Research Article

Impaired Velocity Processing Reveals an Agnosia for Motion in Depth

Martijn Barendregt[1,2], Serge O. Dumoulin[1,3], and Bas Rokers[4,5]

[1]Department of Experimental Psychology, Helmholtz Institute, Utrecht University;
[2]Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam;
[3]Spinoza Center for Neuroimaging, Amsterdam, The Netherlands; [4]Department of Psychology,
University of Wisconsin–Madison; and [5]McPherson Eye Research Institute, University of Wisconsin–Madison

Abstract

Many individuals with normal visual acuity are unable to discriminate the direction of 3-D motion in a portion of their visual field, a deficit previously referred to as a stereomotion scotoma. The origin of this visual deficit has remained unclear. We hypothesized that the impairment is due to a failure in the processing of one of the two binocular cues to motion in depth: changes in binocular disparity over time or interocular velocity differences. We isolated the contributions of these two cues and found that sensitivity to interocular velocity differences, but not changes in binocular disparity, varied systematically with observers' ability to judge motion direction. We therefore conclude that the inability to interpret motion in depth is due to a failure in the neural mechanisms that combine velocity signals from the two eyes. Given these results, we argue that the deficit should be considered a prevalent but previously unrecognized agnosia specific to the perception of visual motion.

Under conditions in which judging the direction of 2-D motion is trivial, the perception of motion in depth (i.e., approaching or receding motion) can be severely impaired. These impairments are traditionally referred to as *stereomotion scotomas*, because the deficits are typically not complete, but rather confined to a part of the observers' visual field (Hong & Regan, 1989; Richards & Regan, 1973). Stereomotion scotomas occur in more than 50% of otherwise healthy observers, are stable over time, and are not predicted by impairments in the processing of monocular information (Barendregt, Dumoulin, & Rokers, 2014). However, the underlying cause of these stereomotion scotomas has remained elusive. Some work has suggested that the deficit may be related to impaired eye vergence (Regan, Erkelens, & Collewijn, 1986). Our recent work, however, suggests that the underlying deficit likely originates at or near the stage of binocular integration, where signals from the left and right eyes are combined (Barendregt et al., 2014).

There are two known binocular cues to motion in depth, changes in binocular disparity over time (i.e., the *CD cue*) and interocular velocity differences (i.e., the *IOVD cue*). Under natural viewing conditions, these two cues co-occur, and the primary functional difference between them arises from a difference in the order of operations: Binocular disparity for an object is computed before the change in disparity over time is computed (Cumming & Parker, 1994; Regan, 1993), whereas a change in a monocular object's position over time (velocity) is computed before the interocular difference in velocity is computed (Harris, Nefs, & Grafton, 2008; Regan & Gray, 2009; Shioiri, Saisho, & Yaguchi, 2000).

Even though the CD and IOVD cues occur simultaneously in most viewing situations, it is possible to isolate them in an experimental setting. Julesz (1971) designed a *dynamic random-dot* stimulus that contains changes in binocular disparity over time, but no coherent motion in

Corresponding Author:
Martijn Barendregt, v/d Boechorststraat 1, 1081BT Amsterdam, The Netherlands
E-mail: barendregt@fastmail.com

either retinal image. Conversely, it is possible to create anticorrelated (Rokers, Cormack, & Huk, 2008) or uncorrelated (Shioiri et al., 2000) stimuli that contain coherent motion in each retinal image but disrupt the processing of changes in binocular disparity over time. At relatively large spatial scales, both cues support the perception of motion in depth (Czuba, Rokers, Huk, & Cormack, 2010; Nefs, O'Hare, & Harris, 2010). However, it is unknown if and to what extent they contribute to the perception of motion in depth at the spatial scale at which stereomotion scotomas occur.

Thus, we set out to identify the neural impairment that underlies stereomotion scotomas, by measuring sensitivity to motion in depth across the visual field in a number of observers with no obvious retinal impairments. We then used cue-isolating stimuli to evaluate the relative contribution of the two motion-in-depth mechanisms. We found that at the spatial scales at which stereomotion scotomas occur, the CD cue contributes little to the perception of motion in depth. Instead, the variation in sensitivity to the direction of motion in depth across the visual field is well predicted by sensitivity to the IOVD cue. These findings indicate that the inability to discriminate motion in depth must be caused by a failure to combine retinal motion signals from the two eyes in visual cortex. We argue that these impairments are more correctly described as a form of visual agnosia, rather than a scotoma (i.e., a blind spot).

Method

Observers

A total of 11 observers (1 female, 10 male, ages 24–35 years) participated in the experiments reported here after giving informed consent. All had normal or corrected-to-normal vision and were able to judge position in depth in stereo displays. All participants were experienced psychophysical observers and, with one exception (one of the authors), were naive to the purpose of the experiments. Our sample size was based on the assumption that the within-participants effect size would be relatively large ($r^2 \sim .25$). The experiments were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Apparatus and display

Stimuli were presented on two 20-in. CRT displays (60-Hz refresh rate, resolution of 1,024 × 768 pixels); each display contained the image for one of the eyes at a simulated viewing distance of 75 cm. Using a mirror stereoscope, in which a set of mirrors redirected each image to the corresponding eye, the observers fused both images into a single binocular image. A pink-noise (*1/f*) background pattern was presented throughout each experiment to facilitate vergence. The stimuli were generated using an Apple Mac Pro computer using MATLAB (The MathWorks, Natick, MA) and Psychophysics Toolbox 3 (Brainard, 1997; Kleiner, Brainard, Pelli, & Ingling, 2007; Pelli, 1997). The experimental setup used has previously been described in more detail (Barendregt et al., 2014).

Stimuli

The stimuli were presented within circular apertures (1.5° in diameter) positioned within an 8.25° radius around fixation. The centers of the apertures ranged from 1.5° to 7.5° in eccentricity, in five equal steps, along eight "spokes" radiating from fixation (i.e., eight locations per "ring"; Fig. 1). This arrangement provided a total of 40 testing locations across the visual field.

Each stimulus consisted of a set of eight dots (0.17° in size), half white and half black, randomly positioned within the gray background (46.7 cd/m²) of an aperture. During each trial, the dots shown to the left eye and the dots shown to the right eye moved in opposite directions, with a monocular speed of 0.6° per second in the main experiment, and with speeds of 0.3° per second and 1.2° per second in two supplemental experiments. The dots were randomly repositioned whenever they reached a binocular disparity of ±0.3°. The starting position of the dots was chosen such that they would not move beyond the edge of the aperture in either monocular image. In every condition, all the dots shared the same position in depth, so that the stimulus defined a single plane that moved through depth.

