Are silencing, ectopic shifts, and receptive field (RF) scaling in cortical scotoma projection zones (SPZs) the result of long-term reorganization (plasticity) or short-term adaptation? Electrophysiological studies of SPZs after retinal lesions in animal models remain controversial, because they are unable to conclusively answer this question because of limitations of the methodology. Here, we used functional MRI (fMRI) visual field mapping through population RF (pRF) modeling with moving bar stimuli under photopic and scotopic conditions to measure the effects of the rod scotoma in human early visual cortex. As a naturally occurring central scotoma, it has a large cortical representation, is free of traumatic lesion complications, is completely reversible, and has not reorganized under normal conditions (but can as seen in rod monochromats). We found that the pRFs overlapping the SPZ in V1, V2, V3, hV4, and VO-1 generally (i) reduced their blood oxygen level-dependent signal coherence and (ii) shifted their pRFs more eccentric but (iii) scaled their pRF sizes in variable ways. Thus, silencing, ectopic shifts, and pRF scaling in SPZs are not unique identifiers of cortical reorganization; rather, they can be the expected result of short-term adaptation. However, are there differences between rod and cone signals in V1, V2, V3, hV4, and VO-1? We did not find differences for all five maps in more peripheral eccentricities outside of rod scotoma influence in coherence, eccentricity representation, or pRF size. Thus, rod and cone signals seem to be processed similarly in cortex.

Functional MRI | Scotopic | Plasticity | Adaptation | Population receptive fields

Pressing question in visual neuroscience is, “To what extent can adult human visual cortex reorganize after the removal of visual input?” This question can be studied through the effects of retinal lesions (causing scotomas), in which input from the retina has been removed, but cortical representations of the scotoma projection zone (SPZ) remain intact. Accordingly, emphasis must be placed on teasing apart effects of scotomas that relate to short-term cortical adaptation from those of long-term cortical plasticity (1) (terminology review is in ref. 2). Here, we investigate this question in human cortex by using functional MRI (fMRI) to measure the immediate cortical SPZ responses in the unique paradigm of the naturally occurring rod scotoma.

The photoreceptors in humans can be divided into two classes: cones, which are primarily responsible for vision under high-luminance (photopic) conditions, and rods, which are primarily responsible for vision under low-luminance (scotopic) conditions when the cones are inactive. The cones are an order of magnitude more highly concentrated in the fovea relative to the periphery, where they inform our most detailed visual experience (3). In contrast, the greatest concentrations of rods are more than ~1° eccentric from fixation and become increasingly sparse toward fixation until they are completely absent. This roughly circular rod-free zone covers a radius of ~0.6–0.8° of visual angle about the fixation point (diameter = ~1.25–1.7°) (4, 5). Under scotopic conditions, a scotoma arises from these foveal, rod-free zones, because no photoreceptors are stimulated within these regions (6, 7). Perceptual and fMRI estimates of the rod scotoma range from ~1° to 2° of visual angle because of the rod-sparse region surrounding the fovea and individual variability (6–9).

The properties of the rod scotoma make it an excellent candidate for studying the removal of visual input. First, the scotoma exists in all normal human subjects under scotopic conditions (5, 7). Second, the scotoma is located in the central fovea, which has large swaths of early visual cortex devoted to its analysis (10–12). Third, the scotoma arises because of the central fovea’s complete lack and surrounding paucity of rod photoreceptors, allowing for a very close comparison with retinal lesions in animal models (5). Fourth, there is indirect evidence that the rod contributions to cortical activity are very similar to those of the cones, allowing for comparisons of changes in the properties of the cortical neurons overlapping the scotomas arising from either scotopic conditions or direct retinal lesions (6, 7, 13, 14). Fifth, the rod scotoma is completely reversible on return to photopic conditions, allowing for the measurement of ectopic cortical responses caused by short-term cortical adaptation without contamination from long-term reorganization, such as that seen in the relatively permanent developmental foveal scotomas of rod monochromats (7).

Keys to the use of the rod scotoma in the evaluation of cortical plasticity are the questions, “To what extent do the retinal differences between rod and cone photoreceptors influence cortical processing, and do any affects vary across cortical regions?” Rods have larger receptive fields (RFs) than cones and greater connectivity density with ganglion cells (4, 5), but do these differences survive center-surround mutual inhibitory networks to be measurably different at the cortical level (15, 16)? To answer all of these questions, the cortical effects of the rod scotoma must be differentiated from any effects caused by differences between rod and cone input.

To investigate the effects of the rod scotoma in human early visual cortex, we presently compared the retinotopic responses in...
early visual field maps V1, V2, V3, hV4, and VO-1 between photopic and scotopic conditions in normal adults. We expect three types of short-term adaptive responses from neurons in the SPZ of any scotoma in visual space. First, neurons with RFs completely eclipsed by the SPZ should be silenced, resulting in a reduction of neural activity to the spontaneous firing rate (Fig. 1A). At this population-level fMRI measurement, this effect will be reflected by a reduction in coherence. Second, neurons with RFs partially eclipsed by the SPZ should have an apparent ec-
topic shift of their preferred centers, because they will continue to respond to the remaining (now decreased) visual space. Such e
topic shifts occur whether the preferred center of that neuron is within the SPZ (Fig. 1B) or adjacent (Fig. 1C). Third, it is expected that neurons with RFs partially eclipsed by the SPZ may show a scaling of their RF sizes, although whether these increase or decrease in size is difficult to predict. Such neurons’
new RF spans will necessarily be reduced by the overlap with the
SPZ, but their RF sizes may also be increased because of changes
in feedback activity or a reduction in lateral inhibitory connec-
tions to nearby neurons that have also been silenced or shifted to
eccentric locations by the scotoma (1, 2, 17–20). The combination
of these effects could also lead to no observable change at this
level of measurement.

