × 0.75°, luminance: 0.33 cd/m^2) was presented 5° to the right of the screen center on the vertical midline. The anchor stimulus remained visible for the rest of the trial. After a random delay between 100 ms and 180 ms from the anchor's onset (a variation which we found separately to have little or no effect, see Experiment 2), a whole-field random texture was shown for 51 ms. At various times relative to the mask onset, a colored probe dot (red color, radius: 0.75°, luminance: 13.42 cd/m^2) was flashed for 17 ms. In sessions testing horizontal localization, the probe dot was presented always on the horizontal meridian while its horizontal position was varied across trials (−2.5°, 1°, 8.75°, and 12.5° relative to screen center). In sessions testing vertical localization, the probe dot was presented always on the vertical meridian while its vertical position was varied across trials (−7.5°, −3.75°, 3.75°, and 7.5° relative to screen center). Subjects were instructed to report the probe
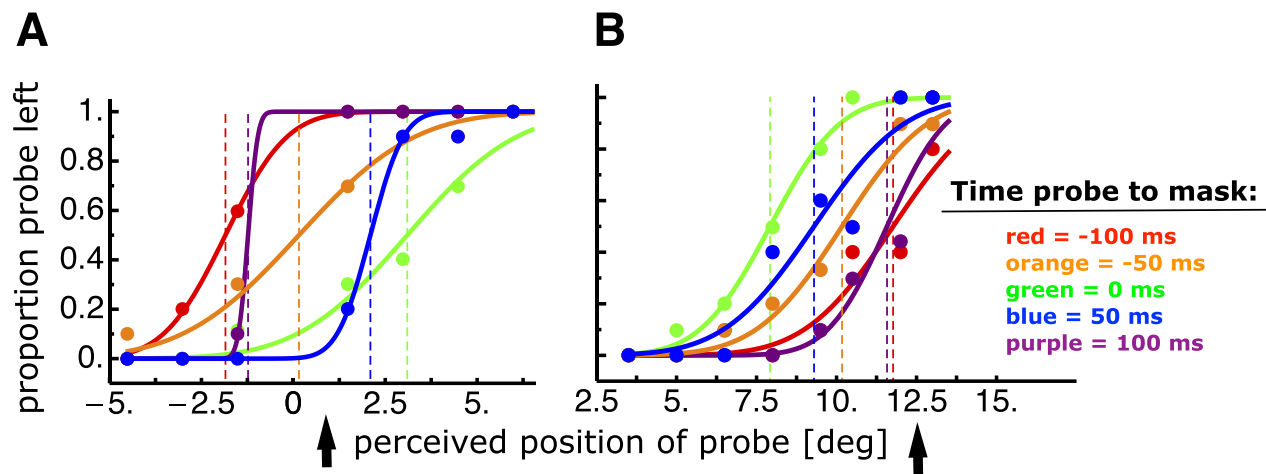
Figure 2. (A) Sample psychometric functions from one representative subject for the five different timings of probe presentation relative to mask onset. The probe dot position (1° horizontally offset from the fovea) is indicated by the black arrow. The anchor location was 5° horizontally offset from the fovea. (B) Same conventions as in (A) except that the probe was at 12.5°.

position with respect to a comparison stimulus that appeared 500 ms later. The comparison stimulus was presented in all experiments in a range between −1.5° and +6° around stimulus location in one of eight equiprobable positions. Each of these positions was tested 10 times, pseudorandomly intermixed. A full psychometric function was generated for each probe position and each time of appearance relative to mask onset and a cumulative Gaussian distribution was fitted to the data.

Results

Figure 2 shows sample psychometric functions for probe stimuli presented at 1° (Figure 2A) and for probe stimuli presented at 12.5° (Figure 2B) in the horizontal testing conditions. To check that the probe was visible at the different eccentricities and onset times relative to the mask, we analyzed the precision of localization across the different conditions using the slope of the psychometric functions (the "just noticeable differences," JNDs). If the probe was not seen at all, the psychometric functions would be flattened. There was a trend for larger JNDs (less precision) for the probes presented near the fovea within 50 ms of the mask for the subject shown in Figure 2A. However, on average no statistical differences in JNDs were found for different probe onset times and probe eccentricities across the five subjects (repeated measures ANOVA).

