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Stereomotion scotomas occur after binocular combination

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ABSTRACT

Stereomotion scotomas are a surprisingly common visual impairment that result in an observer's inability to accurately report the direction of an object's motion in depth in restricted parts of the visual field. In this study we investigated the role of binocular cues to motion in depth. Using stimuli containing only non-stationary cues to stereomotion, we measured sensitivity across the visual field and identified areas of significant impairment in stereomotion processing in over 50% of otherwise healthy observers. These impairments vary idiosyncratically in extent and location between observers. We established that these impairments occur for a variety of visual stimuli, as long as they share the property that stimulus motion is exclusively defined by interocular and velocity differences. We tested for concordant impairments at relatively early stages along the visual pathway, i.e. changes in sensitivity across the visual field to local eye-dominance, monocular motion or instantaneous binocular disparity. Although we find variability in sensitivity across the visual field of our observers for all visual tasks, this variability across visual field locations did not correlate with the impairments in stereomotion processing. We therefore conclude that these stereomotion scotomas are due to impaired processing of dynamic cues after the stage of binocular combination.

1. Introduction

Everyday activities such as playing sports, driving a car or just navigating the world depend on the ability to perceive motion in depth. Despite its importance, the ability to perceive motion in depth can be impaired in a large proportion of otherwise healthy observers (Hong & Regan, 1989; Regan, Erkelens, & Collewijn, 1986). These impairments are specific to regions of the observers' visual field in which they are not able to judge whether an object is moving towards or away, termed stereomotion scotomas (Richards & Regan, 1973). The nature and underlying cause of these visual impairments have received little attention and therefore remain poorly understood. We investigated whether these stereomotion scotomas are specific to either a deficit in early visual processing of the binocular cues to motion in depth or rather the result of deficient processing in a later stage of the visual hierarchy.

In natural scenes an object moving towards or away from an observer produces both monocular and binocular cues to motion in depth. We consider only binocular cues and their monocular constituent signals here because we are specifically interested in stereomotion processing. The visual system can use two binocular cues to motion in depth: changing disparity over time (CD) and interocular velocity differences (IOVD) (Harris, Nefs, & Grafton, 2008; Regan & Gray, 2009). The visual system processes these two cues independently (Rokers, Cormack, & Huk, 2009) and there is mounting evidence that the cues make independent contributions to the percept of motion in depth (Brooks & Stone, 2004; Brooks, 2002; Czuba et al., 2010; Nefs, O'Hare, & Harris, 2010; Rokers, Cormack, & Huk, 2008; Shioiri et al., 2008; Shioiri, Saisho, & Yaguchi, 2000).

In order to identify stereomotion scotomas we measured sensitivity to the direction of motion in depth across the visual field in our observers. To exclude possible contributions from instantaneous binocular disparity, we used a set of stimuli that were specifically designed to contain only non-stationary cues to stereomotion. Specifically, in previous work the stimulus consisted of a small rectangular bar that was moved back and forth in depth (Hong & Regan, 1989; Regan, Erkelens, & Collewijn, 1986). Such a stimulus is confounded because it contains static cues to the direction of motion in depth (instantaneous disparity at the start and end of motion). To circumvent this issue, we used a drifting grating pattern within a Gaussian aperture. Because of the periodicity of the grating, instantaneous disparity would be uninformative of the direction of motion. In order to ensure that the measured sensitivity for stereomotion is not specific to certain stimulus

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parameters, we also used a different stimulus (moving dots) to independently verify the location of any stereomotion scotomas.

Next, we considered the possible underlying causes for stereomotion scotomas in early stages of visual processing. As illustrated in Fig. 1 the binocular percept of 3D motion can be computed by processing monocular signals in two separate ways, corresponding to the two binocular cues to motion in depth (CD, IOVD). We hypothesized that a deficit in processing of either the monocular velocities ($V_{L,R}$) or binocular disparity (D_t) could be the underlying cause of the stereomotion scotomas, since either of those deficits could result in a less reliable stereomotion signal (V_{3D}). Another possible cause for the scotomas, binocular rivalry, is not directly represented in Fig. 1, but would most likely occur prior to extracting these cues.

We were particularly interested in this question, since visual sensitivity for each of the constituent cues to stereomotion varies across the visual field. Stereomotion scotomas might therefore be the result of a specific impairment at one of these stages of stereomotion processing. Specifically, sensory eye dominance in binocular onset rivalry has shown to be anisotropic across the visual field (Carter & Cavanagh, 2007; Xu, He, & Leng, 2011). Additionally, there is variability in sensitivity to binocular disparity (Blakemore, 1970; Julesz, 1971; Westheimer & Truong, 1988), as well as directional anisotropy of motion sensitivity (Ball & Sekuler, 1980; Edwards & Badcock, 1993; Georgeson & Harris, 1978; Giaschi et al., 2007; Raymond, 1994) across the visual field. We therefore compared the variability in sensitivity to these cues with the variability in the locations of observers' stereomotion scotomas.

