Motion Thresholds in Retinitis Pigmentosa

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Minimum displacement thresholds, or $d_{\text{min}}$, were measured in 29 subjects with retinitis pigmentosa (RP) and 10 subjects with normal vision. The results showed that RP can affect an observer's ability to judge the correct direction of motion in a random-dot pattern. The majority of RP subjects had elevated $d_{\text{min}}$. They required a larger displacement to perceive the correct direction of motion. Only 5 of the 29 RP subjects had thresholds within two standard deviations of the mean of the normal-observer distribution. Moreover, three RP subjects were unable to detect the correct direction of motion regardless of the displacement magnitude, and four RP subjects consistently reported motion in the opposite direction at small displacements. The results cannot be explained by abnormal temporal processing or a reduction in the effective luminance. There was a statistically significant correlation ($r = 0.72, P < 0.001$) between log threshold and log MAR, consistent with the hypothesis that a reduction in the spatial density of the photoreceptors contributes to the motion-threshold elevation. Motion thresholds also were measured in subjects with normal vision under conditions of simulated “photoreceptor” dropout. The results showed that a random elimination of information from over 25% of the image positions significantly elevates motion thresholds. These results also support the spatial-density reduction hypothesis. Invest Ophthalmol Vis Sci 33:2411-2422, 1992.

A traditional view of the visual impairment of people with retinitis pigmentosa (RP) is limited to progressive visual-field loss and night blindness. Many of the subjective reports and performance difficulties experienced by RP patients are considered in terms of these losses. However, the progressive nature of the disease suggests that at different stages of RP, the visual system may perform anomalous processing of information that may affect visual perception and have consequences for performance.

RP is a progressive retinal degeneration and, as stated above, is characterized by night blindness and visual-field loss typically in the form of a mid-peripheral ring-like scotoma or contracted field. It is also characterized by intraretinal bone-spicule-like pigmentation, narrowed retinal arterioles, vitreous degeneration with cellular debris and pigment dusting, reduced or unrecordable electroretinogram, and loss of foveal reflex. Furthermore, there is no known systemic, metabolic, inflammatory, dietary, toxic, or traumatic cause of the retinal degeneration. Studies have shown there are several genetic and functional subtypes. However, once the retinal degeneration begins, all RP progresses in the same way.

With progression, histopathologic results show a reduction in the spatial density of photoreceptors across the total extent of the retina, a shortening of photoreceptor outer segments, and an enlargement of the inner segments of the remaining photoreceptors. The inner retinal layers appear normal. Even in the early stages of RP, the number of foveal photoreceptors can be reduced by 25% with visual acuity still at 20/20. Visual acuity often remains better than 20/40 until late in the disease, but despite the retention of good visual acuity, a number of studies show changes in foveal function. For example, RP subjects show abnormal foveal contrast sensitivity and abnormal temporal processing.

Two experimental studies have shown abnormal space perception in RP. Temme et al studied three individuals in the early stages of RP. Judgments of the eccentricity of a light flash presented in a Goldmann perimeter suggested that the RP subjects perceived a magnified central visual field. Turano measured the ability of RP subjects to judge the center of a spatial interval defined by two briefly flashed bars of light and contained within the subject's visual field. Some RP subjects exhibited substantial spatial-position dis-
tortions, and some RP subjects had reduced bisection acuity.

The perceptual anomalies in the space domain, combined with abnormal temporal processing, suggest that RP subjects may have abnormal processing of motion. Anomalous motion processing could have serious ramifications for the use of optic flow patterns to guide mobility and control posture, apart from any consequence of restricted visual fields. In the present study, we examine in RP and normally sighted observers a basic measure of motion perception—the minimum displacement necessary for the correct discrimination of motion direction, or $d_{\text{min}}$.

**Materials and Methods**

**Display and Stimuli**

Random-dot patterns have been used extensively to investigate $d_{\text{min}}$.

Consequently, they provide a well established base of normal $d_{\text{min}}$ values under a variety of viewing conditions. Random-dot patterns were generated by an IMAGRAPH (IMAgraph Corp., Woburn, MA) high-resolution graphics display board (1024 X 1024 X 8 bits) controlled by an IBM-AT computer (IBM Corp., Armonk, NY). The patterns were displayed on an Ikegami high-resolution CRT monitor (19 inch diagonal, PI04 phosphor; Ikegami Electronics, Inc., Maywood, NJ). The display was refreshed at a rate of 60 Hz without interlace.