When the probe was presented long before or after mask onset (>100 ms) the probe's perceived position was close to its actual location. In contrast, probes presented around the time of the mask appeared shifted toward the anchor. This attraction amounted to as much as 4° or 50% of the probe-to-anchor separation, and was found for all tested directions, i.e., for stimuli presented to the left or right of (Figure 3A), as well as above or below (Figure 3B) the anchor stimulus. To quantify the compression magnitude we calculated a mislocalization index related to Lappe et al. (2000). The index represents the average difference between the separation of the perceived locations of the outermost probes (−2.5° and +12.5°) and the innermost probes (1° and 8.75°) at mask onset and that reported at 102 ms before mask onset, normalized by the separation reported at 102 ms before mask onset. In this index a value of 1 indicates full compression, while 0 indicates no compression. For horizontal judgments, the compression index of 0.44 ± 0.06 was significantly greater than 0 (paired t test, t[5], $p = 0.0003$).

For vertical judgments (Figure 3B), the compression index was 0.41 ± 0.17, again being significant (paired t test, t[5], $p = 0.012$). The attraction toward the anchor stimulus therefore produced an effective compression of space in all directions around the anchor.

Discussion

Thus, data suggest that the visual anchor dramatically changed the apparent position of the probe stimulus. When the probe dot was shown simultaneously with the mask, probe stimuli at all positions were compressed toward the anchor position. The attraction effect toward the anchor was similar in size to perisaccadic compression toward the saccade target while its time course relative to the mask was similar to that of perisaccadic compression relative to the saccade. The peak mislocalization was seen when the probe stimulus occurred closest to mask onset. This is
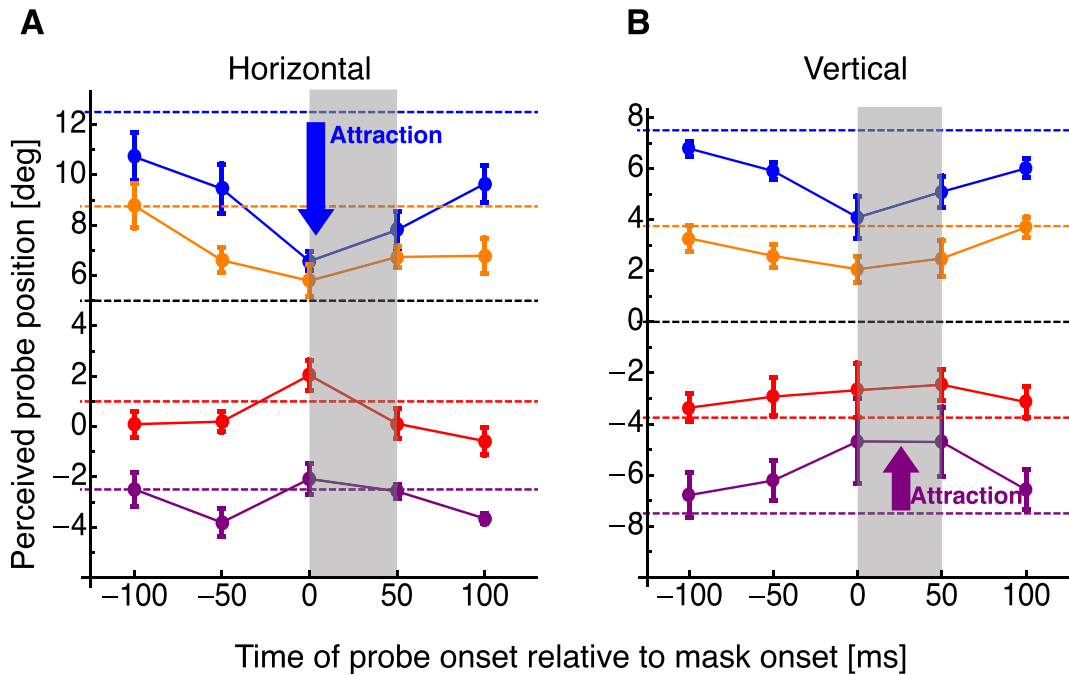
Figure 3. (A) Perceived position of the probe dot measured in the horizontal dimension as a function of presentation time relative to mask onset. Each dot represents the average across subjects. Error bars are *SEM*. Colored dotted lines show the physical positions of the probe dot. The gray dotted line shows the position of the anchor stimulus. The gray shaded area indicates the time when the mask was presented. Fixation was at −10°. (B) Same conventions as in (A) except that the probe dot was displaced vertically relative to the anchor.

consistent with saccade experiments since compression of visual space and suppression of visual sensitivity is strongest at saccade onset. The attraction effect observed is unrelated to the smaller foveal bias reported for flashed visual objects (Kerzel, 2002; Mateeff & Gourevich, 1983; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; O'Regan, 1984; Sheth & Shimojo, 2001; van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999), which shift only in one direction, i.e., toward the fovea.