Each of these predicted scotoma effects must be distinguished
from differences between photopic and scotopic conditions un-
related to the rod scotoma. The RFs of neurons in more pe-
ripheral eccentricities do not overlap with the rod scotoma, but
they perform the same computations as their more central
counterparts. As a result, they measure the effect of rod vs. cone
inputs independent of the rod scotoma, acting as an ideal control
with which the effects of the rod scotoma can be contrasted.
First, because of the difference in luminance that defines photopic
and scotopic conditions, we predict a reduction in coherence.
Second, we predict no change in the locations of cortical RFs.
Third, we test whether there is a change in RF size at the pop-
ulation level. The RFs of rods are larger than cones, and the
retinal ganglion cells receive a greater number of inputs from rods
than cones (4, 5), both of which suggest that we may observe larger
cortical RFs. However, it is possible that, by the time that the
signals reach cortex, center-surround mutual inhibition circuitry
may counter any such increase in RF size, because the larger
retinal RFs contribute to both the centers and surrounds of sub-
cortical and cortical RFs (4, 5, 8, 13–16). Furthermore, any pop-
ulation of RFs in a cortical location, such as a voxel, will have a
degree of dispersion of their preferred centers, which leads to a
larger measured RF for the population as a whole relative to in-
dividual constituent RFs. As such, any change in RF size under
scotopic relative to photopic conditions that survives center-sur-
round mutual inhibitory networks may be indistinguishable from
RF dispersion at the population level (17, 21, 22). Any differences
in these measurements of coherence, preferred center, and size of
populations of RFs caused by the rod scotoma in the central ec-
centricities must extend beyond any differences observed in more
peripheral eccentricities caused by differences between photopic
and scotopic conditions.

Results

To compare cortical activity in early visual field maps between
photopic (luminance = 140 cd/m²) and scotopic (luminance =
0.003 cd/m²) conditions, we collected fMRI data in four subjects
using moving bar stimuli (Fig. 2F) after the subjects adapted to
each luminance condition (SI Materials and Methods). We used
population RF (pRF) modeling to estimate the V1, V2, V3, hV4,
and VO-1 maps and pRFs (22). A pRF for a particular voxel
reflects the central tendency of the sizes (spreads) and centers in
visual space preferentially activated by the RFs of the population
of neurons within that voxel that are activated by a particular
stimulus. An example of the similarity of pRF model fits under
photopic and scotopic conditions is presented in Fig. S1. For
analysis of the measurements of visual field map activity, shifts of
pRF centers, and scaling of pRF sizes, we divided up the ec-
centricity representation in each map in each hemisphere of each
subject into 10 regions of interest (ROIs) spanning 1° of visual
angle along the eccentricity gradient from 0° to 10° centered on
every 0.5°. Each measurement was drawn from these 10 eccentricity
band ROIs for each subject, averaged between hemispheres for
each subject, and then, analyzed across subjects between conditions.
We defined the central ROI in each early visual field maps as
the region where RFs in each voxel overlap the eccentricities that are expected to be
in the rod scotoma as measured in the photopic condition (Fig.
1D). For example, voxels in V1 with a preferred center of 2.5° of
visual angle are estimated by pRF measurements to span ~1° of
visual angle under photopic conditions and thus, would be
expected to span visual space approximately from 1.5° to 3.5°,

Fig. 1. Schematic of the predicted effects of the rod scotoma. (A–C) Black
disks and black circles around them indicate the preferred center and spread
of a neuron’s RF, respectively. Each row, thus, represents neurons with
preferred centers at one specific eccentricity. (Lower) The gray shaded re-

dions indicate the SPZ of the rod scotoma under scotopic conditions. Black
arrows indicate the expected direction of the measured shift of RF centers
caused by interaction of the rod scotoma with a neuron’s RF under scotopic
relative to photopic conditions. (A) Neurons with RFs completely eclipsed by
the SPZ. (B) Neurons with RFs partially eclipsed by the SPZ and centers within
the SPZ. (C) Neurons with RFs partially eclipsed by the SPZ and centers
outside the SPZ. (D) pRF interactions with the rod scotoma. This graph is an
accurately scaled visual representation of the normal pRF sizes (measured
under photopic conditions) for each visual field map (degrees of visual angle

corresponding to the sizes seen here are shown in Fig. S6). Each circle is an
accurately scaled visual representation of the average size of pRFs for the
eccentricities indicated below it in the map indicated on the left. The ec-
centricities labeled at the bottom are the centers of the 1° bins used for 10
eccentricity-band ROIs measured for each visual field map. Filled circles
represent pRFs in eccentricities where the pRF is both large enough and close
enough to the rod scotoma to expect interactions between them. Open
circles represent pRFs at eccentricities outside the expected influence of the
rod scotoma (see also Fig. S3).

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Barton and Brewer
Neural Activity Is Reduced Within the SPZ. Coherence was measured for voxels in each visual field map across the entire stimulated visual field and compared between scotopic and photopic conditions to assess changes in blood oxygen level-dependent signal caused by the differences in luminance (Fig. 3A, SI Materials and Methods, and Fig. S5). Across all five maps, photopic coherence was not statistically significantly greater than scotopic coherence in the more peripheral eccentricities (ps = 0.078–0.897), which indicates that responses in early visual areas are generally robust under scotopic conditions, despite the drastic drop in luminance and the activation of an entirely different class of photoreceptors between photopic and scotopic conditions (Figs. S4A and S5 and Table S2).

These results indicate that there is a specific drop in neural activity in these visual field maps caused by the silencing of neurons with RFs partially or completely eclipsed by the rod scotoma (Fig. S3). The pattern of results across visual field maps is consistent with the pRF sizes for each of the maps (Fig. 1D), such that maps with larger pRFs—hV4 and VO-1, which have proportionally less surface area eclipsed by the rod scotoma—are not only possible for such detailed measurements through the presently used functional (not anatomical) localization (24, 25).