Each display sequence consisted of seven images, each containing 50 random dots. The configuration of the dots in each image was the same, but shifted by a constant amount. Dots lost at the edge of the image were wrapped around to reappear within the opposite boundary. A motion sequence then was created by writing each of the seven images into a different bit plane of the display board and reading them out sequentially through lookup-table manipulation. The eighth bit plane was used to image a blank screen with a fixation cross. Viewing distance was 4.06, 2.49, or 1.27 m, depending on the subject's visual acuity. Observers with visual acuities better than or equal to 20/30 viewed the display at 4.06 m. Observers with visual acuities between 20/30 and 20/50 viewed the display at 2.49 m, and observers with visual acuities worse than or equal to 20/50 viewed the display at a distance of 1.27 m. The window of dots subtended a visual angle of 1.0 X 1.0° at all viewing distances. Each dot was made up of a 3 X 3 pixel square array, with each side subtending a visual angle of 0.67, 1.09, and 2.14 arcmin at viewing distances of 4.06, 2.49, or 1.27 m, respectively. The luminance of the dots was 92.6 cd/m², and the luminance of the display background was 4.92 cd/m² (see Note 1).

**Procedure**

Each trial began with a stationary presentation of a fixation cross positioned in the center of the screen. Next, the fixation cross disappeared and the sequence of seven images was displayed (see Note 2). Each image was displayed for 133.3 msec. The refresh time between successive images was sufficient to switch to the next image. Thus, a motion sequence was approximately 933 msec. Between trials, the screen was spatially uniform and of the same luminance as the background luminance of the display during the trials. The time between subsequent trials was approximately 3.5 sec. A new random dot configuration was generated for each trial, and the direction of the displacement on each trial was up or down, randomly determined. After each trial, the subject indicated whether the dots moved upward or downward by moving the position of a joystick. No feedback was provided.

The method of constant stimuli was used to measure $d_{\text{min}}$. A set of five displacement magnitudes was used in a session. The range of the displacement magnitudes was determined from the results of a minimum of 20 practice trials (see Note 3). Each displacement value was presented 20 times, and the order of presentation of the five displacements was random. Thus, each $d_{\text{min}}$ was determined from a total of 100 trials.

For each subject and condition, the proportion of correct responses per displacement magnitude was calculated. A Weibull function (Equation 1) then was fit to the proportion-correct distribution. The parameter $\alpha$ specifies the threshold (displacement value where observers perform at 82% correct), and the parameter $\beta$ specifies the slope of the psychometric function. A maximum likelihood procedure was used to fit the Weibull function with a simplex maximizing routine.

$$f(x) = 1.0 - 0.5 \times \exp[-(x/\alpha)\beta]$$

**Subjects**

Ten observers with normal vision and 29 observers with RP served as subjects. Normal volunteers were recruited from the laboratory personnel and a subject pool at the Wilmer Institute. The RP subjects were recruited from the Retinitis Pigmentosa Study at the Wilmer Institute. The ages of the RP subjects ranged from 15–66 yr, with a mean age of 40.9 (±14.6) yr. The ages of the normally sighted subjects ranged from
22–74 yr, with a mean age of 36.7 (±16.4) yr. (Table 1 is a list of the subjects’ characteristics.) Viewing was monocular with the subject’s eye of better visual acuity, and the subject’s forehead and chin were supported by a headrest. Visual acuity was measured monocularly on all subjects using the ETDRS acuity chart that was back illuminated at 100 cd/m². All subjects wore their refractive correction during the experiment. Visual fields were obtained from each of the RP subjects on the same day that data were collected for the motion experiment. Visual fields were measured by kinetic perimetry with the Goldmann perimeter, using the II/4e target (15 arcmin test spot at 320 cd/m²) on a background of 10 cd/m². Six of the RP subjects were unilateral. Each had an RP-affected eye and a normal fellow eye (see Note 4). (Unilateral subjects were tested with their RP-affected eye.) Informed consent was obtained from each subject after the nature of the experiment had been described.

Results

Figure 1 shows the psychometric functions of a normally sighted subject (solid symbols) and an RP subject (open symbols) along with the best fitting Weibull functions. Proportion correct is plotted against the displacement magnitude of a single shift. The dmin of the normally sighted subject (JG) was 0.56 arcmin, and the dmin of the RP subject (FD) was 0.95 arcmin. Figure 2 shows the distribution of dmin values of the normally sighted subjects and the RP subjects who performed above chance levels. (Note dmin is plotted on a

Table 1. Subject characteristics

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* Media.
† LogMAR.
‡ Years past critical age.
clr, clear. PSC, posterior subcapsular cataract. na, not applicable.
log scale.) \( d_{\text{min}} \) was not obtained for seven RP subjects. Three RP subjects performed at chance level across all displacements. Interestingly, four RP subjects consistently reported motion in the opposite direction at small displacements and performed at chance level at the larger displacements.