Experiment 2

The onset of an unexpected visual object produces a shift of attention. One could thus argue that the onset of our anchor changed the apparent position of the flashed probe by triggering an attention shift. Shifts of attention can indeed modulate the perceived spatial position of an object (Suzuki & Cavanagh, 1997). Yamada, Miura, and Kawabe (2011) showed that short stimulus onset asynchronies (SOAs) lead to apparent repulsion between cue and probe stimulus, while longer SOAs produce more attraction. To test the role of attentional shifts, we used the setup of Experiment 1 and systematically varied the onset of the anchor. Subjects (four participants, two female and two males,

including one author, mean age: 39 years) localized the probe (presented for 17 ms), which was now always presented simultaneously with the mask (presented for 51 ms) to obtain maximal attraction. A full psychometric function (same procedure as in Experiment 1) was measured for each of the nine different anchor onsets (−306 ms, −204 ms, −102 ms, −68 ms, −34 ms, 0 ms, 34 ms, 102 ms, and 204 ms relative to mask onset).

Results

Figure 4 shows perceived position of the probe dot as a function of anchor onset time. Strong attraction was found when the anchor appeared between −200 ms and −68 ms before the simultaneous onset of probe and mask, thereby confirming the results of Experiment 1. However, when the probe appeared long before (−300 ms) mask onset, the perceived position of the probe dot was close to the baseline localization of Experiment 1 (see Figure 3). Localization was also nearly veridical when the anchor was presented close to mask and probe onset. In order to test whether there is a significant influence of anchor onset time on mislocalization magnitude we chose the anchor onsets at −300 ms as baseline. We binned localization data from anchor onsets before mask onset (−200 ms to −60 ms),
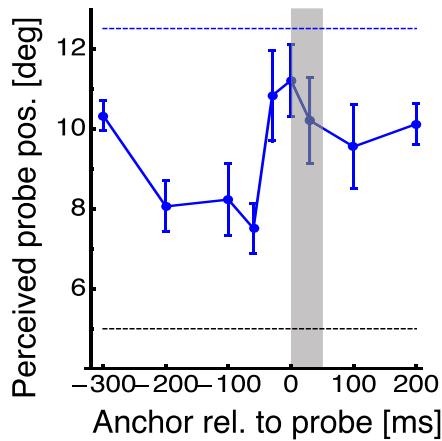
Figure 4. Perceived position of a probe dot that was presented simultaneously with mask onset as a function of anchor onset. The blue dotted line shows the physical position of the probe dot and the black dotted line the physical position of the anchor stimulus. Error bars are *SEM*. The gray shaded area indicates the time when the mask was presented.
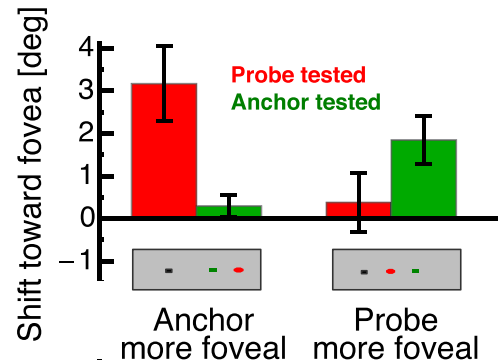

Figure 5. Apparent position shifts of probe and anchor for probe more foveal than anchor compared to anchor more foveal than probe. The shifts of the perceived positions of probes (red bars) and anchors (green bars) are shown with positive values representing a shift toward the fovea. The icons under the bar plot illustrate the relative positions of anchor and probe in the two conditions tested. Error bars are *SEM*.

around mask onset (−30 ms to 30 ms) and after mask onset (100 ms to 200 ms) and compared them to the baseline anchor onsets long before mask onset (−300 ms). Significant mislocalization occurred when the anchor appeared before mask onset (paired t test, t[4], $p = 0.0018$), but not when the anchor was presented around (paired t test, t[4], $p = 0.38$) or after mask onset (paired t test, t[4], $p = 0.09$).

Discussion

The attraction effect reached its maximum when the anchor was presented between 68 ms and 200 ms before mask onset and vanished when the anchor appeared longer than 200 ms before mask onset. This profile is consistent with the time course of transient attention shifts: Nakayama and Mackeben (1989) found that transient attention shifts take around 50 ms to complete. Consistent with our decline of attraction for anchors shown 200 ms before mask onset, Nakayama and Mackeben (1989) found a fallout in their performance measures if the cue-target SOA exceeded 200 ms. Attraction was lowest when anchor and probe appeared simultaneously. This might be in accordance with the idea that short anchor-probe SOAs lead to repulsion and longer ones to attraction. Repulsion would cancel out attraction and shift the probe in the opposite direction. Another explanation for the loss of attraction for very short SOAs might be that in this case both anchor and probe are perceived as simultaneous so the distance between them can be judged directly—"exocentrically"—without reliance on absolute position judgments of each separately (Sogo & Osaka, 2001).