Scotopic and Photopic Visual Field Map Measurements. Typical pRF measurements of the eccentricity and polar angle representations in V1, V2, V3, hV4, and VO-1 under photopic and scotopic conditions are presented in Fig. 2 for the left hemisphere of one subject (Fig. S2). Note the loss of blood oxygen level-dependent response in the central foveal representation (darkest red voxels drop out of the image in Fig. 2B) in the eccentricity representation of V1 under scotopic conditions (Fig. 2B and Fig. S2B, D, and F), consistent with previous findings (6, 7). Interestingly, V2, V3, hV4, and VO-1 did not show a similar loss of signal but rather, a peripheral shift in the central eccentricity representations between photopic and scotopic conditions (red/orange voxels shift to orange/yellow/green in Fig. 2B and Fig. S2B, D, and F). This eccentricity shift represented in the color overlays here is further quantified in graphical form in Fig. 3B. It is likely that this shift was produced as neurons with small RFs within this region in each visual field map that did not overlap the rod scotoma edge were silenced, whereas the neurons with larger RFs overlapping the scotoma border are measured as effectively representing a more peripheral position (Fig. S3B) (17). The moving bar stimulus at this size (Fig. 2F) typically does not produce clear measurements of the polar angle representation within the very central fovea (hence, cyan color in the central photopic polar angle map of V1 in Fig. 2C and Fig. S2A, C, and E) but contrasts with the loss of contralateral responses in this region under scotopic conditions (Fig. 2D and Fig. S2B, D, and F). Outside of this region, the polar angle representations in all visual field maps remained largely unchanged between the two conditions. Because differences in eye movements between conditions could contribute to problems in measuring visual field maps, we confirmed that no significant differences in fixation stability existed between the two conditions (26) (SI Materials and Methods, Fig. S4, and Table S1).

Fig. 2. Visual field maps in photopic and scotopic conditions. (A–D) Pseudocolor overlays on a flattened representation of occipital cortex from the left hemisphere of one subject (S2) represent the position in visual space that produces the strongest response at that cortical location. (A and B) Eccentricity representations. Color legend represents the visual field from 0° to 10° radius of visual angle. (C and D) Polar angle representations. Color legend represents the contralateral hemifield. (A and C) Photopic measurements. (B and D) Scotopic measurements. Boundaries of visual field maps are depicted with dotted (polar angle boundaries between maps of interest) and solid (eccentricity boundaries and edge of measurement) black lines. Coherence ≥ 0.20. (Scale bar: 1 cm along the flattened cortical surface.) (E, Upper) Anatomical orientation legend. (E, Lower) Inflated 3D representation of a medial view of the left hemisphere of subject 2. Inset indicates the region near the calcarine sulcus of the occipital lobe, where the maps were measured. (F) Moving bar stimulus for visual field map and pRF measurements comprised a set of contrast-reversing checkerboard patterns at eccentricities from 0° to 11° radius. One frame is shown for the bar stimulus sequence. Four bar orientations (0°, 45°, 90°, and 135° from vertical) with two motion directions orthogonal to each orientation were used, producing eight different bar configurations. Additional examples are in Fig. S2.

Fig. 3. Coherency, eccentricity shifts, and pRF size changes in central and peripheral eccentricities. (A) Coherence differences. (B) Ectopic eccentricity shifts. Positive numbers indicate shifts of pRF centers outward from the rod scotoma, and negative numbers indicate shifts of pRF centers into the rod scotoma. (C) Scotopic pRF size percentage changes. Positive values indicate larger pRF sizes under scotopic conditions, whereas negative values indicate smaller pRF sizes under scotopic conditions. All data are plotted as a function of the photopic eccentricity in degrees of visual angle. The legend indicates line shading and marker shape for each map. Error bars represent SEMs (Figs. S5–S7).
significantly silenced within the central representation. Conversely, maps with smaller pRF sizes—V1, V2, and V3—which are proportionally more eclipsed by the rod scotoma—do undergo significant silencing of neural activity within the central representation (2, 27).

Voxels with pRFs Overlapping the Rod Scotoma Show an Ectopic Shift in Their pRF Centers. Preferred eccentricity was measured for voxels in each visual field map across the entire stimulated visual field and compared between scotopic and photopic conditions to assess changes caused by the differences in luminance (Fig. 3B and Fig. S6). Across the more peripheral eccentricities of all five maps, there was no significant peripheral shift in pRF locations for scotopic relative to photopic conditions (ps = 0.091–0.740) (Fig. 3B, Fig. S6, and Table S2). However, there was a significant shift peripherally from the rod scotoma in scotopic relative to photopic conditions for the central eccentricities of all five maps (ps = 0.023–0.049) (Fig. 3B, Fig. S6, and Table S2).

These findings pose a significant problem for fMRI and electrophysiological studies of cortical responses to scotomas reporting ectopic responses from a population of neurons in the SPZ as evidence of reorganization without taking into account effects of short-term adaptation (28–33). Here, we achieved the same results in the SPZ of the rod scotoma with short-term exposure to scotopic conditions. In fMRI measurements, each voxel summarizes the summed activity of hundreds of thousands of neurons, but if a substantial number of those neurons is silenced, because their RF is over the scotoma, the summed RF now only draws from the more active, peripheral individual RFs and shifts more eccentric from the scotoma, which we see here. Similarly, in electrophysiological studies of single neurons, these short-term changes in measurements may arise because of a similar effect at the level of the retinal ganglion cells; the RFs of the neurons in this case each may be drawing from several ganglion cells, some of which are silenced within the scotoma, whereas the more peripheral ganglion cells remain active. Studies of long-term cortical plasticity using any measurement must show that any ectopic responses caused by long-term reorganization are above and beyond the effects of such short-term cortical adaptation (2, 17). Note that fMRI measurements of ectopic responses from long-term reorganization have been successfully shown in the rod scotoma SPZs in rod monochromats (which have a condition that produces congenital, bilateral foveal lesions in the rod-free zone) (7) by comparing these ectopic responses in the rod monochromat subjects with rod scotoma SPZ measurements in control subjects.