\( d_{\text{min}} \) of the normally sighted subjects ranged from 0.15–0.58 arcmin. Our estimates of \( d_{\text{min}} \) for normally sighted observers are comparable to previously reported \( d_{\text{min}} \) estimates. \( d_{\text{min}} \) values ranging from 0.15–1.5 arcmin have been reported for random-dot patterns with a two-frame motion sequence and with a multi-frame motion sequence (frame duration = 20 msec). The reported \( d_{\text{min}} \) estimates with random-dot patterns of the present and past studies of normally sighted subjects also are comparable to displacement thresholds obtained with spots of light and gratings. Displacement thresholds less than 0.5 arcmin have been reported for moving stimuli presented with a stationary reference. Thresholds of 1.0–1.5 arcmin have been reported for displays without a stationary reference.

The data of the RP subjects were markedly different from that of the normally sighted subjects. The majority of the RP subjects did not have \( d_{\text{min}} \) values as low as the normally sighted subjects. \( d_{\text{min}} \) ranged from 0.44 arcmin to chance-level performance where \( d_{\text{min}} \) could not be obtained. The mean of the normally sighted subjects was 0.34 arcmin (SD = 0.17). Only 5 of the 29 RP subjects had \( d_{\text{min}} \) values within two standard deviations of the mean of the distribution of normally sighted subjects.

Possible Causes of Elevated \( d_{\text{min}} \) in RP

**Reduced spatial sampling density:** The reduction in the spatial density of the photoreceptors in the RP eye may be the cause of the large \( d_{\text{min}} \) values. Because the intercone spacing in the fovea is approximately proportional to the minimum angle of resolution (MAR; ie, a measure of visual acuity), a high correlation between \( \log d_{\text{min}} \) and \( \log \text{MAR} \) would provide an indirect confirmation of the hypothesis that reduced cone spatial density elevates \( d_{\text{min}} \) in RP subjects. This would be true if the relationship between MAR and intercone spacing in the RP eye was the same as found in the normal eye. However, lens opacities have been shown to affect visual acuities and posterior subcapsular (PSC) cataracts are seen in some patients with RP. We did not want to confound reductions in MAR resulting from decreased spatial density with reductions in MAR resulting from ocular opacities.

Within our clinical sample, six RP subjects had PSC cataracts. We computed Pearson's correlation between \( \log d_{\text{min}} \) and \( \log \text{MAR} \), excluding subjects with lens opacities and subjects who reported motion in the opposite direction or who performed at chance level. Figure 3 shows a scatterplot of the relationship between the two factors. The correlation coefficient was 0.72, \( P < .001 \) (\( \log d_{\text{min}} = -0.306 + 2.282 \times \log \text{MAR} \)). This means that more than 50% of the variance in \( \log d_{\text{min}} \) could be accounted for by \( \log \text{MAR} \), providing indirect support for the view that the reduction in the spatial density of the photoreceptors contributed to the elevation of \( d_{\text{min}} \) in RP. The relationship between \( \log d_{\text{min}} \) and visual acuity has been noted previously based on a similar elevation of Snellen acuity and displacement thresholds with eccentricity.

**Luminance.** Displacement thresholds have been shown to vary inversely with luminance. Legge and Campbell showed that displacement thresholds increased by a factor of 1.75 as the luminance of a small spot decreased from 100 to 1.0 cd/m². Buckingham and Whitaker obtained a similar \( d_{\text{min}} \) increase.
ment for sinusoidal gratings oscillating at low temporal frequencies (factor of 2.0 over mean luminances of 134–3.8 cd/m²). In RP, histopathologic studies show there is a shortening of the photoreceptor outer segments.7-8 With shortened photoreceptor outer segments, the individual receptors would contain less pigment than normal, which could conceivably reduce the effective luminance. A reduction in the quanta-catching ability of the receptors by half is comparable to a two-fold decrease in stimulus luminance. Although this “dark-glasses” explanation has failed to account for losses in visual acuity,33 flash-on-flash sensitivity,34 and temporal sensitivity,14 we ran a control experiment to exclude the possibility that d_min was elevated in RP subjects because of reduced effective luminance. Specifically, we measured the effects of mean luminance on d_min in a random-dot display. Mean luminance was varied over a 1.6 log unit range by means of neutral-density filters (Wratten gelatin filters No. 96; Eastman Kodak Co., Rochester, NY) attached to spectacle frames. Filter densities of 0.4, 1.0, 1.4, and 1.6 log units were used. The use of the neutral-density filters permitted stimulus contrast to remain constant as mean luminance was varied. We measured d_min over a 40-fold range of luminance levels.