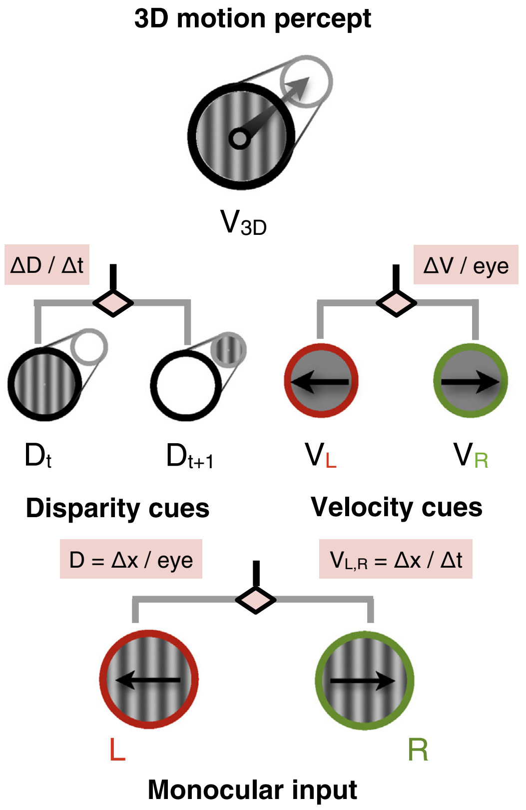

Fig. 1. An estimate of motion in depth can be computed by processing binocular information in two ways. Based on the two retinal images the visual system can extract velocities for each eye ($V_{L,R}$) and compare these velocities to compute the motion in depth (V_{3D}) percept (formula in pink rectangle). The computation of motion in depth can also be based on disparity information. After computing the binocular disparity (D_t) from the retinal images the visual system could track the change in disparity over time (D_{t+1}) as a cue to motion in depth (formula in pink rectangle). A deficit in extracting the monocular velocities or in processing the binocular disparities is hypothesized as a possible cause for the stereomotion scotomas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Briefly, we found evidence for stereomotion scotomas based on non-instantaneous cues in over 50% of our observers. The scotomas varied idiosyncratically in size and location between, but not within, individual observers. We found variability across the visual field in sensitivity at each of the three stages of stereomotion processing in our observers but these variations were not predictive of the location of the stereomotion scotomas. These results lead us to conclude that stereomotion scotomas are not due to binocular rivalry, and occur based on deficits in visual processing after the extraction of retinal motion and binocular disparity. The impairments therefore have to be due to impairments in the processing of the cues underlying stereomotion, i.e. the changing disparity (CD) and/or interocular velocity difference (IOVD) cues, later in the visual hierarchy.

2. Methods

2.1. Observers

A total of 11 observers (1 female, ages 24–38) participated in the experiments. The participants gave informed consent and all had normal or corrected-to-normal vision. All were experienced psychophysical observers and naive to the purpose of the experiments, with the exception of the three authors. The experiments were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus and display

All stimuli were presented using a mirror stereoscope. The setup consisted of two 20″ CRT displays (85 Hz, 1024 × 768 pixels) with each display containing the image for one eye at a simulated viewing distance of 75 cm. The luminance of the two displays was linearized using standard gamma-correction procedures, and the mean luminance was 46.7 cd/m^2. The observer viewed the images through a set of mirrors that redirected each image to the corresponding eye. Vergence was facilitated by a $1/f$ noise background pattern. In addition a small fixation dot and a fixation cross of nonius lines was presented in the center of the display to help the observer maintain fixation and monitor vergence during the experiments. (See Fig. 2 for an example of the stimulus display). The stimuli were generated using a Apple Mac Pro computer using Matlab (Mathworks, Natick, MA, USA) and the Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

2.3. Stimuli

The stimuli were presented within circular apertures (1.5° diameter) positioned within a 7.5° radius around fixation. The centers of the apertures ranged from 1.5° to 7.5° eccentricity in 5 equal steps and were laid out in a spoke-wheel pattern with 8 locations per 'ring' (see Fig. 2). This arrangement provided a total of 40 testing locations across the visual field.

2.3.1. Stereomotion sensitivity

We measured stereomotion sensitivity in three different experiments. In the first stereomotion sensitivity experiment, the stimulus consisted of a sinusoidal grating (2 cycles/°) drifting laterally at 4 cycles/s within a stationary spatial envelope (2-dimensional Gaussian, sigma 0.25°, falling to 1% luminance at 0.56° eccentricity, Fig. 2A). These stimulus parameters were used based on previous work which showed that stereomotion sensitivity is highest at a

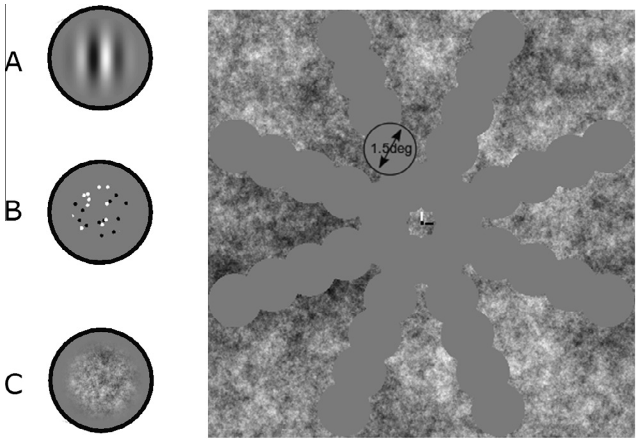

Fig. 2. Example of the stimulus display for one eye. Each eye's image contained 40 locations (gray circles) across the visual field where sensitivity would be assessed. The displays for the two eyes were identical except for the fixation cross and the stimulus. (A) The stimulus for the stereomotion and ocular dominance experiments consisted of a sinusoidal grating pattern. (B) In the stereomotion and lateral motion experiments, the stimulus consisted of randomly positioned black and white translating dots. (C) In the static depth experiment the stimulus was a randomly generated circular patch of pink ($1/f$) noise with horizontal offset between the two eyes. Movies of all the stimuli used in the experiment can be found in the Supplementary materials.