Voxels with pRFs Overlapping the SPZ May Scale pRF Sizes. pRF sizes were measured for voxels in each visual field map across the entire stimulated visual field and compared between scotopic and photopic conditions to assess changes caused by the differences in luminance (Fig. 3C and Fig. S7). The scaling of pRF sizes was evaluated using a measure of the percentage change in pRF sizes between luminance conditions: pRF size percentage change = (scotopic pRF size/photopic pRF size – 1) × 100. Positive values would indicate a larger pRF size under scotopic conditions, whereas negative values would indicate smaller pRF sizes under scotopic conditions. Across the more peripheral eccentricities of all five maps, there was no significant pRF size scaling in scotopic relative to photopic conditions (ps = 0.200–0.628) (Fig. 3C, Fig. S7, and Table S2). There was also not a significant difference in pRF size percentage change between photopic and scotopic conditions for V2, V3, or hV4 (ps = 0.131–0.436). However, there was a marginally significant pRF size percentage decrease in the central eccentricities for V1 (P = 0.062) and a significant increase for VO-1 (P = 0.015) (Fig. 3C, Fig. S7, and Table S2).

These results indicate that scaling is quite variable among maps because of the rod scotoma; decreasing, not changing, and increasing pRF sizes were all observed. It is possible that these changes reflect differences in attentional modulation from higher-order visual field maps or perhaps, differences in the properties of the individual maps, such as differences in initial pRF sizes or lateral connectivity (2, 17, 18, 34). For the more peripheral eccentricities, these results indicate that there is no observable cortical difference at this measurement level in pRF size between the rod and cone processing pathways.

Discussion
In summary, the central eccentricities of these visual field maps, with pRFs overlapping the SPZ, generally (i) reduced their coherence because of silenced neurons, (ii) shifted their pRF centers more eccentric from the rod scotoma, and (iii) had variable results regarding scaling of their pRF sizes (increase, decrease, and no change). Each of these measurements was independent of long-term plasticity, which has particularly important implications for the interpretation of studies of cortical reorganization. Although several electrophysiological and fMRI studies propose long-term cortical reorganization as the primary mechanism for silencing, ectopic shifts, and pRF scaling within the SPZ (29, 31–33, 35), we have acquired a similar pRF-level measurement and shown that these responses can arise during short-term cortical adaptation in the representation of pRFs with some overlap with the SPZ.

In contrast, the more peripheral eccentricities of these visual field maps, with pRFs independent of the rod scotoma, (i) had no statistically significant reductions in coherence, (ii) did not shift their pRF centers, and (iii) did not scale their pRF sizes. Although there was no significant reduction in coherence, there tended to be a nonsignificant drop in coherence. Crucially, the drop in coherence observed in the central eccentricities is larger than in the midperiphery. In general, these results act as an ideal within-subject, within-map control, differentiating the effects of the rod scotoma from the luminance drop between photopic and scotopic conditions. Furthermore, these results indicate that retinal differences between rod and cone photoreceptors do not translate to measurable differences at the cortical level of these five visual field maps.

Comparisons with Studies on the Cortical Effects of Other Retinal Scotomas. Keys to understanding cortical responses to scotomas are the following questions. Are silencing, ectopic shifts, and RF scaling in cortical SPZs the result of short-term adaptation and thus, the expected immediate response of the visual system to a removal of visual input? Alternatively, do such responses primarily arise over a longer period after more extensive cortical reorganization? Scotomas caused by trauma or disease are challenging for human SPZ studies, because they tend to be permanent, monocular, variable in retinal thicknesses, and difficult to compare across patients because of variability in retinal or cortical location and time of onset. The blind spots, although they are omnipresent, naturally occurring scotomas, are located in the midperiphery, where there is less cortex devoted to visual analysis, and the RFs are larger relative to the fovea (4, 5, 10). Not surprisingly, fMRI studies of the blind spot can only localize a small area of V1 corresponding to the blind spot, which does not make it ideally suited for these questions of ectopic responses and plasticity (36, 37). Artificial, reversible scotomas caused by stabilization of the stimulus on the retina are transient and most effective in the periphery (38), making them difficult to measure in early visual areas with fMRI because of the comparatively slow temporal resolution of fMRI and the relatively smaller amount of cortex devoted to peripheral processing (10, 11, 39, 40).
As a result, many researchers have focused on studying long-term reorganization in early visual cortex in cat and monkey in response to induced binocular retinal lesions, but even these studies have very controversial results (2, 41). Some groups using electrophysiology have reported silencing, ectopic shifts, and pRF scaling from V1 neurons within the SPZ that they use as evidence of cortical reorganization weeks to months after the retinae were lesioned (28–33). However, because these studies typically measure only immediate postlesion and long-term (weeks to months) time points, they cannot differentiate responses in the SPZ caused by short-term adaptation from those arising from long-term reorganization (Fig. S3). The retinal tissue surrounding the experimentally lesioned site takes up to 2 wk to recover normal function after initial swelling from such lesion-inducing procedures as photocoagulation, which prevents accurate measurements immediately after the retinal lesion (27, 28, 42). Furthermore, measurements of short-term adaptation in these cases are inherently confounded by the effects of this retinal stunning that surrounds the true retinal lesion.