Figure 4 shows d_min values of a normally sighted observer at dot luminances of 2.32–92.50 cd/m². The results show that across the range of luminance levels tested, d_min varied only by a factor of two. The reduction in luminance levels by a factor of 40 is equivalent to a reduction of 97.5% in the quanta-catching ability of the receptors. A two-fold increase in d_min could not account for the elevated d_min values found in the majority of the RP subjects—i.e., at least four-fold after exclusion of reverse and chance performance. Therefore, it is unlikely that d_min was elevated in RP subjects solely because of a decrease in effective luminance.

**Opposite Direction of Motion**

A puzzling aspect of the RP results is the reported perception of opposite direction of motion from 13% of the RP subjects (4 subjects out of 29). To illustrate, in Figure 5 we have plotted psychometric functions of the four subjects with data of a normally sighted subject. Proportion correct is plotted against displacement magnitude. Chance-level performance and chance-level performance ±SD (calculated from the binomial-frequency distribution) are indicated as dotted lines drawn at 0.5, 0.72, and 0.28 proportion correct, respectively. Ninety-five percent of the chance-level scores should fall within ±2 standard-deviations of the mean.

As displacement magnitude increased to approximately 4 arcmin, the proportion correct increased for the normally sighted subject. However, the psychometric functions of the four RP subjects were markedly different from that of the normally sighted subject. For two of the RP subjects (AH and KP), performance was at chance level for the smallest displacements, fell close to 0% correct (consistently chose the wrong direction) for displacements at about 2 arcmin, then returned to chance level for larger displacements. A third subject performed at 0% correct for displacements smaller than approximately 5 arc-
Displacement (arcmin)

Fig. 5. Proportion correct is plotted against displacement magnitude of the four RP subjects who reported opposite direction of motion (AH, open circles; LL, closed triangles; LT, open triangles; and KP, open diamonds) and a normally sighted subject (JG, closed squares). Chance-level performance is indicated by a dotted line drawn at 0.5 proportion correct. The dotted lines drawn at 0.72 and 0.28 represent chance-level performance ± 2 standard deviations. Solid lines connect data points.

min, then performed close to chance for displacements at about 7 arcmin. The fourth RP subject performed at about 30% correct for the smallest displacements, then performed at chance level for displacements of about 2 arcmin. At a displacement of approximately 1 arcmin, all four subjects had scores that fell below the 95% confidence interval for chance performance, indicating that the results are not merely variance around chance level. Three of the four subjects performed below the 95% confidence range for chance level across displacements of 1–3 arcmin.

A review of the subjects’ characteristics (Table 1) shows that the four RP subjects who reported motion in the opposite direction have no remarkable features that would distinguish them from the RP subjects who reported motion in the correct direction. Three of the four subjects had visual acuities of 20/20 (LT) or 20/25 (LL and KP). One subject, AH, had a reduced visual acuity of 20/160 and a PSC cataract. In Table 1, we have listed estimates of years past visual-field-loss onset or critical age (ie, YPCA), which is an index of disease progression extrapolated from Goldmann visual-field data. Notice that disease progression, likewise, does not differentiate the RP subjects who report opposite-direction motion from RP subjects who see motion in the correct direction.

Perception of Opposite Direction of Motion Disappears With Parafoveal Viewing

To determine whether the phenomenon of opposite-direction motion perception was specific to foveal stimulation or whether it occurred at other retinal locations, we measured $d_{\text{min}}$ at a parafoveal location in the same RP subjects who reported opposite-direction motion. A display configuration similar to that described by Baker and Braddick was used to confine the dots in eccentricity. Fifty dots were randomly positioned within two vertically oriented rectangular windows instead of the previously used centrally positioned square window. The procedure for obtaining $d_{\text{min}}$ was the same as described above.