We used three main stimulus conditions in the experiment (Fig. 2). In the full-stimulus condition, the position of each dot was correlated both between the eyes (binocular correlation) and from frame to frame (temporal correlation), so that the stimulus contained both CD and IOVD cues. In the CD-stimulus condition, we isolated the CD cue by randomly repositioning the dots in the image plane on every frame (every 17 ms) while coherently increasing or decreasing their binocular disparity. Perceptually, the resulting stimulus looked like the static of a poorly tuned television moving through depth. In the IOVD-stimulus condition, we isolated the velocity component by anticorrelating the dots in the two eyes, which greatly reduced the percept of position in depth. This stimulus still contained interocular velocity differences, and we have previously shown that observers retain the ability to judge the direction of motion in depth for such stimuli (Rokers et al., 2008).
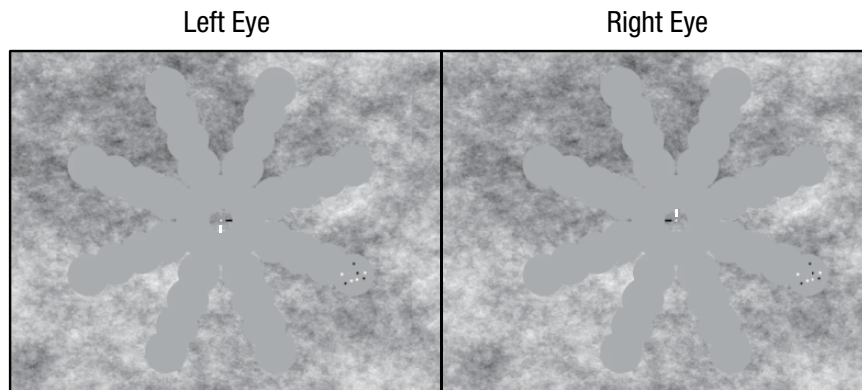
Fig. 1. Illustration of the stimulus displays for the left and right eyes. On each trial, a stimulus consisting of eight white and black dots was presented at 1 of 40 locations ranging from 1.5° to 7.5° in eccentricity, in five equal steps; there were eight locations per "ring." In this illustration, a stimulus is displayed in a location in the lower right visual field.

Procedure

The stereoscope was initially adjusted to accommodate the typical interocular distance. Prior to each session, observers could make further changes if needed so that the nonius markers in the display appeared to be aligned both horizontally and vertically. Observers were instructed to maintain continuous fixation on the central fixation dot.

Stimuli were presented in a blocked design; each block comprised a complete sampling of the visual field for one stimulus condition. A total of 800 trials (40 locations × 20 repetitions) were presented during each block, with the location of the stimulus pseudorandomly distributed across trials. As a result, observers could not predict the location in which the stimulus would appear on any given trial.

On every trial, a stimulus that randomly moved either toward or away from the observer was presented for 500 ms. The stimulus moved through a cylindrical volume (based on the maximal disparity) and "wrapped around" when it reached either extreme (near or far) of the volume. The instantaneous disparity at any point throughout the trial could not serve as a potential cue to the direction of motion in depth in any condition in any of the experiments. For the supplemental experiments, which used slower (0.3° per second) and faster (1.2° per second) dot speeds than the main experiment, we chose to keep all other parameters (e.g., the size of the volume) identical to those used in the main experiment. As a result, the dots in the supplemental experiments wrapped around either more (dots moving 1.2° per second) or less (dots moving 0.3° per second) frequently than the dots in the main experiment. In all the experiments, we chose the dot plane's starting position in depth randomly on each trial, so that the starting (and ending) positions could not serve as a cue to motion in depth. Note also that because

of the stimulus wrapping, the starting and ending positions of the dot plane were identical except in the experiment with the slower dot speed.

In the main and supplemental experiments, observers reported the perceived direction of motion (i.e., toward or away from them) of each stimulus after its offset. In the constant-disparity experiment, which used stimuli that did not vary in depth, they instead reported the perceived position in depth (i.e., near or far) of each stimulus. Responses were made by pressing one of two keys (up- or down-arrow key). Thus, each task was a two-alternative forced-choice task.

Data analysis

For each observer in each condition, we calculated the percentage of correct responses for every position in the visual field. We then determined whether these percentages were significantly different from chance performance ($p < .05$, binomial tests). We also assessed sensitivity to position and motion in depth by calculating d'. Given that the results were essentially identical for percentage correct and d', we report here only results from the analyses of percentage-correct scores.

To determine if performance with stimuli containing a single cue predicted performance with stimuli containing both cues (i.e., full-stimulus condition), we fitted linear mixed-effects models to the data. We entered observer as a random effect to account for any overall differences in task performance between observers. All linear models were fitted using the *fitlme* function in the Statistics Toolbox for MATLAB, and we used restricted maximum likelihood to estimate variance.

To compare models obtained for different cues and different stimulus speeds, we used a likelihood ratio test. We tested the assumption that the observed responses
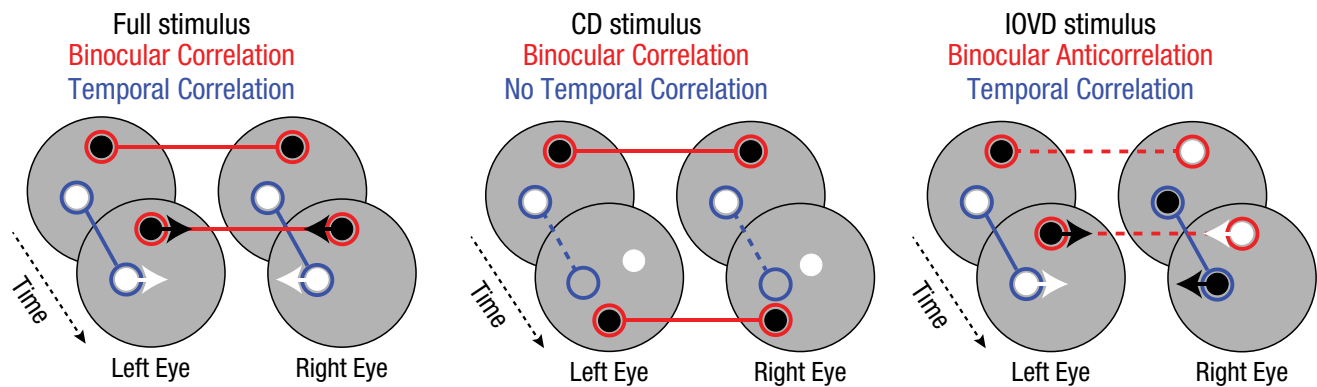
Fig. 2. Illustration of the stimuli used in the experiments. Two example dots (one black, one white) are shown for the two eyes and two moments in time. The arrows indicate the direction of motion for each dot (when applicable), outline circles connected by solid lines indicate binocular correlation, and outline circles connected by dashed lines indicate noncorrelation or anticorrelation. In our full-stimulus condition, dots of the same color were presented at corresponding locations in the two eyes at every point in time. Thus, the left- and right-eye images were both binocularly and temporally correlated in this condition. In the changing-disparity (CD) condition, we isolated the changing binocular disparity over time by randomly repositioning the dots on every frame (over time) while systematically changing their binocular disparity. In the interocular-velocity-difference (IOVD) condition, we anticorrelated the dots in the left- and right-eye images; that is, corresponding dots had opposite contrast in the two eyes. Although anticorrelation of the dots does not remove the disparity information entirely, that information is greatly degraded relative to the velocity information.

were more likely to occur under one model compared with another model. We used the *compare* function in the Statistics Toolbox for MATLAB and computed *p* values to determine if the likelihood ratio of two models deviated significantly from a reference chi-squared distribution.