In contrast, other groups using electrophysiology and fMRI report no evidence of ectopic responses in the macaque V1 SPZ after weeks of recovery and therefore, no cortical reorganization (2, 27). It is important to note that none of these studies can measure the same neuron at multiple time points, but rather, they measure activity from active neurons in similar locations, resulting in potential sampling biases that further complicate their interpretations (2, 27). Similar conflicting measurements have been seen in human patients with bilateral foveal lesions from age-related macular degeneration, with some fMRI studies claiming extensive recovery within the V1 SPZ, whereas again, others showed no evidence for reorganization (7, 18, 35, 43–45). Thus, the predicted and measured effects on (p)RFs caused by short-term adaptation and long-term reorganization are very difficult to differentiate (Fig. S3).

To avoid a potential overestimation of the extent of long-term cortical reorganization and recovery within the SPZ, measurements must be able to determine that long-term reorganization has occurred that is greater than both what can be attributed to short-term adaptation, as described here, and what can be attributed to the recovery of the stunned retinal tissue. Often, one could argue that silencing, shifting, and scaling of (p)RFs in response to a scotoma are short-term adaptations that are simply the result of transitory short-term cortical reorganization in many cases. Our goal here was to use measurements of the human rod SPZ to allow for detailed evaluation of immediate human cortical responses to the reversible removal of visual input.

Our data are largely consistent with and extend the recent findings that central retinal lesions caused by age-related macular degeneration and simulated lesions in the central (5° and 7.5° radius) visual field in control subjects show ectopic pRF shifts, silencing, and scaling in V1 caused by cortical short-term adaptation rather than long-term reorganization (17, 18). We note that our data differ in our measurements of a small, marginally significant decrease in pRF size in V1 caused by the rod scotoma, whereas these studies showed an increase in V1 pRF size caused by age-related macular degeneration and artificial scotomas. One possibility for this difference is that our bar stimulus, which spans the central visual field, may have elicited a greater perception of filling in than the expanding ring and rotating wedge stimuli used in the prior studies, leading to alterations in pRF dynamics (46). We have compared such differences in perceptual filling in between these stimulus types in other measurements and do find greater perceptual filling in for the bar stimulus (47). Another factor may be the differences in the sizes of the scotomas; the previously measured scotomas are much larger, on average, than the rod scotoma presently measured. The larger scotoma increases the average pRF size affected by the scotoma because of the well-documented enlargement in pRF size from the representation of central fixation to that of the periphery in visual field maps (22).

Interestingly, we do observe increases in pRF sizes caused by the rod scotoma for larger pRFs, which we measured in VO-1, consistent with these previous findings in V1 (Fig. 1D shows a model of pRF sizes by map and eccentricity). We do not believe that this difference in V1 pRF sizes arises from the different photoreceptors activated in each study (rods vs. cones). We expect that any such differences in the rod vs. cone visual pathways would be evident across our analysis of the peripheral eccentricities of the visual field (7). However, we see no differences between photopic and scotopic conditions in the relatively more peripheral eccentricities of any of five visual field maps.

**Rod Pathways in Cortex.** Comparatively few studies have examined the contributions of the rod system to cortical activity. Our measurements support the studies of scotopic psychophysics and retinal circuitry, which suggest that most, if not all, retinal ganglion cell types—and thus, the cone pathways—contribute to scotopic vision (13, 14, 48). Outside of the region of interactions with the rod scotoma, we do not measure any differences in visual field map organization or pRF properties across our measurements out to 10° of visual angle between photopic and scotopic conditions, suggesting that these regions in these visual field maps receive similar cone and rod inputs, at least for this level of processing.

With measurements of cortical activation under scotopic vision, Hadjikhani and Tootell (6) also showed similar peripheral responses between photopic and scotopic conditions in V1, V2, V3, and what they measured as V8 (analogous to our hV4 and VO-1) (39), comparable with our findings. However, Hadjikhani and Tootell (6) observed a significant lack of activity in the central representations of their four maps, which is in contrast to our findings of shifts of the central representations to more parafoveal regions in all five maps. We do observe significant decreases of activity, which indicate that many neurons in pRFs overlapping the rod scotoma have reduced activity or are silenced. These differences may have arisen from variations in (i) measurement methodology (traveling wave vs. pRF modeling), (ii) signal-to-noise ratios, and (iii) effects arising from the stimulus types, such as perceptual filling in. Our moving bar stimulus, for example, likely produced a greater effect of filling in, which might be reflected in top-down influences producing activity in foveal V2, V3, hV4, and VO-1 (19, 47). Along these lines, a recent study by Williams et al. (19) showed that feedback from higher cortical areas can produce differential effects in the fovea vs. the periphery of early visual cortex. Specifically, object stimuli presented in the periphery produced responses in foveal retinotopic cortex but not peripheral retinotopic cortex. It is possible that a similar feedback mechanism contributes to the coherence changes, ectopic shifts, and pRF size changes measured here along the scotoma border.

Additionally, Hadjikhani and Tootell (6) observed no activation of the region of hV4 and VO-1 (V8) under scotopic conditions throughout their entire measured visual field, concluding that those maps were cone-only color-processing maps. We observe significant activation of both hV4 and VO-1 when only rods are active, indicating that, although these maps may be involved in color processing, they are not cone-exclusive. From our data, it seems that rod signals are passed through all maps in the early stages of the visual system. There seems to be no differences in any of our measurements of the peripheral eccentricities, indicating that the maps handle rod signals very similarly to cone signals.