For comparison purposes, a subset of the normally sighted subjects and RP subjects who participated in the foveal-viewing condition was tested at parafoveal locations of 1.25 or 2.5°. Table 1 shows the results of the normally sighted and RP subjects. At 1.25° eccentricities,
tricity, \( d_{\text{min}} \) values of four normally sighted subjects ranged from 0.34–0.49 arcmin. At an eccentricity of 2.5°, the normal \( d_{\text{min}} \) values ranged from 0.30–1.33 arcmin. The normal \( d_{\text{min}} \) values obtained at 1.25 and 2.5° eccentricity are comparable to those reported by Baker and Braddick.\(^{23}\) Of the RP subjects who reported motion in the correct direction in the foveal-viewing condition, 10 subjects were tested at an eccentricity of 1.25° and had \( d_{\text{min}} \) values ranging from 0.51–2.87 arcmin. Six subjects were tested at 2.5° eccentricity and had \( d_{\text{min}} \) values ranging from 0.36–2.05 arcmin. One of the three RP subjects who performed at chance level across all displacements in the foveal-viewing condition was tested at an eccentricity of 2.5° eccentricity. She continued to perform at chance level across all displacements.

Most interesting are the results of the RP subjects who reported opposite-direction motion in the foveal-viewing condition. In the parafoveal-viewing condition, all four RP subjects reported motion in the correct direction. The three RP subjects tested at an eccentricity of 2.5° had \( d_{\text{min}} \) values (0.55, 0.90, and 1.14 arcmin) within the normal range. Only one of the four RP subjects (AH) was tested at 1.25° eccentricity. She had a significantly elevated \( d_{\text{min}} \) value of 7.56 arcmin. Unfortunately, we did not test each of the four RP subjects at both eccentricities, 1.25 and 2.5°. Therefore, we are unable to determine whether all of the RP subjects who reported opposite-direction motion in the foveal-viewing condition would have elevated \( d_{\text{min}} \) values at the smaller eccentric location (1.25°). The results demonstrated that the perception of opposite-direction motion in the present study occurred only under the foveal-viewing condition. That the same four RP subjects who reported opposite-direction motion in the foveal-viewing condition did not report the paradoxical motion in the parafoveal-viewing condition demonstrates the result is not merely an artifact of misunderstood instructions or response strategies.

**Simulation of “Photoreceptor” Dropout**

The psychophysical results show that RP can affect an observer’s ability to judge the correct direction of motion in a random-dot pattern. The majority of RP subjects required a larger displacement to perceive the correct direction of motion. Moreover, some RP subjects were unable to detect the correct direction of motion, regardless of the displacement magnitude. A few RP subjects consistently reported motion in the opposite direction. The statistically significant correlation of log \( d_{\text{min}} \) and log MAR suggests that the reduction in spatial density of the photoreceptors may contribute to the elevation in \( d_{\text{min}} \).

One way to view the task in the present experiment is to think of the observers as detecting the spatio-temporal correlation of the random dots across successive frames. With photoreceptor dropout, a dot that stimulates functional photoreceptors on successive frames would have potential for producing a motion signal. A dot that fails to stimulate functional photoreceptors over successive frames may not be capable of producing a motion signal.

To determine whether a loss in the spatio-temporal correlation of the random dots across successive frames, by itself, could account for the significantly elevated \( d_{\text{min}} \) or perception of opposite direction of motion in a random-dot pattern, we simulated “photoreceptor” dropout in normally sighted subjects by randomly eliminating visual information from a specified number of image positions and measured \( d_{\text{min}} \).

**Methods**

The methods were the same as described above, with the following exceptions. The motion sequence was restricted to two frames instead of seven because of space and memory limitations of the computer imposed by the simulation requirements. The viewing distance was 1.25 m. At this viewing distance, each of the 50 bright dots subtended a visual angle of 2.17 × 2.17 arcmin, ie, a 3 × 3 pixel array (see Note 5). “Photoreceptor” dropout was simulated in the following manner. An invisible array was superimposed upon the 1 deg\(^2\) window, and it remained fixed throughout the session. The invisible array consisted of values indicating the “functional status” for each underlying pixel, ie, simulated “photoreceptor.” A nonfunctional status meant that a random dot assigned to that pixel location, initially or through a displacement, would not be visible (see Fig. 6 for an illustration of the display). Each dropped-out unit consisted of a 3 × 3 pixel array (2.17 × 2.17 arcmin). The number of nonfunctional pixels relative to the total number of pixels defines the dropout percentage.

Within a session, each of five displacement magnitudes was presented 40 times. Across sessions, the percent dropout was varied. Subjects included one naive observer (FA) and two experienced psychophysical observers (KT and FT), all of whom had corrected or uncorrected visual acuities of 20/16.