Results

We measured sensitivity to motion in depth across the visual field and aimed to evaluate the relative contribution of the CD and IOVD cues to motion sensitivity. We determined that 7 of our 11 participants had a stereomotion scotoma in part of their tested visual field.
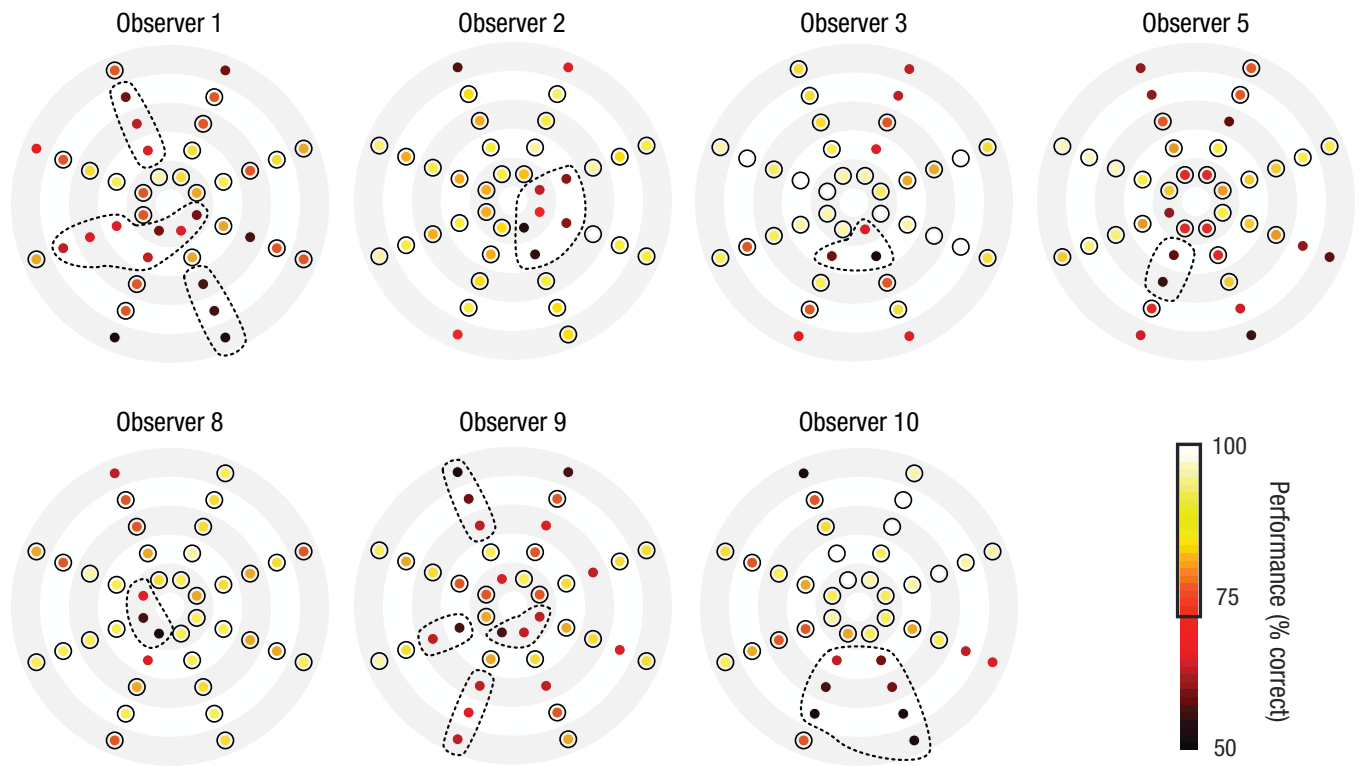
Substantial variability of sensitivity to motion in depth across the visual field

Figure 3 shows the percentage of correct responses across the visual field in the full-stimulus condition for the 7 observers with stereomotion scotomas (see Fig. S1 in the Supplemental Material available online for results for all observers). Sensitivity to motion in depth varied greatly across the visual field. For each of these observers, motion discrimination was nearly perfect in some locations of the visual field, but dropped to chance level in other locations. In some cases, these drops were abrupt, such that locations at which performance was nearly perfect were separated by as little as 1.5° of visual angle (center to center) from locations at which performance was random. For an example, see the results for Observer 3 in Figure 3.

Figure 3 shows the locations in the visual field (to be conservative, we excluded peripheral locations unless they were part of a more extensive scotoma) where these observers were not able to discriminate between a stimulus moving toward them and a stimulus moving away from them, that is, the locations of the observers' stereomotion scotomas. In previous work, we showed that these regions are stable over time, and persist across a range of stimulus parameters, such as duration and contrast. Moreover, the impairments are specific to the perception of motion in depth. Changes in sensitivity to binocular rivalry, static disparity, and lateral motion across the visual field do not explain these impairments (Barendregt et al., 2014; Hong & Regan, 1989; Regan et al., 1986).

Sensitivity to changing disparity over time does not predict differences in motion sensitivity

Changes in disparity that occur over time as an object moves toward or away from the observer have traditionally been considered the primary cue to motion in depth (Cumming & Parker, 1994; Nefs et al., 2010). To assess if the location of stereomotion scotomas can be explained by a local deficit in the processing of changing binocular disparity, we compared our observers' sensitivity to motion in depth in the full-stimulus and CD-stimulus conditions (see Fig. 4a for results for 3 representative observers with stereomotion scotomas and see Fig. S2 in the Supplemental Material for all observers' performance in the CD-stimulus condition). We found that sensitivity

Fig. 3. Sensitivity to motion in depth across the visual field for the 7 observers with stereomotion scotomas. Each plot shows the percentage of correct responses at each location in the visual field for a single observer. A black circle around a dot indicates performance that was significantly different from chance. The dashed outlines indicate regions where performance did not differ significantly from chance in multiple contiguous locations (i.e., the locations for which a stereomotion scotoma was identified).

to the CD cue was generally poor across the whole visual field, and there were no regions with systematically low sensitivity that corresponded to stereomotion scotomas.

To quantify how well sensitivity to motion in depth as measured by the full-stimulus condition was predicted by sensitivity to the CD cue, we fitted a linear mixed-effects model to the combined data of all observers. Figure 4b shows the best-fitting regression lines for the individual observers and for the overall model. Sensitivity to the CD cue did not predict sensitivity to motion in depth across the visual field as measured with stimuli containing both binocular cues, $F(1, 75) = 2.55$, $p = .115$. This result suggests that stereomotion scotomas are not due to variable sensitivity to changing disparity across the visual field.