Finally, we note that our measurements average across all polar angles within each eccentricity band. Interestingly, there is growing evidence for perceptual and neural asymmetries between the dorsal and ventral visual fields, with improved motion, global processing, and coordinate spatial judgments in the lower...
visual field and improved visual search, local processing, and
categorical judgments in the upper visual field, especially for
the left visual field (49–53). Such variations would not be apparent in
our measurements based on eccentricity from fixation, which
grouped the polar angles. Although such differences would be
unlikely to have an effect on our results here, it may be of interest
to future studies to investigate potential differences between these
quarter-field representations as well as between hemispheres.

Conclusions
The use of the rod scotoma provides an excellent, reversible, accessi-
able approach for investigating the short-term responses to
scotomas as well as the cortical differences between rod and cone
inputs, which we describe here. Claims of long-term cortical re-
organization after macaque

Materials and Methods
Subjects. Four subjects (two females) ages 24–36 years old participated in this study.
All subjects had normal or corrected-to-normal visual acuity. The
perimetric protocol was approved by the Institutional Review Board at University of California, Irvine, and informed consent was obtained from
all subjects.

Experimental Design. Each subject underwent two fMRI scan sessions, which
involved collecting 1 T1-weighted anatomical volume, 2 T1-weighted
plane anatomic scans, and 16 functional visual field mapping scans (moving
bar stimulus) under both photopic (luminance = 140 cd/m²) and scotopic
(luminance = 0.003 cd/m²) conditions (38 scans per condition). Our data
analysis used pRF modeling to estimate the visual field map organization and
pRF sizes and centers (22) (SI Materials and Methods).

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and Applications, eds apaegaeoung DY, Smirnakis SM, Christopoulos G (InTech,
Supporting Information

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SI Materials and Methods

Anatomical Data. Scanning was conducted at the University of California, Irvine, on the 3T Philips Achieva MR Scanner with an eight-channel sensitivity encoding (SENSE) imaging head coil. One high-resolution whole-brain anatomical dataset was acquired for each subject [T1-weighted 3D magnetization-prepared rapid acquisition with gradient echo (MPRAGE), 1-mm³ voxels, repetition time (TR) = 8.4 ms, echo time (TE) = 3.7 ms, flip = 8°, SENSE factor = 2.4]. We used custom software (mrVista from Stanford University; white.stanford.edu/software) (1) to segment white matter, which was hand-edited to minimize segmentation errors. Gray matter was grown from the segmented white matter to form a 2- to 4-mm layer covering the white matter surface. The cortical surface was then represented as a mesh at the white-/gray-matter border, which was used to render a smooth 3D cortical surface and flatten the cortical representation for visualization of the visual field maps (2).

In addition, one anatomical in-plane image was acquired before each set of functional scans with the same slice prescription as the functional scans but a slightly higher spatial resolution (1 × 1 × 3-mm voxels). These anatomical image slices were physically in register with the functional image slices to align the functional data with the high-resolution anatomical data. This alignment was performed by first, a manual coregistration and then, a semi-automated 3D coregistration algorithm, which used a mutual information method (3, 4).

Functional Data. The same 3T scanner was used to collect the functional MR data, with ~35 axial slices oriented approximately parallel to the calcarine sulcus (T2-weighted, gradient echo imaging, TR = 2 s, TE = 30 ms, flip = 90°, SENSE factor = 1.7, reconstructed voxel size of 1.875 × 1.875 × 3 mm, no gap). We analyzed fMRI data using the same custom Matlab mrVISTA software. For each subject, data in each fMRI session were analyzed voxel by voxel with no spatial smoothing. The mean value of the blood oxygen level-dependent (BOLD) signals was examined for potential head movements. No motion correction algorithm was applied here, because all scans had less than one voxel of head motion. The time series from each scan was high-pass filtered to remove low-frequency sources of physiological noise and averaged together to form one mean time series for each subject, which was then used in the pRF model analysis (5).

Stimulus Presentation. Stimuli were generated using the Psychophysics Toolbox (6) in the Matlab programming environment on a Dell Optiplex desktop. Stimuli were back-projected onto a screen at the head end of the bore of the magnet by a Christie DLV1400-DX DLP Projector (spatial resolution: 1,024 × 768 pixels, refresh rate: 60 Hz). Subjects viewed the display on an angled front surface mirror mounted on the head coil close to their eyes with a viewing distance of ~70 cm. Head movements were minimized with padding and tape. Photopic conditions (maximum luminance = 140 cd/m²) consisted of our standard setup for visual field mapping experiments, with lights of the scanning room turned on and a neutral density filter over the projector’s wave guide. Scotopic conditions (maximum luminance = 0.003 cd/m²) during scanning were created by blacking out all light sources in the scanner room and placing additional neutral density filters over the projector’s wave guide. Subjects were dark-adapted for 35–40 min before any set of scotopic scans and light-adapted for at least 10 min before any set of photopic scans (7, 8). We also verified dark adaptation at the start of each scotopic scan session by testing each subject’s inability to perceive stimuli within the central 2° radius from fixation (i.e., within the rod scotoma).

Visual Field Mapping Stimuli. The moving bar stimulus was comprised of achromatic (mean luminance ~50 cd/m²) dynamic checkerboard contrast patterns (~90% contrast) and spanned a visual field subtending a maximum radius of 11° of visual angle (Fig. 2F). The contrast pattern of the bar aperture consisted of rows that appeared to be moving in the opposite direction to adjacent rows, with each column spanning the length of the bar aperture and each row spanning its width. The bar apertures were displaced in discrete steps every 2 s in synchrony with the fMRI volume acquisition. Modulation of the checkerboard contrast pattern was metameric to modulation of a 500-nm light. The contrast pattern motion created a 2-Hz temporal frequency, and the motion direction changed randomly every 2–3 s. Four bar orientations (0°, 45°, 90°, and 135° from vertical) with two motion directions orthogonal to each orientation were used. This stimulus set produced eight different bar configurations and a total presentation time of 192 s at one cycle per scan. Four mean luminance periods were inserted in the last 12 s of each 48-s period at a frequency of four cycles per scan. To aid fixation under scotopic conditions, subjects maintained fixation on one of two large central crosses, which alternated between spanning either the diagonals from the corners of the field of view or the midpoints of each of the sides of the field of view. The same two alternating fixation crosses were used in both scotopic and photopic luminance conditions. The lines of each fixation cross were roughly 0.5° wide, and they randomly switched between the two positions every 2–4 s as a drifting bar moved passed across the visual field. Subjects attended to these moving bar apertures and responded with a button press to an intermittent, subtle change in the motion direction of the checkerboard pattern (not in sync with the visual stimulus position changes or mean luminance periods).