**Results**

First, no displacement magnitude or dropout level produced the perception of opposite-direction motion. The data of three normally sighted subjects, with the best linear fits, are shown in Figure 7. \( d_{\text{min}} \) is plotted against percent dropout. Subjects FT and FA performed at chance level with 50% dropout. As shown, performance at 12% dropout was similar to performance at 0% dropout. However, at dropout levels of
Fig. 6. A schematic of the display used in the simulation experiments. Shown is a subset of the dots used in the display. Solid dots represent the position of the dots in frame 1, and open circles represent the position of the dots in frame 2 after an upward uniform displacement. The grid represents the invisible array with nonfunctional positions indicated by cross-hatching. Dots assigned to nonfunctional positions (through the initial random assignment or displacement) did not appear on the screen.

25% and greater, \(d_{\text{min}}\) increased significantly with percent dropout (see Note 6).

In the simulation experiment, the average number of dots per frame varied inversely with dropout percent. The average number of dots per frame with 0% dropout was 50. At 50% dropout, the average number of dots (that consisted of a minimum of four pixels) per frame was 36. (Because pixels were randomly dropped out, and not whole dots, the number of remaining dots did not equal 25 at a dropout level of 50%.) The decrease in performance with increasing dropout percent may be attributed to the reduced number of dots per frame. As a control experiment, we measured \(d_{\text{min}}\) at 0% dropout with 36 dots per frame. Table 2 shows a comparison of the \(d_{\text{min}}\) values obtained with 50 dots at 0% and 50% dropout and the \(d_{\text{min}}\) values obtained with 36 dots at 0% dropout. Performance with 36 dots at 0% dropout was slightly lower than performance with 50 dots at 0% dropout, suggesting that the number of dots affects \(d_{\text{min}}\). Greater, however, is the difference in \(d_{\text{min}}\) values obtained with patterns of the same average number of dots (36) per frame but different dropout levels (0% vs. 50%). The elevated \(d_{\text{min}}\) values with dropout in the simulation experiment cannot be explained solely on the basis of a decrease in the number of dots correlated across frames relative to the number of uncorrelated dots—ie, S/N.

**Discussion**

The results of the study show that RP can affect an observer's ability to detect the correct direction of motion in a random-dot pattern. The majority of RP subjects required a larger displacement to correctly judge the direction of motion. Moreover, some RP subjects were unable to judge the correct direction of motion regardless of the displacement magnitude. A few RP subjects consistently reported motion in the opposite direction. What do we know about RP that could account for these results?

Abnormal Temporal Processing and Reduced Effective Luminance Cannot Explain Results

As already stated, it has been demonstrated that RP subjects show abnormal temporal processing. In our study, however, abnormal temporal processing would not be expected to play a role in elevating \(d_{\text{min}}\) because it presumably reflects the spatial properties of the motion system, ie, it is based on the minimum amplitude of motion, not velocity.\(^{24,33}\) This expectation was realized in the lack of a significant correlation (\(r^2 = 0.103\),
P = 0.103) in a subset of the subjects (n = 27) for the magnitude of $d_{\text{min}}$ and critical flicker frequency (CFF; CFF measures are reported in Table 1).

Another RP characteristic, shortened photoreceptor outer segments,7,8 also does not appear to account for the elevation in $d_{\text{min}}$. The results of a control study showed that reduced effective luminance alone could not account for the magnitude of $d_{\text{min}}$ in RP.

### Photoreceptor Dropout Can Account for the Elevation in $d_{\text{min}}$

The relationship between log $d_{\text{min}}$ and log MAR, together with the simulation results, suggests that photoreceptor dropout can account for the elevation in $d_{\text{min}}$. A reduction in the spatial sampling density alone may affect $d_{\text{min}}$ by selectively affecting motion-sensor subunits of small receptive fields or by introducing aliased spectral energy.

**Selective loss of small receptive-field subunits:** Random photoreceptor dropout may selectively affect motion-sensor subunits of small receptive fields. A local motion sensor often is modelled as having a pair of subunits with receptive fields—a symmetric-antisymmetric pair or a displaced pair of symmetric detectors.36-39 Each subunit is sensitive to the spatial po-

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**Table 2. Effects of dot number on $d_{\text{min}}$**

<table>
<thead>
<tr>
<th>Subject</th>
<th>0% dropout (50 dots)</th>
<th>0% dropout (36 dots)</th>
<th>50% dropout (50 dots*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>KT</td>
<td>0.94</td>
<td>1.08</td>
<td>3.80</td>
</tr>
<tr>
<td>FT</td>
<td>0.71</td>
<td>1.23</td>
<td>chance</td>
</tr>
</tbody>
</table>

* Average number of dots per frame is 36.
position and spatial frequency (or size) of the retinal image. At a single retinal locus, many local motion sensors coexist with subunits optimally sensitive to different spatial frequencies. The peaks of the receptive fields are spatially separated by a distance proportional to the subunit receptive-field size, and the temporal decay functions are separated by a time, before the signals from the two subunits are compared.