Poor sensitivity to changing disparity is not caused by diminished sensitivity to static disparity

Our results suggest that changes in binocular disparity over time do not serve as a cue to motion in depth in the spatially restricted stimulus conditions that reveal the existence of stereomotion scotomas. These results are consistent with previous findings that changing disparity

cues require a large field stimulus to be effective (Czuba, Rokers, Huk, & Cormack, 2012). We wanted, however, to exclude the possibility that our observers performed relatively poorly in the CD-stimulus condition because the stimuli contained poor cues to binocular disparity, on which the extraction of changing disparity cues necessarily depends. This possibility was a particular concern given that we refreshed the location of the dots in the CD stimuli on each display frame (every 17 ms).

To evaluate sensitivity to static disparity in our stimulus arrangement, we conducted a constant-disparity experiment in which the stimuli from the CD-stimulus condition in the main experiment were presented at a constant depth (at 0.15° disparity, halfway through the trajectory in the main experiment) either closer or further away in depth relative to the fixation point. Note that in this experiment, all dots were still refreshed on each frame, but the plane defined by the dots did not move through depth. The task for the observers was to indicate the position of each stimulus in depth. We found that all observers were able to perform this task at better than chance levels across nearly all tested locations (right column of Fig. 4a). To test whether observers' sensitivity to static disparity was predictive of their performance in the
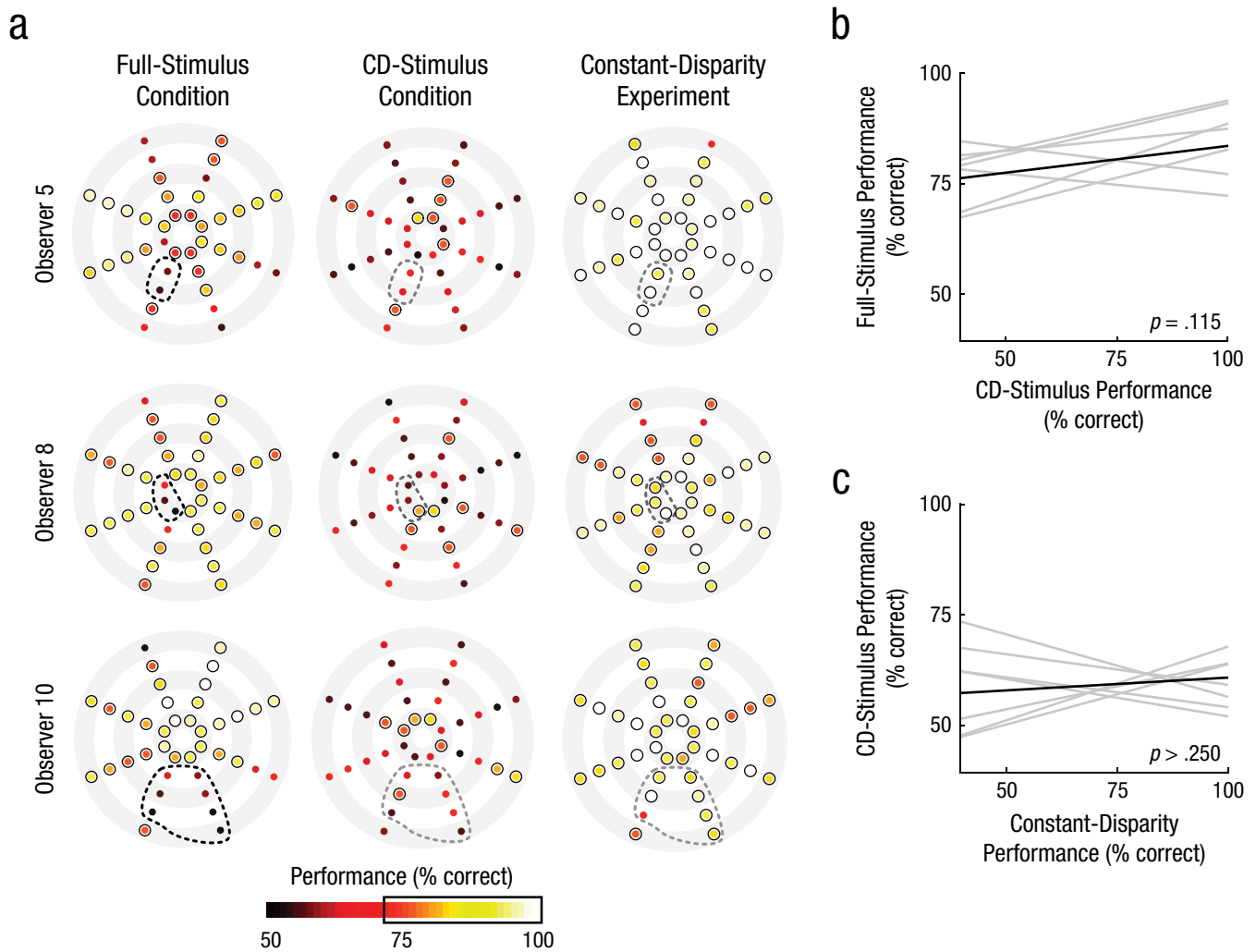
Fig. 4. Results for sensitivity to binocular disparity. The plots in (a) show the percentage of correct responses for 3 representative observers in the full-stimulus condition and changing-disparity (CD) condition of the main experiment and in the constant-disparity experiment, which assessed observers' sensitivity to position in depth. The dashed outlines show the locations of the stereomotion scotomas identified in the full-stimulus condition. The graphs on the right show the association between (b) accuracy in the full-stimulus condition and in the CD-stimulus condition and (c) accuracy in the CD-stimulus condition and in the constant-disparity experiment. In each graph, the gray lines are the best-fitting regression lines for each of the 7 observers with stereomotion scotomas, and the black line indicates the best overall fit of a linear mixed-effects model. The *p* values reflect the probability that the observed linear relationship between the independent (fixed-effect) and dependent variables was simply due to chance.
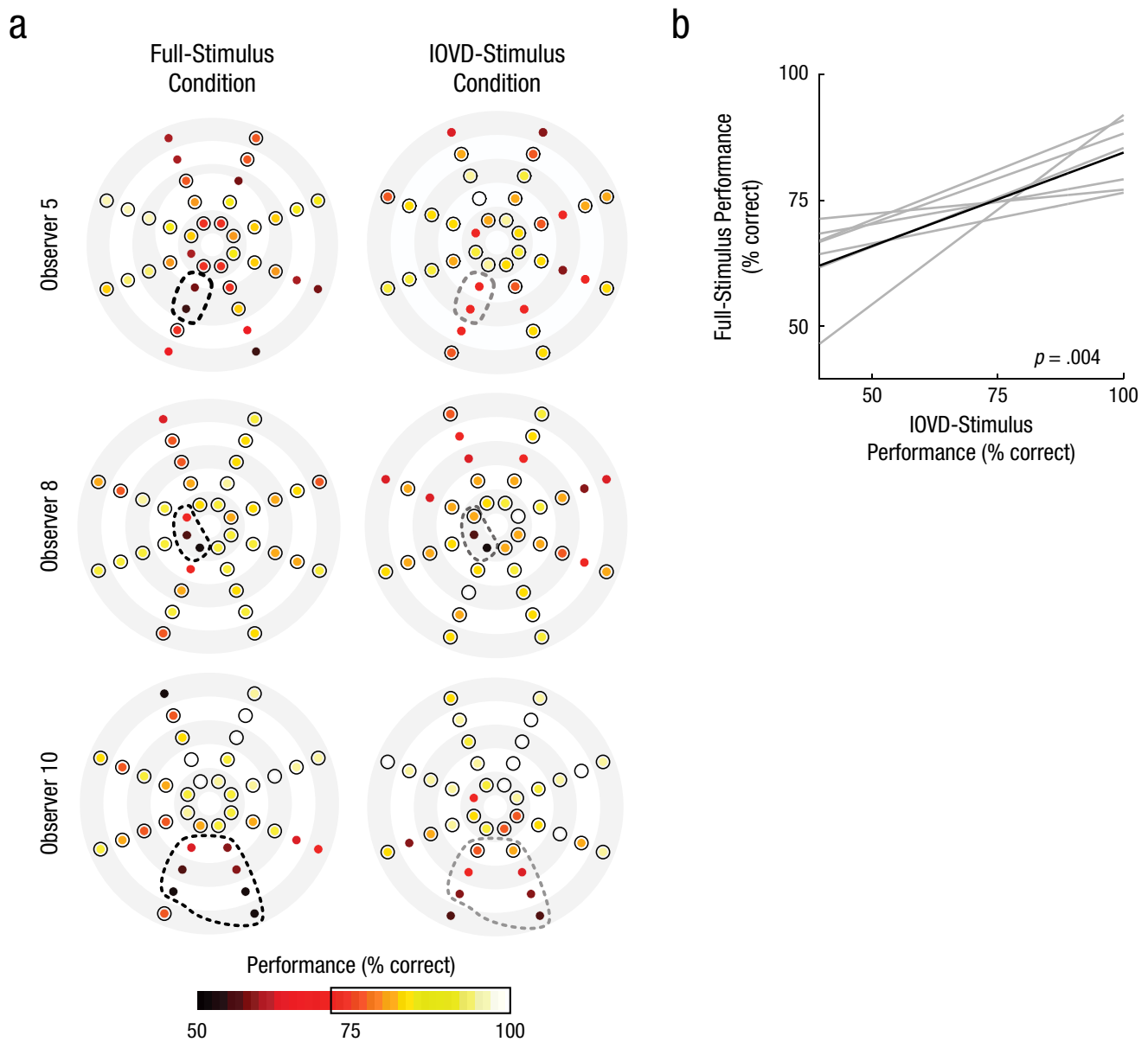
CD-stimulus condition in the main experiment, we fitted a linear model using the data from that condition and the constant-disparity experiment. Sensitivity to static disparity did not significantly predict sensitivity to changing disparity across the visual field, $F(1, 4.2) = 0.89$, $p > .250$ (Fig. 4c).