monocular speed of $\sim$2°/s (Czuba et al., 2010) and our pilot data which showed that this spatial frequency produces the strongest percepts of motion in depth for this size of the Gaussian envelope.

In the second stereomotion experiment we used the same procedure as the first experiment but the stimulus consisted of moving dots rather than drifting grating patterns. A group of randomly distributed black and white dots (Fig. 2B, dot diameter 0.06°) was presented moving laterally at 2°/s in opposite directions in the two eyes. Because the disparity range was limited this created a percept of the dots continuously wrapping through a cylindrical volume.

In the final stereomotion sensitivity experiment we used the exact same stimulus configuration as the first experiment (drifting grating, Gaussian aperture) but with varying contrast levels (5%, 7.5%, 10%, 20%, 100% contrast). Because the additional variable (contrast) increases the number of trials needed for each observer, we confined the stimulus to a single eccentricity 'ring' that would include a region of reduced stereomotion sensitivity (as measured by the previous two methods) in each observer. Because we had 5 levels of contrast as well as 5 different eccentricities in the previous experiments, this resulted in the same number of trials for this experiment and the previous ones.

In order to identify a possible underlying cause for the impairments relatively early in the visual pathway, we conducted four experiments that measured extent of eye dominance (2 experiments), sensitivity to static binocular disparity, and sensitivity to lateral motion, in the same locations across the visual field. Movies of all stimuli used in the experiments have been included in the Supplementary materials.

2.3.2. Eye dominance

To measure sensory eye dominance we used a binocular rivalry paradigm and two types of stimuli. The first stimulus was a stationary version of the 2 cycles/° grating pattern used in the stereomotion experiment (Fig. 2A) but oriented ±45° (counter)clockwise in the two eyes. The second stimulus was the drifting 2 cycles/° grating pattern used previously, but instead of drifting horizontally, this grating drifted vertically, in opposite direction (up-/downward) in the two eyes. Both stimuli were designed to create binocular rivalry, instead of binocular fusion, so that in the absence of strong eye dominance the percept could alternate between the left- and right-eye stimuli.

2.3.3. Binocular disparity

To measure sensitivity to disparity-based static depth, a patch of randomly generated pink ($1/f$) noise (Fig. 2C) was presented within the same Gaussian aperture as the grating stimuli. The use of a $1/f$ noise patch over a stationary grating was necessary because the periodicity of the latter would have rendered the disparity signal ambiguous (i.e. a binocular 'match' could be found in either direction). The patch was displaced, inside the aperture, between the two eyes to create a binocular disparity of ±0.1° (6 min of arc).

2.3.4. Lateral motion

In the motion sensitivity experiments the stimulus consisted of a set of randomly distributed black and white dots (Fig. 2B, dot size 0.08°) contained within a 2° circular aperture centered on one of the 40 locations in the same way as in the other experiments. This larger diameter of the aperture was necessary because pilot experiments showed that a 1.5° aperture (which would correspond more closely to the Gaussian apertures) was too small to perform the task, even at 100% dot coherence. On each frame the dots would be repositioned at either a random location or according to a set direction (left or right) and displacement ($\mathrm{d}x = 0.3^\circ$, $\mathrm{d}t = 45$ ms). The number of dots that would displace coherently was fixed at 50% (value based on pilot study using staircase-method) and the signal and noise dots were randomly selected on each frame-interval. A total of four sets of dots were presented interleaved to prevent 'streaks' and tracking of individual dots (Newsome & Pare, 1988). The dots where presented binocularly but with the exact same configuration in the two eyes.

2.4. Procedure and task

The stereoscope was initially adjusted so that the vergence demand was appropriate for the viewing distance given a typical interocular distance. Prior to each session, the observer made further adjustments so that the nonius markers were aligned both horizontally and vertically, and vergence was comfortable. Observers were instructed to maintain fixation at all times during the experiment.

All experiments followed a similar presentation procedure. In the stereomotion experiments the grating stimulus drifted (or dots moved) in opposite horizontal directions in the two eyes creating a binocular percept of motion drifting towards or away from the observer. On each trial the stimulus was presented for a single 250 ms interval in one of the 40 possible locations. Observers were asked to maintain fixation at the center of the display at all times, so that this procedure mapped sensitivity to the stimuli across the visual field. After stimulus offset observers responded via a key press. For each observer, 20 repetitions of each of the 40 locations were pseudo-randomly distributed across trials, ensuring that the observer was unable to predict the location for any given trial. In the stereomotion experiments, the observer performed a 2-alternative forced-choice (2AFC) task on the direction of motion (towards/away) of the stimulus on each trial.