Presumably, the stimulus must traverse a minimum distance of the receptive fields of the underlying subunits to elicit a motion percept. Psychophysical studies have shown that observers can correctly judge the direction of motion ($d_{\text{min}}$) of a sinusoidal grating (spatial frequency range of 0.85–3.4 cycles/deg) when it is shifted by approximately $1/30^{\circ}$–$1/25$ of its spatial cycle. For patterns that contain more than one spatial-frequency component, $d_{\text{min}}$ appears to be determined by the highest perceptible spatial-frequency component of the stimulus. Boulton and Hess have shown that a pattern composed of two gratings (0.85 and 3.4 cycles/deg) requires a displacement of approximately $1/30^{\circ}$–$1/25$ of the 3.4 cycles/deg grating’s spatial cycle to enable subjects to correctly judge the direction of motion.

Because high spatial-frequency subunits have small receptive-field excitatory centers, it is most likely that these subunits will be affected first by photoreceptor dropout. As the number of subunits decreases, the S/N ratio will decrease, and eventually, the S/N ratio may fall below the level necessary to produce low motion thresholds.

**Aliased spectral energy:** Photoreceptor dropout will result in a lower sampling density, which, depending on the spatial-frequency content of the stimulus, may introduce added spectral energy into the retinal image. Sampling arrays can faithfully reconstruct images when the spatial frequency content is below the Nyquist limit (ie, half the sampling rate). Energy from spatial frequencies above the Nyquist limit, however, is transformed into spurious low frequencies (ie, aliasing or harmonic distortions). Because the photoreceptor dropout is diffuse and seemingly random in the early stages of RP, the sampling array most likely will be irregular. An irregular sampling array aliases the spectral energy into broadband noise.

The aliased spectral energy could stimulate a wide range of local motion sensors with different spatial and temporal properties, thereby producing spurious motion signals for false directions and speeds. The increase in spurious motion-direction signals would increase the ambiguity of the motion signal and decrease the S/N.

One way to more fully examine the role of aliasing in the perception of opposite-direction motion is to measure $d_{\text{min}}$ at various spatial frequencies using stimuli that are localized in space and spatial-frequency (eg, gabor patch). Opposite-direction motion perception should occur only at spatial frequencies higher than the Nyquist limit. (A spatially localized patch permits an examination of a potentially nonhomogeneous sampling array.)

**Eye Movements in RP Are Unknown**

Legge and Campbell found that displacement thresholds decreased significantly in the presence of an annulus surrounding the stimulus. One hypothesis was that the annulus may have increased fixation accuracy. If eye movements act as ‘‘noise,’’ above which object movements must be perceived, then factors that decrease fixation accuracy might increase $d_{\text{min}}$. There is no priori reason to expect RP subjects to have anomalous eye movements. The little data that have been collected on eye movements in RP subjects (ie, refixation patterns) indicate that eye movements in RP subjects are similar to those of normally sighted subjects.

**What Could Account for the Perception of Opposite-Direction Motion?**

In the discussion above, we described how a reduced irregular sampling array might elevate $d_{\text{min}}$. However, it is difficult to see how the explanations could account for the perception of opposite direction of motion in random-dot patterns. Recent studies in human motion perception in the extrafoveal retina have shown that undersampling can result in the perception of opposite-direction motion of periodic patterns. The studies showed that for sinusoidal gratings, perceived direction of motion is veridical near the Nyquist limit and reverses direction between one and two times the Nyquist limit. For the perception of opposite-direction motion to occur with random-dot patterns, which have spectral energy across a broad range of spatial frequencies (each presumably producing local motion signals), the aliased energy would have to produce a strong enough motion signal in the opposite direction to bias the system against the correct-direction-of-motion signals generated from sensors fed by unaliased frequencies. It is difficult to imagine a system that could produce aliased energy sufficient to bias the motion system yet support visual resolutions of 20/25 or better.