Taken together these results lead us to conclude that the CD cue is not predictive of sensitivity to motion in depth across the visual field at the relatively small spatial scale at which stereomotion scotomas can occur. In addition, we conclude that sensitivity to disparity per se was not impaired in our observers and that their generally poor performance in the CD-stimulus condition was not caused by a problem detecting binocular disparity in our displays.

### Sensitivity to the IOVD cue predicts differences in motion sensitivity

Next, we investigated failure to combine velocity signals from the two eyes as a potential cause for stereomotion scotomas. Figure 5a shows the percentage of correct responses across the visual field in the IOVD-stimulus condition of the main experiment, along with the corresponding results from the full-stimulus condition, for 3 observers in whom we identified a stereomotion scotoma (results for

a

Full-Stimulus
Condition

IOVD-Stimulus
Condition

b

Fig. 5. Results for sensitivity to interocular velocity differences (IOVDs). The plots in (a) show the percentage of correct responses for 3 representative observers in the full-stimulus condition and the IOVD-stimulus condition of the main experiment. The dashed outlines show the locations of the stereomotion scotomas identified in the full-stimulus condition. The graph in (b) shows the association between accuracy in the full-stimulus condition and in the IOVD-stimulus condition. The gray lines are the best-fitting regression lines for each of the 7 observers with stereomotion scotomas, and the black line indicates the best overall fit of a linear mixed-effects model. The *p* values reflect the probability that the observed linear relationship between the independent (fixed-effect) and dependent variables was simply due to chance.

all observers in the IOVD-stimulus condition are presented in Fig. S3 in the Supplemental Material). Comparison of performance in the two conditions suggests that an inability to combine velocity signals from the two eyes may underlie these visual deficits. The locations of poor performance with stimuli in which binocular disparity was disrupted but interocular velocity signals were present matched the locations of the stereomotion scotomas.

To quantify how well sensitivity to motion in depth, as measured by the full-stimulus condition, was predicted by sensitivity to the IOVD cue, we fitted a linear regression model to the combined data of all observers. Figure 5b shows the best-fitting regression lines for the individual observers and for the overall model. The regression analysis revealed that sensitivity to the IOVD cue significantly predicted sensitivity to motion in depth as

Stimulus Speed
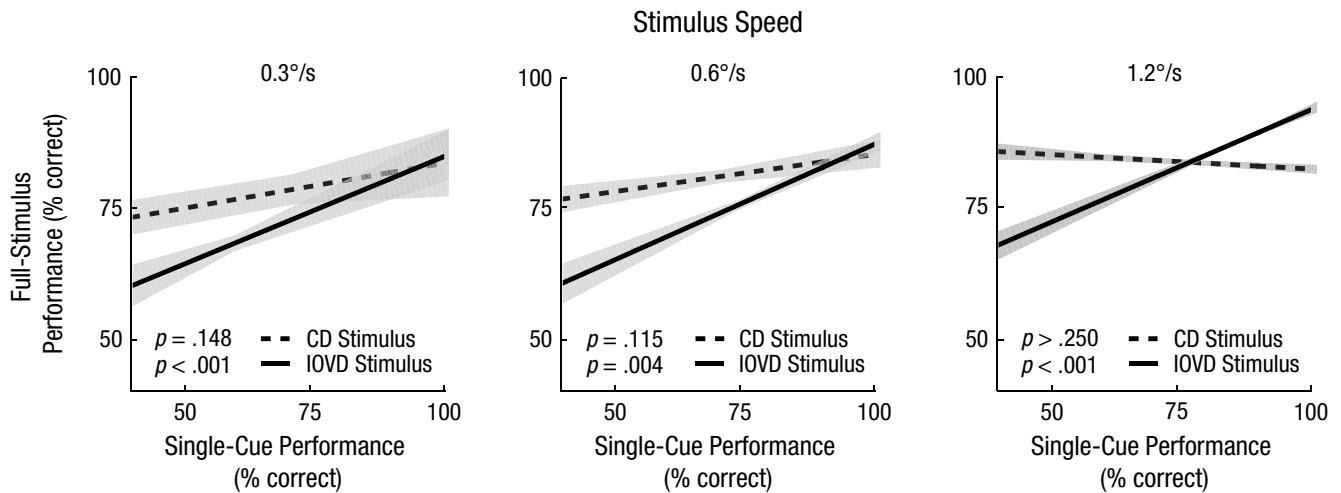
Fig. 6. Results from linear mixed-effects models: predicted performance in the full-stimulus condition as a function of performance in the single-cue conditions (changing disparity, or CD, and interocular velocity difference, or IOVD). From left to right, the panels represent results for data collected using stimuli with monocular speeds of 0.3° per second, 0.6° per second, and 1.2° per second. The shaded regions represent 95% confidence intervals of the linear fits.