The binocular rivalry experiments followed a similar presentation procedure but with a longer stimulus duration (500 ms). In pilot experiments we did not observe significant rivalry at the shorter 250 ms duration used in the stereomotion assessment. To determine if rivalry nonetheless might be a contributing factor to the stereomotion scotomas, based on previous reports of variation in eye dominance across the visual field (Carter & Cavanagh, 2007; Stanley, Carter, & Forte, 2011), we assessed rivalry using the longer stimulus duration. The task for the observer was to indicate on each trial which of the two possible percepts (clockwise/counterclockwise orientation, upward/downward motion) was observed. If there was no exclusive dominance of one percept the observer was instructed to report the "more predominant" of the two.

In the static depth experiment the stimulus was presented for 250 ms and the observer indicated whether the stimulus was perceived "in front" or "behind" the plane of fixation, as defined by the fixation cross and the 1/*f* noise background.

The motion sensitivity experiment had a presentation duration of 500 ms (the task proved too difficult at shorter durations) on each trial. The task for the observer was to report the perceived direction of motion (left/right) of the coherently moving dots.

2.5. Data analysis

In order to quantify the stereomotion sensitivity of each observer, the percentage of correct responses was computed for each location in the visual field. To determine the stability of the measured stereomotion sensitivity we tested each observer on three separate days and computed the Pearson correlation coefficient across locations between the separate datasets. We generally observed good session-to-session agreement and subsequently combined data from three sessions for each observer to increase statistical power. The percentages correct were then plotted in a visual field map (e.g. Fig. 3) where each sample location is represented by a colored circle. A black contour marks locations where the percentage of correct responses was significantly different from chance ($p < 0.05$, uncorrected). We opted to use an uncorrected statistical criterion because we were interested in identifying locations where performance did not differ significantly from chance. Adopting such a criterion makes us relatively conservative in classifying a location as lying within a stereomotion scotoma.

Each of the other experiments was also repeated on three separate days and then subsequently combined to increase statistical power. The data from these experiments were analyzed in the same manner as the stereomotion experiment, i.e. using the percentage of correct responses in each location of the visual field, with the caveat that for the binocular and motion rivalry experiments there was no 'correct' response. For these experiments we computed the percentage of correct responses to the stimulus presented in the left eye. This produced a percentage between 0% and 100%, where 100% (0%) indicates that the observer always reports the stimulus that was presented in the left (right) eye and 50% means that the observer's responses showed no bias of one eye over the other. Locations in the visual field where this value was significantly different from 50% ($p < 0.05$, uncorrected) therefore indicated locations where one of the eyes was dominant.

3. Results

In the experiments described here we aimed to measure the sensitivity to stereomotion across the visual field for individual observers and to establish whether the location of deficits in stereomotion sensitivity was reproducible over multiple testing days.

3.1. Regions of stereomotion insensitivity in ~50% of observers

We quantified the sensitivity to stereomotion across the visual field for individual observers across three separate sessions using Gabor patterns (Fig. 2A). We plotted the sensitivity in a visual field map for each observer, providing a visual reference for the relative sensitivity across the visual field. In Fig. 3 the visual field maps for eight individual observers are shown. The colormap indicates the percentage of correct responses at each location in the visual field with 50% indicating total inability to determine direction of motion in depth (chance level) and 100% indicating perfect ability. A black contour indicates locations where the percentage correct is significantly different from chance ($p < 0.05$, uncorrected).

Fig. 3A shows the visual field map for a single observer with accurate stereomotion discrimination performance in all measured locations (in all locations the percentage correct responses is significantly above chance). The variability in the percentage correct across locations is relatively small and only shows a slight decrease over the 1.5–7.5° range of eccentricity. A second observer is shown in panel (B) of Fig. 3. For this observer the variation in percentage correct responses is much greater across the visual field. In the lower, central part of the visual field the observer was unable to