An alternative explanation has been suggested by Albert Ahumada based on a dual-system theory. According to the theory, the perception of directional motion results from the difference between the signals of two systems, each having motion thresholds that depend upon the ratio of directional to total energy. A frame-of-reference system (perhaps the ocular-motor system) integrates motion information over a large region and averages out more receptor noise, whereas
an object-motion system computes motion information over local receptive fields. Signals of the frame-of-reference system are subtracted from signals of the object-motion system to stabilize the motion. The failure of the object-motion system to respond could lead to paradoxical motion. This theory suggests that paradoxical motion could be seen by normals if the correct parameters could be found to selectively disable the object-motion system.

In conclusion, we have demonstrated that RP can affect an observer’s ability to detect the correct direction of motion in a random-dot pattern. The majority of RP subjects required a larger displacement to reliably judge the correct direction of motion, whereas others reported motion in the opposite direction. We have postulated a number of hypotheses for explaining the elevation in $d_{min}$ in RP. However, we remain puzzled by the report of opposite direction of motion by some RP subjects, especially because it occurs at displacements comparable to normal threshold levels. As explained in our discussion, only very special conditions should produce this type of phenomenon. This study was a first step in the investigation of motion processing in RP.

The results demonstrated that in all stages of RP there is abnormal foveal motion processing. Further studies are needed to examine motion-direction discrimination at faster speeds and discrimination of speed in the fovea and peripheral retina.

Notes

1. Luminance was measured with a 6 × 6 square pixel array instead of the actual dot size (3 × 3 pixel square array) because of the aperture size limits of the spotmeter. Calibrations made with a 9 × 9 pixel square array yielded the same value within the measuring accuracy of the spotmeter.

2. $d_{min}$ typically is measured in motion-sequences that consist of two frames, ie, a single shift. The multiple-shift display was used in the present study to increase the probability that the RP subjects would not miss the trial. In pilot studies, the RP subjects sometimes missed the presentation of the motion sequence altogether. Increasing the number of displacements (and thus the total motion-sequence duration) eliminated the problem. Although past work has demonstrated temporal recruitment effects on motion perception, the use of a 133.6 msec frame duration in the present experiment minimized summation effects across frames. However, it is possible that RP subjects may experience temporal recruitment in the present experiment because of slowed temporal processing in RP eyes. If this is the case, $d_{min}$ would be lower with the multiple-shift display than a single-shift display.

3. Subjects who were unable to consistently report the correct direction of motion across a wide range of displacement values during practice were tested at values in the range of 0.36–22.0 arcmin.

4. The fellow eyes of the unilateral RP subjects were diagnosed as normal, based on the following criteria: normal fundus appearance, normal electroretinogram, normal visual acuity, normal Goldmann visual fields, and normal dark-adapted perimetry.

5. The size of the dropout unit used in the simulation experiments was $2.17 \times 2.17$ arcmin (the size of a clump of approximately 16 photoreceptors). The choice of the dropout unit size was arbitrary. The experiment was set up to examine the effects of random elimination of visual information. It was not meant to mimic dropout of single photoreceptors per se, because we do not know if that is how photoreceptors drop out in RP. We only know that the number of photoreceptors is reduced. To investigate the difference in effects between single-photoreceptor drop out and multiple-photoreceptor drop out, we conducted an analysis in which the dropout unit was $0.36 \times 0.36$ arcmin. Observer KT was the subject. The results of the experiment show that, in both cases, $d_{min}$ increases systematically with increasing dropout, albeit at a slower rate when the dropout unit is smaller. With a $0.36 \times 0.36$ arcmin dropout unit, $d_{min}$ doubled at a dropout percentage of 75%. With the larger dropout unit, $d_{min}$ doubled at around 35%. A critical factor appears to be the relative size of the visual information to the dropout unit.

6. To determine whether the estimates of $d_{min}$ were artificially high at dropout levels of 0 and 12% because of truncation effects (minimum displacement was 0.72 arcmin), we ran one of the subjects (KT) at two viewing distances (1.25 and 2.5 m). A single-pixel displacement was equal to 0.36 arcmin at a viewing distance of 2.5 m and 0.72 arcmin at a viewing distance of 1.25 m. $d_{min}$ was 0.70 arcmin with 0% dropout and 0.86 with 12% dropout at the 2.5 m viewing distance. At the 1.25 m viewing distance, $d_{min}$ was 0.93 arcmin with 0 and 12% dropout. Although the difference in $d_{min}$ values at the different viewing distances could be due to truncation effects, the difference also may be explained as subject variability. Whatever the reason, there is little difference in $d_{min}$ values for the 0 and 12% dropout conditions.

Key words: $d_{min}$, displacement thresholds, retinitis pigmentosa, low vision, photoreceptor sampling

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