measured by the full-stimulus condition, $F(1, 7.3) = 17.29$, $p = .004$.

Thus, the location of a stereomotion scotoma, as measured by a stimulus containing both binocular cues to motion in depth, is best predicted by the observer's sensitivity to the IOVD cue across the visual field. Sensitivity to the CD cue is uniformly poor across the visual field and therefore does not predict the location of a scotoma.

Findings are robust across stimulus speed

Previous studies suggest that sensitivity to the CD and IOVD cues depends on the monocular speed of the stimulus, and that peak sensitivity for the CD cue is exhibited at a slower stimulus speed than is peak sensitivity to the IOVD cue (Czuba et al., 2010; Wardle & Alais, 2013). We specifically chose the monocular speed of 0.6° per second in our main experiment because this speed is closer to peak sensitivity for the CD cue than to peak sensitivity for the IOVD cue. Naturally, this left open the possibility that the existence of stereomotion scotomas is specific to a particular speed, or that stereomotion scotomas have different causes at different stimulus speeds.

We therefore repeated our main experiment at both halved (0.3° per second) and doubled (1.2° per second) monocular speeds with all observers. In each of these supplemental experiments, we tested whether sensitivity to the CD or IOVD cue was more predictive of sensitivity to motion in depth in the full stimulus. Figure 6 shows predicted accuracy in the full-stimulus condition as a function of accuracy in the CD- and IOVD-stimulus conditions for all three different monocular speeds. Sensitivity to the CD cue did not significantly predict performance

in the full-stimulus condition at any speed—0.3° per second: $F(1, 6.5) = 2.59$, $p = .148$; 0.6° per second: $F(1, 75) = 2.55$, $p = .115$; 1.2° per second: $F(1, 92.7) = 0.41$, $p > .250$. Conversely, we found that sensitivity to the IOVD cue significantly predicted performance in the full-cue condition at all three stimulus speeds—0.3° per second: $F(1, 7.1) = 26.04$, $p < .001$; 0.6° per second: $F(1, 7.3) = 17.29$, $p = .004$; 1.2° per second: $F(1, 6.3) = 72.20$, $p < .001$. Further, using a likelihood ratio (LR) test to compare the linear mixed-effects models for the CD- and IOVD-stimulus conditions, we found that for all speeds, sensitivity to the IOVD cue better explained performance in the full-cue condition—0.3° per second: LR = 81.26, $p \sim 0$; 0.6° per second: LR = 73.33, $p \sim 0$; 1.2° per second: LR = 71.06, $p \sim 0$.

Considering the contributions of the individual cues in combination does not improve prediction of stereomotion sensitivity

In normal viewing situations, the two binocular cues are both present. Therefore, the contribution of the CD cue to perception of motion in depth might not be significant when considered in isolation, but might contribute in a combined model. To test this possibility, we fitted linear models using both performance in the CD-stimulus condition and performance in the IOVD-stimulus conditions as predictors. Using an analysis of variance, we tested the contribution of the two cues in this combined model. We did not find a significant contribution of sensitivity to the CD cue at any stimulus speed—0.3° per second: $F(1, 11.4) = 1.66$, $p = .221$; 0.6° per second: $F(1, 5.8) = 0.91$, $p > .250$; 1.2° per second: $F(1, 85.9) = .80$, $p > .250$.

Conversely, sensitivity to the IOVD cue did contribute significantly to the model at each speed—0.3° per second: $F(1, 6.8) = 28.59$, $p = .001$; 0.6° per second: $F(1, 6.3) = 56.57$, $p < .001$; 1.2° per second: $F(1, 6.5) = 73.12$, $p < .001$. Further, we did not find that the combined model predicted sensitivity to stereomotion better than a model based only on sensitivity to the IOVD cue (likelihood ratio test, all p values $> .88$).

Sensitivity to retinal motion does not predict stereomotion sensitivity

The IOVD cue depends on the combination of retinal motion signals from the two eyes. It is therefore possible that stereomotion scotomas are simply due to impaired sensitivity to retinal motion. We therefore incorporated data from a 2-D motion-discrimination task reported in a prior study (Barendregt et al., 2014). Using a linear mixed-effects model of the data for the 4 observers who participated in both studies, we found that performance on the 2-D motion-discrimination task did not predict performance in the full-stimulus 3-D-motion condition of the main experiment, $F(1, 4) = 0.79$, $p = .43$.

However, we did find variability in sensitivity to 2-D motion in our prior study (see Fig. S4 in the Supplemental Material). Variation of sensitivity across the visual field has been shown for other stimulus properties, such as binocular rivalry (Carter & Cavanagh, 2007) and even face processing (Afraz, Pashkam, & Cavanagh, 2010), but remains an underexplored area of research. Poor performance with the 2-D motion stimuli in our prior study should not be taken as evidence for a 2-D motion agnosia, because the stimuli were presented near threshold for all observers. The 3-D motion stimuli in that study were always presented at full (100%) contrast, and performance with similar 2-D motion stimuli would essentially have been at ceiling. We reduced the contrast of those stimuli to expose any variability in sensitivity to 2-D motion across the visual field. Further research is needed to explore the reliability and stability of the observed variability in 2-D motion sensitivity.

Discussion

We investigated the cause of stereomotion scotomas, a deficit in the processing of visual motion that occurs in more than 50% of otherwise healthy observers (Barendregt et al., 2014; Hong & Regan, 1989). Given that stereomotion scotomas are not associated with any clear retinal impairment or with a deficit in the processing of retinal information, we investigated whether they might result from failures in the processing of one or both of the known binocular cues to motion in depth. We did not find a significant contribution of the CD cue, alone or in combination with the IOVD cue,

to the sizable impairments in the perception of motion in depth in observers with stereomotion scotomas. Instead, we found that the location of deficits in motion perception was best predicted by the locations in which there was a lack of sensitivity to the IOVD cue. This was true even when we used motion stimuli with a very slow speed, which privileged the use of the CD cue. Taken together, our results show that the cause of stereomotion scotomas is a deficit in the binocular combination of retinal velocity cues. Given these findings, we argue later in this section that the deficit should be considered a prevalent but previously unrecognized agnosia specific to the perception of visual motion.