Assessment of Fixation Stability. Subjects were required to fixate their eyes under photopic conditions, where the fixation cross is clearly visible at the center of vision, and scotopic conditions, where the center of the fixation cross overlaps the rod scotoma. As a result, we checked the possibility that differences in fixation stability may have affected our results. Previous work modeling the effects of eye movements shows that eye movements would have relatively uniform effects across the entire visual field and that the measurements of visual field maps using pRF modeling remain relatively unaffected by artificial or central scotomas that could produce a small to moderate range of eye movements (9–12). Each of our effects is only over a portion of the visual field (either central or peripheral eccentricities). As a precaution, our fixation stimuli were specifically designed to minimize differences in eye movements and fixation difficulty between conditions by being large and extending to the borders of the field of view (13). Additionally, the fixation cross changed from a large X shape to a large + shape at jittered intervals to diminish consistent effects of fixation stability and additional aid fixation. Our subjects also underwent extensive training and practice with our stimuli under both photopic and scotopic conditions as well as other many other studies that require fixation. Subjects who are experts at fixating, such as our subjects were, perform better than nonexperts at fixation tasks (9, 14).

Eye tracking was provided by an MRI-compatible long-range remote tracking system (Applied Science Laboratories). Any
scans with excessive eye movements were discarded from additional analysis (<1% of all scans). To confirm that eye movements did not differ between photopic and scotopic conditions, additional analyses were performed. The degree to which eye movements occurred during a scan can be measured as the variability of BOLD modulation in the eyes (Eyes ROI) (9). If the SD of the BOLD signal in the Eyes ROI across subjects between photopic and scotopic conditions was significantly different, it would indicate that there were differences in eye movements (Fig. S4 and Table S1). However, a paired samples t test reveals no difference between photopic and scotopic conditions [t (2) = −0.318, P = 0.781], indicating that eye movements did not significantly vary between conditions and thus, did not significantly contribute to our results. For comparison, scotopic eye movements were compared with an eye saccade task, where subjects were asked to make a series of saccadic eye movements from fixation to positions in the midperiphery of the presently measured visual field. As expected, a paired samples t test revealed a significant difference between scotopic and eye saccade scans [t (2) = −5.070, P = 0.037], indicating that eye movements were not a significant factor in scotopic scans.

To rule out the possibility that the difference between scotopic and eye saccade scans in the Eyes ROI was caused by some other factor unrelated to eye movements, we compared the SD of BOLD modulation in V1 between the conditions (Fig. S4 and Table S1). As expected, a paired samples t test reveals no difference between scotopic and eye saccade scans [t (2) = −2.339, P = 0.144], indicating that the difference observed between the scans in the Eyes ROI is related to the difference in eye movements between the conditions. Similarly, there was no difference between photopic and scotopic scans in the SD of BOLD modulation in V1, which was revealed by a paired samples t test [t (2) = 0.574, P = 0.624]. In sum, although it was unlikely that differences in fixation may have influenced our results, these measurements confirm that there was no significant difference in eye movements between luminance conditions.

**pRF Modeling Analysis.** We used the pRF modeling method to estimate the V1, V2, V3, hV4, and VO-1 visual field maps and pRFs. The pRF for a particular voxel is defined as the region of visual space that preferentially activates that cortical site (complete details are in ref. 5). In each voxel, the BOLD response to our stimuli was predicted using a 2D Gaussian pRF model with parameters of preferred center location (x, y) and size (σ); The predicted fMRI time series was calculated by convolving the model pRF with the stimulus sequence and BOLD hemodynamic response function (15, 16). The pRF parameters for each voxel minimized the sum of squared errors between the predicted and observed fMRI time series for the bar apertures.

Each voxel was independently evaluated in terms of the variability of the time series explained by the best-fitting model. In the typical traveling wave measurement of visual field maps, each voxel is independently assigned a coherence value, which is equal to the amplitude of the BOLD signal modulation at the stimulus frequency divided by the square root of the power of the BOLD modulation at all other frequencies except the first and second harmonics. pRF modeling uses percentage variance explained as a primary measurement of goodness of fit; here, we convert to coherence values for comparison with typical phase-encoded traveling wave visual field mapping studies (5, 17–19). Only voxels with coherence values exceeding 0.20 corresponding to that voxel’s peak response to the stimuli presented were considered for additional analysis (20, 21). We have measured the noise in visual cortex using baseline measurements in early visual cortex with a combination of approaches, including photopic and scotopic visual stimuli (bars, wedges, and rings) with traveling wave and pRF modeling methods. Our measurements show maximum baseline noise levels for coherence (from traveling wave measurements) of 0.15 and variance explained (from pRF modeling measurements) of 0.624.

Eccentricity \( \sqrt{(x^2 + y^2)} \) and angle \( \tan^{-1}(y/x) \) were derived from the 2D Gaussian models and are plotted on the unfolded cortical surface measured in each subject (Fig. 2 and Fig. S2). The pRF model prediction assumed full stimulation of the visual field out to 11° radius; the model was not constrained by the expected presence of the rod scotoma (11). The sizes of pRFs (σ in degrees of visual angle) are presented as a function of eccentricity collapsed across subjects (Fig. S7).