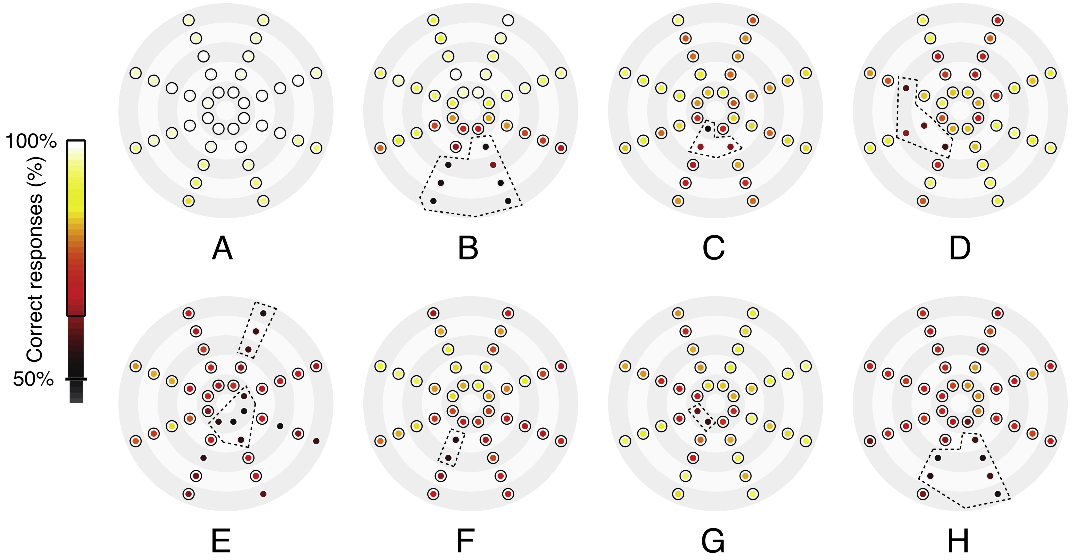

Fig. 3. Stereomotion sensitivity across the visual field for eight observers. Points in the graph correspond to visual field locations on a range of eccentricities (1.5–7.5° in 5 equal steps, indicated by gray/white rings) and polar angles (8 steps of 45° per eccentricity). The colors indicate percentage of correct responses as shown in the colorbar. The black contour marks locations where the performance was significantly above chance, with the threshold as indicated by the black box in the colorbar. The observer in the top left figure has near perfect performance across the whole visual field, and is representative for 4 out of the 11 observers we tested. All of the 7 other observers have a distinct region (at different locations) in the visual field where the performance is not significantly different from chance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reliably discriminate the direction of motion in depth, yet in the rest of the visual field and at the same eccentricities, this observer was perfectly able to do so (performance up to 100% in some locations). A third observer shown in Fig. 3C has a region of poor stereomotion discrimination performance located very close to the center of the visual field (at 1.5° and 3° eccentricity), demonstrating that the decreased sensitivity is not an overall effect of visual field eccentricity. The other five observers shown in Fig. 3 all have a region of poor stereomotion discrimination performance in their visual field, although the locations and sizes differ between observers.

Measuring changes in stereomotion performance in terms of percentage correct has the potential to confound changes in sensitivity with changes in response bias. To exclude the possibility that our results are merely reflecting a difference in response bias across the visual field, we also computed d' as a direct measure of stereomotion sensitivity. The details and results are included in the Supplementary materials (Figs. S1 and S2). We found that the percentage correct correlates very strongly with d' ($R^2 = 91\%$, $p < 0.0001$, $N = 8$) and only weakly with response bias ($R^2 = 4\%$, $p < 0.001$, $N = 8$).

We find stable impairments in stereomotion perception in 64% of our observers (7 out of 11, all shown in Fig. 3 and Supplemental Fig. S1). Within the same observer performance could vary as much as 50%, from chance (50%) to ceiling performance (100% correct), at identical eccentricities. The location and size of the impairments varied idiosyncratically across observers and could be as close as 1.5° from fixation.

3.2. Locations of stereomotion insensitive regions are stable over time

To test the stability of the measured visual field over time, we tested each participants on three separate sessions divided over multiple days using the same stimulus (Fig. 2A). These sessions were separated by at least a day and up to several weeks in some participants. Fig. 4 shows visual field maps for three observers in three separate sessions. Any region indicated with dotted lines is the region of poor stereomotion discrimination as inferred from the combined data (see Fig. 3A, B and F). Although there is session-to-session variability in the percentage correct responses within locations, the threshold level is never reached for the locations that lie within the marked region. In general we observe reliable session-to-session stability in all observers (correlation from 1st to 3rd session: $r = 0.60$, $p < 0.0001$, $N = 7$). Thus we conclude that the stereomotion scotomas are stable over time.

3.3. Locations of stereomotion insensitive regions are stable over stimulus parameters

In order to assess whether the measured sensitivity to stereomotion across the visual field is specific to the stimulus parameters used in this study, we repeated our visual field measurements using a stimulus with different characteristics (moving dots, Fig. 2B). Fig. 5 shows a comparison of the measured stereomotion discrimination performance at a single eccentricity using the Gabor and moving dots stimuli for two observers (Fig. 3E and F). Three observers participated in this moving dots experiment. Performance was correlated between the two different stimuli when combined across observers ($r = 0.68$, $p < 0.001$). These effects are on the same order as the session-to-session variability we observed within observers using the drifting grating stimuli.

To assess the stability of the scotomas as a function of stimulus contrast, we varied the contrast of the Gabor stimulus (Fig. 2A) and measured a psychometric curve to quantify contrast sensitivity at 8 locations at a single eccentricity (Fig. 5C). At very low contrasts (5–10% Michelson contrast) the performance decreases in all visual field positions, but above these values stereomotion sensitivity remained constant over a large range of contrasts (20–100% Michelson contrast). This shows that sensitivity to stereomotion is not simply the result of different contrast sensitivity inside and outside the stereomotion scotoma. In summary, we found that the stereomotion scotomas were stable across different stimuli and a wide range of stimulus contrasts.