Experiment 3

While a recent, sudden onset is necessary to induce the attraction effect, we wondered whether the anchor stimulus had to be displayed continuously for the effect to appear. In Experiments 1 and 2 the anchor remained visible until the end of the trial. The main manipulation of Experiment 3 was to test the attraction effect with an anchor onset time nearly as short as that of the probe stimulus. We thus presented the anchor stimulus for only 51 ms in green color. The probe was flashed for 17 ms in red color and to induce maximal attraction, the probe was always presented simultaneously with the mask, in order to produce the strongest mislocalization (see Figure 3A). The similar presentation duration of anchor and probe also allowed us to test the influence of temporal order. The anchor therefore was presented pseudorandomly either 68 ms before or 68 ms after probe onset. We then asked subjects (three participants, two female and two male, including one author, mean age: 26 years) to localize either the probe or the anchor relative to the subsequently presented standard bar. We tested two probe positions, one more foveal (at 1°) and one more peripheral (at 12.5°) than the anchor (which was at 5°).

Results

Figure 5 shows the amount by which either the probe or the anchor shifted toward the fovea. The temporal order (anchor first vs. probe second) had no significant effect (repeated measures ANOVA, $df = 1$, $F = 8.161$, $p = 0.251$). Data were collapsed across temporal order.

Since all values in Figure 5 are positive, both probe and anchor shifted toward the fovea. In Experiment 1, compression was seen toward the stationary anchor whether the probe was more foveal or more eccentric than the anchor. In contrast, in Experiment 3 the shift was always of the more peripheral toward the more foveal stimulus when the anchor had the same properties as the probe. In particular, on trials where the anchor was more foveal, the attraction effect, the shift of the probe toward the anchor, remained identical to that seen in the earlier experiments. Thus, the flashed anchor attracted the more peripheral probe, no matter which appeared first. In these trials, the anchor itself was localized almost veridically. However, on trials where the probe was more foveal, the perceived probe position hardly shifted and instead the anchor was mislocalized toward the probe, again independently of temporal order of probe and anchor. In the case where the presentation duration of probe and anchor were both brief, the stimulus presented closer to the fovea acted as an anchor attracting the other stimulus while hardly shifting itself.

Discussion

When the anchor was flashed briefly like the probe, temporal order of the two had little influence. Instead, proximity to the fovea determined the direction of attraction: The more foveal stimulus always attracted the other irrespective of temporal order. This finding clearly argues against an attentional shift as the main source of the effect. An attentional focus should always be drawn to the first stimulus and so the first stimulus should always attract the second if attention were the sole factor determining the shift. However, rather than timing, we found position to be the determining factor.

General discussion

Previous studies have shown an effect of a first flash on localization of a second test (McCourt & Jewell, 1999; Pratt & Arnott, 2008; Suzuki & Cavanagh, 1997) also using a mask as we did. But these studies typically showed a repulsion of the second test by the first. One study reported that the repulsion changed to attraction for longer intervals between probe and comparison stimulus (Yamada et al., 2011). While this account might be true for stationary anchors, it does not explain the results of our Experiment 3, where the anchor was flashed. In that case the temporal order of anchor and probe did not influence attraction. Other studies tested mislocalization during fixation as a control for non-saccadic factors in mislocalization and found much

smaller attraction shifts than those reported here (Eggert, Ditterich, & Straube, 2001; Sheth & Shimojo, 2001). The main difference between their procedures and ours is that we introduced a brief visual mask, which, like a saccade, increased the spatial uncertainty of the stimuli, broadening their position distributions.

Although the attraction effect was time-locked to the onset of the anchor, shifts of visual attention cannot account for all of the results: When both the probe and the anchor were flashed, the direction of attraction was not determined by visual order but by position. Although an attentional account would predict that the first stimulus should attract the second, we found that the more foveal stimulus attracted the more peripheral one, irrespective of which was first. Wardak, Denve, and Hamed (2011) found small effects of attention shifts on the perceived position of briefly flashed probes, which were masked. Their measured shifts were approximately 0.3° at an eccentricity and spacing similar to ours where we measured shifts of as much as 4°. One significant difference in their procedure was that they presented two anchors, either one of those could be the attended cue. Since our experiments suggested that the position and timing of the anchor was more important than attention in generating attraction, it is plausible that the nonattentional component of the attraction effects might cancel in the region between the two anchors.