Relation to previous work on stereomotion scotomas

Our results show that stereomotion scotomas occur specifically as a result of impairment in processing visual cues that vary over time. Although previous work (Hong & Regan, 1989; Richards & Regan, 1973) provided evidence for the existence of this impairment, it did not explicitly distinguish between sensitivity to instantaneous and time-varying cues to motion in depth. Moreover, we focused on the contribution of binocular cues because previous work (Barendregt et al., 2014) suggested that stereomotion scotomas are due to a failure at or after the stage of binocular combination. This implied that the deficit had to be due to a problem in the processing of one or both of the two binocular cues to motion in depth: changing disparity over time or interocular velocity differences.

The inability to detect motion in depth from the CD cue is not due to an inability to extract binocular-disparity signals

We emphasize that the observers in our experiments had no trouble detecting binocular disparity per se, despite the fast stimulus refresh rate. In our constant-disparity experiment, we found that across the visual field, all observers were easily able to judge position in depth of a stationary stimulus under otherwise identical conditions. This is consistent with previous reports that stereopsis per se is limited mainly by monocular luminance mechanisms (Gheorghiu & Erkelens, 2005b). However, previous studies have also shown that the temporal frequencies that can be used for the perception of motion from disparity are quite low (Gheorghiu & Erkelens, 2005a). Thus, poor performance in detecting motion from changes in disparity is not the result of limitations in extracting binocular-disparity signals per se, but instead

derives from poor sensitivity to the CD cue in displays that use a small spatial extent.

Contributions of the CD cue to motion perception

We used stimuli that wrapped in depth, so that they did not contain static binocular-disparity cues to motion in depth. Previous work, however, has provided evidence of stereomotion scotomas even when the stimuli contained such cues (Hong & Regan, 1989). Taken together with our observers' poor performance in the CD-stimulus condition, this seems to suggest that binocular-disparity cues do not contribute significantly to perception of motion in depth at all. Although disparity cues can contribute to the perception of motion in depth, such contributions seem to be restricted to situations in which the motion is slow (Czuba et al., 2010) and spans a large part of the visual field (Czuba et al., 2012; Sakano, Allison, & Howard, 2012). A careful investigation of the role of stimulus size on the perception of motion in depth from changing binocular disparity would therefore be beneficial.

Contributions of the IOVD cue to motion perception

Our results indicate that deficits in motion perception are closely linked to an observer's ability to utilize the IOVD cue in visual displays. When we isolated the contribution of this cue by eliminating instantaneous binocular disparity as a cue and disrupting the CD cue, the resulting performance was highly predictive of performance with stimuli containing all binocular cues. Given that the deficit could not be explained by sensitivity to either retinal motion or binocular disparity, it is likely not due to a problem in the extraction of motion signals per se, or to a binocular imbalance, but rather due to a failure in the integration of motion signals from the two eyes. Thus, our findings show that the underlying cause of stereomotion scotomas is a failure to combine velocity signals between the eyes, and point to a deficit in cortical areas that are involved in motion processing.

Alternative explanations

One might consider that these deficits are due not to a failure in the processing of motion signals, but to other factors, such as stimulus contrast. Although there is some evidence that perception of motion in depth is more sensitive to stimulus contrast than is perception of frontoparallel motion in similar 2-D stimuli (Fulvio, Rosen, & Rokers, 2015), previous work explicitly investigating the effects of stimulus contrast in visual displays very similar to the ones used here has shown that these specific

deficits in perception of motion in depth are relatively robust to manipulations of contrast (Barendregt et al., 2014).

Because we tested for a very specific visual deficit, we necessarily used artificial stimuli that isolated the stimulus features of interest, and this could have introduced cue conflicts. Using a simple model of cue interaction, we demonstrated that having both cues available was not necessarily better than having access only to the velocity-based cue. However, this model probably underestimates the actual contributions of the different cues in normal viewing situations, in which having both cues available likely leads to better performance than does having access only to the velocity-based cue. Although it is well known that there can be substantial interindividual differences in sensitivity to the CD and IOVD cues (Nefs et al., 2010; Allen, Haun, Hanley, Green, & Rokers, 2015), we accounted for this by modeling the individual participant's performance as a random factor in all our analyses.

We did not explicitly monitor observers' eye movements in these experiments. The short presentation duration and the randomized order of the stimulus locations ensured that making eye movements would not be informative for performing the task. If observers had actively made eye movements toward the locations at which the stimuli were presented, their performance either should have been close to uniform across the visual field or should have declined as a function of eccentricity. Moreover, there should not have been significant correlations between sensitivity across the different stimulus types and speeds. Because we found significant and reliable variability in sensitivity across different stimulus types and speeds, we feel confident that eye movements toward the stimulus locations cannot explain our results.

Motion agnosia

We propose that the deficit we investigated in these experiments should be considered a previously unrecognized type of visual agnosia. Whereas a scotoma is a localized loss of visual acuity, or a blind spot, visual agnosias are characterized by an inability to discriminate a specific feature of visual stimuli despite normal basic visual function. Individuals with what have been called stereomotion scotomas are unable to discriminate the direction of motion in depth in some locations in the visual field, but they are not blind in those locations; rather, they are unable to interpret what they see there.

Visual agnosias are frequently associated with a cortical lesion (Riddoch, 1917), but this is not a necessary condition. For example, prosopagnosia can exist in the absence of any lesion and is congenital in some cases (Kennerknecht et al., 2006). Unlike other visual agnosias, the motion agnosia we have described here is quite

common and is typically restricted to part of the visual field. A likely reason for this clear restriction to a region within the visual field is that neurons that are sensitive to motion in depth have smaller receptive fields compared with neurons that are impaired in other types of agnosia, such as those that are required for the recognition of objects or faces. It is currently not known if other forms of visual agnosia can also be spatially restricted, but our results suggest that this might be an interesting avenue of further research.

Identifying the neural mechanisms involved in visual agnosias is often complicated by the fact that a large number of visual cues contribute to visual perception (Avidan, Hasson, Malach, & Behrmann, 2005). However, because there are only two cues that support the binocular perception of motion in depth, we were in a unique situation to investigate the underlying neural cause of this particular form of visual agnosia.