3.4. Potential early visual mechanisms underlying stereomotion scotomas

We considered early visual mechanisms involved in stereomotion processing (Fig. 1) that could be impaired in the case of stereomotion scotomas. We identified and tested three mechanisms of early processing that might have been impaired: eye dominance, binocular disparity, and lateral motion. We quantified variability

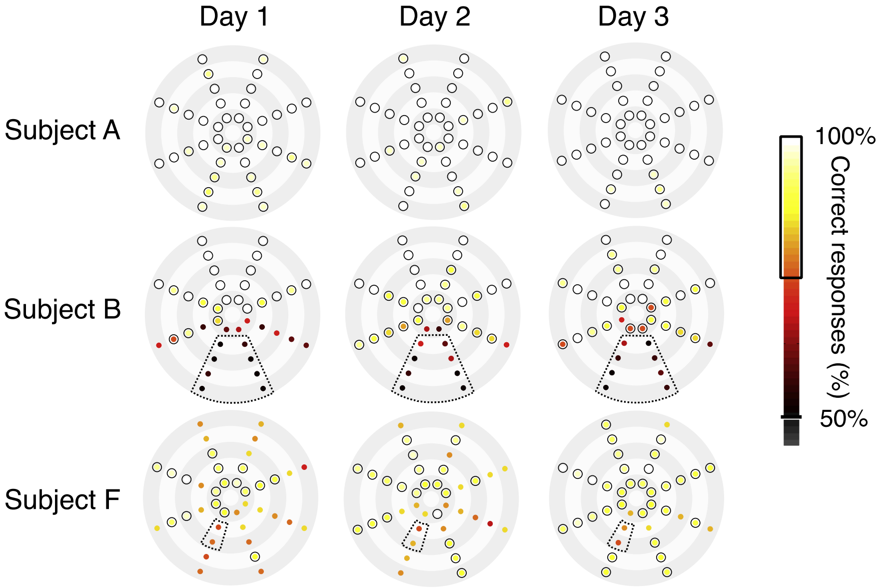

Fig. 4. Stereomotion sensitivity maps for three observers on three separate days with intervals ranging from one day to several weeks. The marked region indicates the location of possible stereomotion scotomas based on the cumulative data shown in Fig. 3. Although there is variation in the percentage of correct responses from session to session, locations within the scotoma (marked region) are not significantly different from chance in any of the sessions.

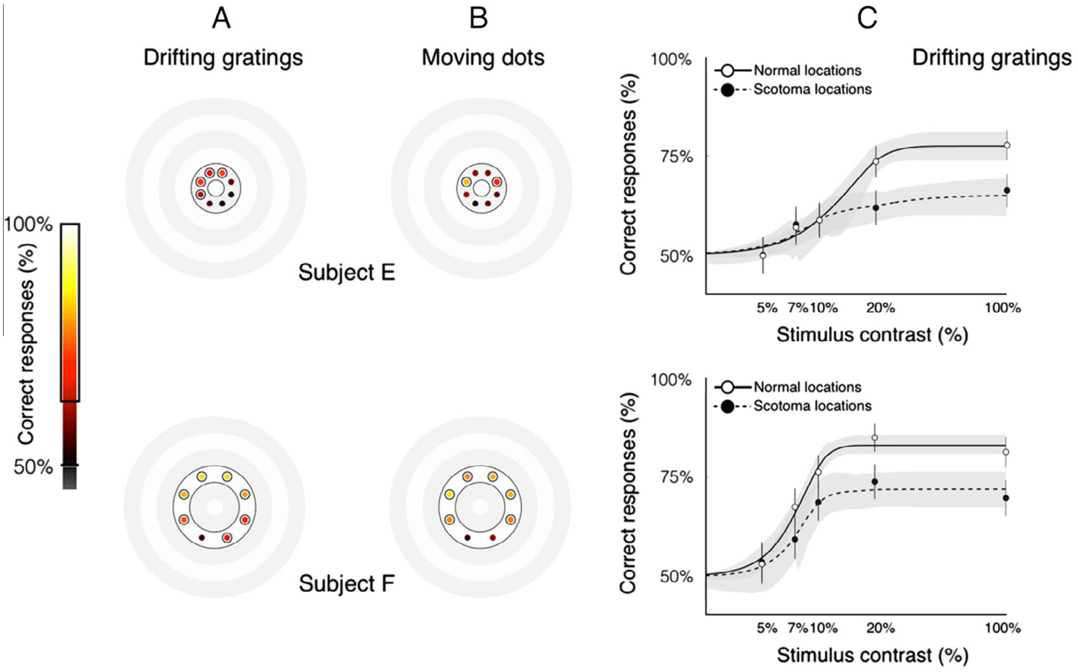

Fig. 5. Comparison of stereomotion sensitivity in two observers as measured by three different tasks. All panels (A, B, C) display the results from the same two observers. (A) Percentage of correct judgments when using a drifting grating. (B) Percentage of correct judgments when using moving dots. Both panels A and B plot percentage of correct responses as a function of visual field position. The performance for the two different stimuli (A: grating vs B: dots) are significantly correlated $r = 0.63$ ($p < 0.0001$). C: Percentage of correct responses as a function of Michelson contrast (5–100%). Here we presented the drifting grating pattern at different contrast levels. The two lines represent the average of the measurements taken at either the normal (open symobls) or scotoma locations (solid symbols, also in panel A&B). Performance remains relatively stable across a wide range (20–100%) of stimulus contrasts.

across the visual field of our participants for each of these three possible mechanisms in a series of experiments.