The compression effect that we observed is large enough in the foveal direction to be relevant for perisaccadic mislocalization, specifically for probes more peripheral than the saccade target where the shift is seen opposite to the saccade vector (Ross et al., 2001). The perifoveal compression effect we report here resembles perisaccadic compression in its magnitude and time course. Perisaccadic compression usually starts 75 ms before saccade initiation and peaks at saccade onset (Ross et al., 2001). As in our Experiment 1, probe dots are also compressed in orthogonal direction to the saccade path (Kaiser & Lappe, 2004). A computational model explains these shifts by an alteration of the receptive field structure triggered by oculomotor feedback (Hamker, Zirnsak, Calow, & Lappe, 2008). To induce attraction the anchor must be shown at least 68 ms before probe and mask onset. This is consistent with perisaccadic compression, which does not occur when no saccade target is shown before saccade initiation (Zimmermann et al., 2012). Previous studies had investigated whether a displacement of the visual scene, simulating the effects of a saccade, is sufficient to induce mislocalization. Two studies (Honda, 1995; Morrone, Ross, & Burr, 1997) reported only mislocalization in direction of the displacement. Ostendorf, Fischer, Gaymard, and Ploner (2006), however, found compression comparable to our results,
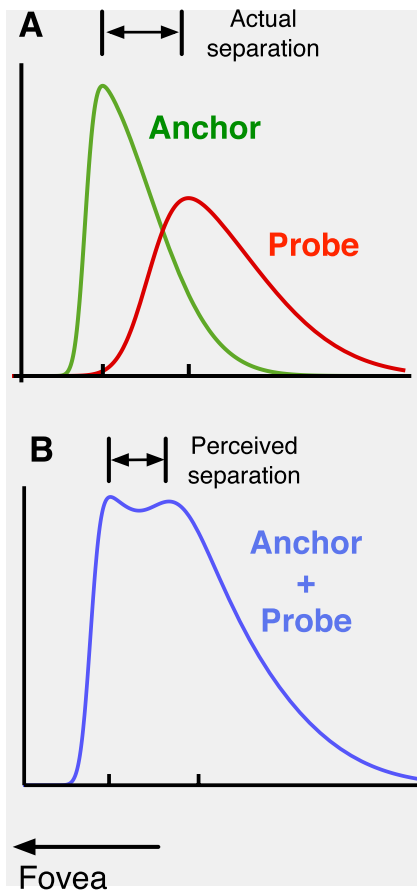
Figure 6. Proposed model of perifoveal attraction. The neural activity distributions for the transient onsets of the anchor (green curve) and the probe (red curve) are broadened by the mask and the distribution is naturally asymmetric to the peripheral side because of cortical magnification. When the anchor and probe distributions overlap and sum (blue curve) the peak of the more peripheral distribution will shift toward the more foveal location, producing an apparent attraction of the probe to the anchor.

most probably because of the reduced contrast of the probe stimulus.

We offer a speculative interpretation of these compression effects in terms of interactions between the anchor and probe activity distributions on a neural representation that determines perceived location (see Figure 6). We can see the shifts in perceived location as similar to the shifts seen in perceived orientation following adaptation (see review in Clifford, Wenderoth, & Spehar, 2000) where the activity distributions for the test are shifted by the pattern of sensitivity changes across the population induced by adaptation. Rather than effects of adaptation, here we look simply at the sum of two activity distributions where the peaks indicate the location of each stimulus and these peaks are shifted by the overlapping distributions. Normally, the target-related distributions of stimuli like our anchor and probe would have only a narrow spread

around their actual location but we suggest that the mask broadens this spread (e.g., Battaglia, Jacobs, & Aslin, 2003), perhaps by eliminating the normal inhibitory surrounds, in particular for transient stimuli. Others have shown that cortical magnification stretches the spread of the target-related activity distribution on the peripheral side (Essen, Newsome, & Maunsell, 1984) and an asymmetry in the distribution may cause an asymmetry in the shift. In particular, when both distributions overlap and sum up, the peak of the more peripheral stimulus shifts toward the more foveal stimulus, but the more foveal stimulus does not shift much, resulting in apparent attraction of the probe toward the anchor that is stronger in the peripheral to foveal direction. Note, however, any correspondence between our data and the classic effects of overlapping response distributions may only be coincidental.

Keywords: mislocalization, compression, fixation

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