Relation to binocular visual disorders

Motion agnosia is clearly a disorder of binocular vision. The deficit is not present for lateral motion directions, but is distinct from other disorders of the binocular visual system. Other visual impairments, such as poor stereo vision, typically extend across the entire visual field and tend to occur as the result of developmental visual disorders, such as amblyopia, although there is also evidence that poor stereo acuity is more common in normally sighted observers than previously thought (Hess, To, Zhou, Wang, & Cooperstock, 2015). However, other disorders of the binocular visual system result in problems with perceiving binocular visual stimuli in general, whereas motion agnosia is a problem with discriminating a specific feature of binocular stimuli.

Conclusion

In sum, we studied a deficit in the ability to discriminate the direction of motion in depth in part of the visual field. We did not find that sensitivity to the CD cue contributes significantly to this prevalent deficit. Instead, we found that the cause is a failure to properly combine retinal velocity signals in visual cortex. We therefore argue that this deficit is best described as a novel type of visual agnosia.

Action Editor

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Author Contributions

M. Barendregt designed the experiments and collected the data. M. Barendregt performed the data analysis under the supervision of B. Rokers and S. O. Dumoulin. M. Barendregt drafted

the manuscript, and S. O. Dumoulin and B. Rokers provided critical revisions. All the authors approved the final version of the manuscript for submission.

Supplemental Material

Additional supporting information can be found at http://pss .sagepub.com/content/by/supplemental-data

References

Afraz, A., Pashkam, M. V., & Cavanagh, P. (2010). Spatial heterogeneity in the perception of face and form attributes. *Current Biology*, *20*, 2112–2116. doi:10.1016/j.cub .2010.11.017

Allen, B., Haun, A. M., Hanley, T., Green, C. S., & Rokers, B. (2015). Optimal combination of the binocular cues to 3D motion. *Investigative Ophthalmology & Visual Science*, *56*, 7589–7596. doi:10.1167/iovs.15-17696

Avidan, G., Hasson, U., Malach, R., & Behrmann, M. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 2. Functional neuroimaging findings. *Journal of Cognitive Neuroscience*, *17*, 1150–1167. doi:10.1162/0898929054475154

Barendregt, M., Dumoulin, S. O., & Rokers, B. (2014). Stereomotion scotomas occur after binocular combination. *Vision Research*, *105*, 92–99. doi:10.1016/j.visres.2014.09.008

Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Carter, O., & Cavanagh, P. (2007). Onset rivalry: Brief presentation isolates an early independent phase of perceptual competition. *PLoS ONE*, *2*(4), Article 343. doi:10.1371/journal .pone.0000343

Cumming, B. G., & Parker, A. J. (1994). Binocular mechanisms for detecting motion-in-depth. *Vision Research*, *34*, 483–495.

Czuba, T. B., Rokers, B., Huk, A. C., & Cormack, L. K. (2010). Speed and eccentricity tuning reveal a central role for the velocity-based cue to 3D visual motion. *Journal of Neurophysiology*, *104*, 2886–2899. doi:10.1152/jn.00585.2009

Czuba, T. B., Rokers, B., Huk, A. C., & Cormack, L. K. (2012). To CD or not to CD: Is there a 3D motion aftereffect based

on changing disparities? *Journal of Vision*, *12*(4), Article 7. doi:10.1167/12.4.7

Fulvio, J. M., Rosen, M. L., & Rokers, B. (2015). Sensory uncertainty leads to systematic misperception of the direction of motion in depth. *Attention, Perception, & Psychophysics*, *77*, 1685–1696. doi:10.3758/s13414-015-0881-x

Gheorghiu, E., & Erkelens, C. J. (2005a). Differences in perceived depth for temporally correlated and uncorrelated dynamic random-dot stereograms. *Vision Research*, *45*, 1603–1614. doi:10.1016/j.visres.2004.12.005

Gheorghiu, E., & Erkelens, C. J. (2005b). Temporal properties of disparity processing revealed by dynamic random-dot stereograms. *Perception*, *34*, 1205–1219. doi:10.1068/p5404

Harris, J. M., Nefs, H. T., & Grafton, C. E. (2008). Binocular vision and motion-in-depth. *Spatial Vision*, *21*, 531–547. doi:10.1163/156856808786451462

Hess, R. F., To, L., Zhou, J., Wang, G., & Cooperstock, J. R. (2015). Stereo vision: The haves and have-nots. *i-Perception*, *6*(3). doi:10.1177/2041669515593028

Hong, X., & Regan, D. (1989). Visual field defects for unidirectional and oscillatory motion in depth. *Vision Research*, *29*, 809–819.

Julesz, B. (1971). *Foundations of cyclopean perception*. Chicago, IL: University of Chicago Press.

Kennerknecht, I., Grueter, T., Welling, B., Wentzek, S., Horst, J., Edwards, S., & Grueter, M. (2006). First report of prevalence of non-syndromic hereditary prosopagnosia (HPA). *American Journal of Medical Genetics, Part A*, *140*, 1617–1622. doi:10.1002/ajmg.a.31343

Kleiner, M., Brainard, D., Pelli, D. G., & Ingling, A. (2007). What's new in Psychtoolbox-3? [Abstract]. *Perception*, *36*(Suppl. 1), S14.

Nefs, H. T., O'Hare, L., & Harris, J. M. (2010). Two independent mechanisms for motion-in-depth perception: Evidence from individual differences. *Frontiers in Psychology*, *1*, Article 155. doi:10.3389/fpsyg.2010.00155

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Regan, D. (1993). Binocular correlates of the direction of motion in depth. *Vision Research*, *33*, 2359–2360.

Regan, D., Erkelens, C. J., & Collewijn, H. (1986). Visual field defects for vergence eye movements and for stereomotion perception. *Investigative Ophthalmology & Visual Science*, *27*, 806–819.

Regan, D., & Gray, R. (2009). Binocular processing of motion: Some unresolved questions. *Spatial Vision*, *22*, 1–43. doi:10.1163/156856809786618501

Richards, W., & Regan, D. (1973). A stereo field map with implications for disparity processing. *Investigative Ophthalmology & Visual Science*, *12*, 904–909.

Riddoch, G. (1917). On the relative perceptions of movement and a stationary object in certain visual disturbances due to occipital injuries. *Proceedings of the Royal Society of Medicine*, *10*(Neurol Sect), 13–34. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2017643/?tool=pmcentrez

Rokers, B., Cormack, L. K., & Huk, A. C. (2008). Strong percepts of motion through depth without strong percepts of position in depth. *Journal of Vision*, *8*(4), Article 6. doi:10.1167/8.4.6

Sakano, Y., Allison, R. S., & Howard, I. P. (2012). Motion aftereffect in depth based on binocular information. *Journal of Vision*, *12*(1), Article 11. doi:10.1167/12.1.11

Shioiri, S., Saisho, H., & Yaguchi, H. (2000). Motion in depth based on inter-ocular velocity differences. *Vision Research*, *40*, 2565–2572.

Wardle, S., & Alais, D. (2013). Evidence for speed sensitivity to motion in depth from binocular cues. *Journal of Vision*, *13*(1), Article 17. doi:10.1167/13.1.17