3.4.1. Eye dominance

We measured sensory eye dominance in two related experiments, one using stationary and one using vertically drifting Gabor patterns (Fig. 2A). Both experiments reveal significant variability in eye dominance across the visual field. In Fig. 6A eye dominance is reported as the percentage of responses that correspond to the stimulus orientation or motion direction presented in each eye, ranging from 100% right dominant (observer always reported stimulus in right eye) to 100% left dominant (always reported stimulus in left eye). We compared eye dominance based on the stationary Gabor (orientation) with eye dominance based on the drifting Gabor (motion) stimulus. We found a significant correlation between the two eye dominance experiments ($r = 0.28$, $p < 0.001$, $N = 4$), suggesting that motion-based and orientation-based rivalry share a common mechanism. However, we did not find a significant correlation between the performance in the stereomotion experiment and eye dominance ($r = 0.005$, $p = 0.94$, $N = 7$ for orientation rivalry and $r = 0.08$, $p = 0.32$, $N = 4$ for motion rivalry).

3.4.2. Binocular disparity

We quantified sensitivity to instantaneous binocular disparities by the percentage of correct responses when judging position in depth (near/far) for all observers with a stereomotion scotoma. We found that the sensitivity was stable over time (correlation from 1st to 3rd session: $r = 0.45$, $p < 0.0001$, $N = 7$) but we found no significant correlation between discrimination performance in the binocular disparity experiment and the stereomotion

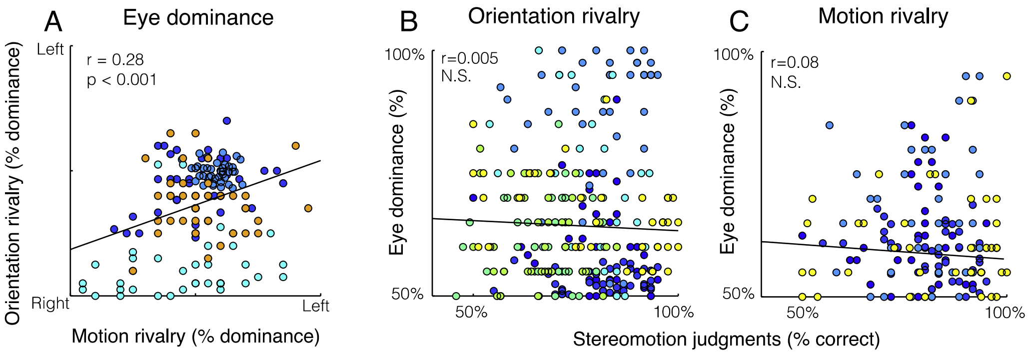

Fig. 6. (A) Measured eye dominance (in%) for 4 observers in two different experiments (different colors indicate different observers). The data shows a significant correlation between the results for the orientation stimulus (stationary grating pattern rotated ±45) and the motion stimulus (grating pattern drifting either up- or downward). (B & C) Measured eye dominance (vertical axis) as a function of stereomotion discrimination in observers with a stereomotion scotoma. We did not find a significant correlation between the performance in stereomotion discrimination and eye dominance with either of the two stimuli used to measure eye dominance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

experiment (Fig. 7A, $r = 0.08$, $p = 0.81$, $N = 7$). These results indicate that the variability in sensitivity to the binocular disparity cue is not predictive of the observed deficits in stereomotion processing.

3.4.3. Lateral motion

In Fig. 7B we show the percentage of correct responses (between 50% and 100%) to the direction of motion (left/right) for 6 observers with a stereomotion scotoma (correlation from 1st to 3rd session: $r = 0.27$, $p < 0.05$, $N = 6$). We did not find a significant correlation between performance in the lateral motion experiment and the stereomotion experiment ($r = 0.01$, $p = 0.13$, $N = 6$). These results indicate that the variability in sensitivity to lateral motion are not predictive of the observed deficits in stereomotion processing.

In order to exclude stimulus duration as an explanation of differences in task performance, we ran an additional version of the main experiment where we presented the stimulus (drifting grating pattern) for 500 ms. The results are included in the Supplementary data (Fig. S3). The percentage correct at 250 ms and 500 ms presentations is significantly correlated ($R^2 = 0.89$, $p < 0.0001$) demonstrating that a longer presentation time does significantly alter the results.

In summary, we find clear evidence for local variation across the visual field in each of the three tested mechanisms. The results presented here are correlations over all subjects' data, however we also computed the individual correlations per subject and performed a GLM analysis. In all cases we do not find a systematic relationship between the variability in discrimination performance across the visual field for binocular rivalry, binocular disparity, or lateral motion and the location of stereomotion scotomas.

4. Discussion

Our results demonstrate that over 50% (7 out of 11) of otherwise healthy observers have impairments in the perception of 3D motion in regions of their visual field. We find that these stereomotion scotomas can vary idiosyncratically in eccentricity, polar angle and size between, but not within, observers. These scotomas are stable in size and position in the visual field within individual observers over time and a variety of stimulus parameters. We subsequently investigated possible causes of these common deficits in 3D motion perception relatively early in visual processing. Specifically we hypothesized that either binocular rivalry, or deficits in the processing of either lateral motion or binocular disparity formed the basis of these deficits in 3D motion perception. Although the observers showed variability across the visual field for all three candidate mechanisms, none of these deficits in visual processing was predictive of the locations of the stereomotion scotomas.

We designed the stimuli so that instantaneous disparity was excluded as a possible cue. Nonperiodic stimuli will inherently contain such instantaneous disparity cues, and previous work did not explicitly distinguish between the instantaneous and time-varying cues (Hong & Regan, 1989; Regan, Erkelens, & Collewijn, 1986; Richards & Regan, 1973). We showed that these instantaneous disparity cues are not the basis for the stereomotion deficits since the scotomas persist even when the cues are eliminated, and variability in sensitivity to instantaneous binocular disparity across the visual field does not predict stereomotion performance.

Some variability in measured performance across the visual field could be the result of an observers' inability to maintain fixation throughout the experiment. We did not explicitly monitor eye movements but using a short presentation time and randomizing the stimulus location on every trial ensured that eye movements would not be informative to the task. In fact, the significant session-to-session and stimulus-to-stimulus reliability of our findings would be unlikely if the differences in performance across the visual field were purely due to eye movements, and we therefore do not believe our results are driven by eye-movements.

All stimuli were presented at full contrast, except in the one experiment where we explicitly assessed stereomotion sensitivity as a function of stimulus contrast. When asked informally, all observers reported that they could easily see the stereomotion stimuli, in all but the lowest (5%) contrast condition, but that they were simply unable to judge their motion in depth. This indicates that the observers had no trouble perceiving motion in the stimuli but they specifically had trouble judging the direction of motion in depth. Some observers reported that they perceived lateral motion, as if binocular rivalry was occurring. Although, we did find regions of strong eye dominance in accordance with recent findings by Carter and Cavanagh (2007), our analysis showed that there was no systematic relationship between these percepts of binocular rivalry and the location of the stereomotion scotomas.

Other observers reported motion transparency, which can occur when two drifting gratings are superimposed (Adelson & Movshon, 1982; Wallach, 1935), and especially when the gratings differ in spatial frequency, relative direction, speed or contrast (Hupé & Rubin, 2004; Kim & Wilson, 1993; Kooi et al., 1992; Smith, 1992; Victor & Conte, 1992). A recent model has been proposed (Hedges, Stocker, & Simoncelli, 2011) that unifies those perceptual phenomena, but it is unclear why a propensity for perceptual coherence or transparency would vary across the visual field.

Previous work has suggested that the perception of stereomotion might rely more on the processing of velocity rather than disparity cues. For example, sensitivity to changing disparity is often a poor predictor of 3D motion discrimination (Harris & Watamaniuk, 1995), and that psychophysical performance on velocity-isolating stimuli seems to better predict 3D motion performance away from

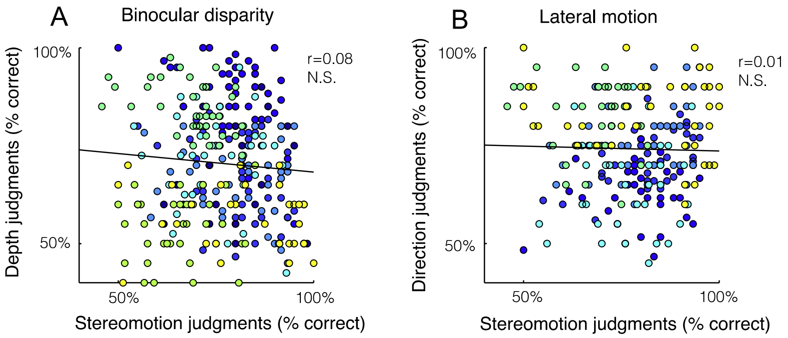

Fig. 7. (A) Performance on the depth discrimination task (judging position in depth) as a function of the performance on the stereomotion task (judging direction in depth) for all observers with a stereomotion scotoma. (B) Same for the lateral motion direction judgment task. For both visual tasks we did not find a correlation between performance on the task and performance on the stereomotion discrimination task.

fixation (Czuba et al., 2010). Of course our present findings suggest that sensitivity to lateral motion might be a poor predictor of the ability to perceive 3D motion as well, and care should be taken in attempting to isolate contributions of the constituent cues. Previous work (Nefs, O'Hare, & Harris, 2010) demonstrated large inter-individual differences in the relative contributions of each cue to 3D motion perception. Therefore, it could be the case that the underlying cause for stereomotion scotomas is different across individuals. However, the inseparability of the changing disparity and interocular velocity cues to motion in depth in our current experiments precludes any strong inferences about their relative contribution based on our results.

In sum, we conclude that the commonly occurring stereomotion scotomas are due to deficits in relatively late stages of visual processing. While we do find variability of sensitivity to local ocular dominance, lateral motion sensitivity and static disparity sensitivity, these do not co-vary with the location of stereomotion scotomas. Given the hierarchical organization of the visual system (Van Essen & Maunsell, 1983), we posit that stereomotion scotomas are not the result of an impairment in the processing of the constituent cues, but rather the result of an impairment in the processing of the later stage cues underlying stereomotion proper, i.e. the changing disparity (CD) and/or interocular velocity difference (IOVD) cues.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2014.09.008.

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