**Definition of Visual Field Maps.** We define a visual field map as a complete map by the following criteria: (i) it represents a complete contralateral hemifield of visual space (visual field maps vary in the degree to which their pRFs extend into ipsilateral space, and therefore, we ignore the extent of ipsilateral representation in this definition; also, we group the discontinuous V2 and V3 dorsal/ventral quarterfields into complete hemisphere representations), (ii) both a polar angle and an eccentricity representation must be present, and (iii) the polar angle and eccentricity representations are orthogonal to one another (22). When presented with reversals in polar angle or eccentricity representations, which denote the borders between visual field maps, we split the reversal evenly between the two maps. Here, we follow widely established conventions for the definitions of the posterior and ventral occipital visual field maps V1, V2, V3, hV4, and VO-1 (Fig. 2 and Fig. S2) (19, 21, 23–25).

**References**


Fig. S1. pRF model fits for a single typical V1 voxel at the rod scotoma edge. The measurements for A and B were taken under photopic conditions from the same voxel at the edge of the rod scotoma in V1 of subject 3, whereas C and D were under scotopic conditions. A and C show representations of visual space and the portion of it represented by the population of neurons in this V1 voxel (the result of the pRF model fit). Red/yellow colors depict the regions of visual space represented by the example voxel. Green color represents no response. B and D show the percentage of BOLD modulation over time. The black dotted lines represent actual data; the solid blue lines represent the pRF model fit. The variance explained (Var. Expl.) by each model fit is displayed above each graph. Note the correspondence between the pRF model fit and the data in each case. dva, Degrees of visual angle.

Fig. S2. Eccentricity maps in photopic and scotopic conditions. (A–F) Pseudocolor overlays on a flattened representation of occipital cortices from three subjects represent the eccentricity position in visual space that produces the strongest response at that cortical location. Data for subject S2 are presented in Fig. 2. (A, C, and E) Photopic measurements. (B, D, and F) Scotopic measurements. Boundaries of visual field maps are depicted with dotted (boundaries along polar angle reversals) and solid (boundaries along eccentricity reversals and the edge of measurement) black lines. Coherence ≥ 0.20. (Scale bar: 1 cm along the flattened cortical surface.) (G, Upper) Color legend represents the visual field from 0° to 11° radius. (G, Lower) Moving bar stimulus for visual field map and pRF measurements comprised a set of contrast-reversing checkerboard patterns at eccentricities from 0° to 11° radius. One frame is shown for the bar stimulus sequence. Four bar orientations (0°, 45°, 90°, and 135° from vertical) with two motion directions orthogonal to each orientation were used, producing eight different bar configurations. (H, Upper) Anatomical orientation legend. (H, Lower) Inflated 3D representation of a medial view of a representative left hemisphere from which all data were taken. The black dotted line indicates the region near the calcarine sulcus of the occipital lobe, where the maps were measured.
Models to explain ectopic responses in scotoma projection zones (SPZs). (A) Model 1 assumes that ectopic responses of neurons with RFs in the SPZ are not an aspect of the normal RF organization of the visual system but happen only after extensive cortical reorganization. Model 2 assumes that ectopic responses of neurons with RFs in the SPZ are the expected response of the normal RF organization of the visual system. The key time point to differentiate between these two models is immediately after the onset of a scotoma, which for all scotomas induced by damage, is contaminated by stunning of cells in and around the lesion site. The rod scotoma is a naturally occurring, reversible scotoma that can be applied noninvasively to a primate without inducing damage and rendering immediate measurements of RFs interacting with the SPZ uninterpretable. (B–E) Potential confounds in measurements of long-term reorganization and short-term adaptation. Upper represents the RF of a cortical neuron or the pRF of a single voxel, which is completely eclipsed by a retinal scotoma. Lower represents the RF of a cortical neuron or the pRF of a single voxel, which is partially eclipsed by a retinal scotoma. In each panel, solid lines indicate an active cortical (p)RF, and dotted lines indicate a silenced, original cortical (p)RF. B represents the original cortical (p)RFs, with dots as the preferred centers and circles as the spreads. (C) Here, both (p)RFs are silenced because of a combination of the retinal scotoma and the adjacent retinal stunning, which occurs in studies involving the creation of a direct lesion to the retinae (1–3). This combination of scotoma and retinal stunning effectively broadens the silenced cortical region. D represents the new effective cortical (p)RFs after recovery from retinal stunning (~2 wk in retinal lesion studies using photocoagulation) but before extensive long-term reorganization. Note that (Upper) the totally eclipsed cortical (p)RF remains silenced, whereas (Lower) the partially eclipsed (p)RF is active for the portion of the p(RF) that was silenced by retinal stunning. Such recovery from retinal stunning is impossible to differentiate at this point from long-term cortical reorganization. In addition, D also depicts the immediate measurements of scotomas, such as the rod scotoma presented here or artificial scotomas (4), which do not involve retinal stunning. This type of short-term (p)RF change must be accounted for in studies of long-term reorganization. E represents examples of potential long-term reorganization for these cortical (p)RFs. In Upper, the cortical (p)RF that was initially fully covered by the scotoma has now shifted to represent new regions of visual space. However, in Lower, this same shift into new territory cannot be distinguished by these (p)RF measurements from the measurements of the expected leftover (p)RF seen in D, Lower.

Fig. S4.  Eye movement measurements. Each graph represents the BOLD signal modulation in percentage over time for one scan for an individual subject. Measurements for A–C are taken from (D) the Eyes ROI. In general, the more that the subjects moved their eyes, the higher the variations in BOLD as measured by the SDs for measurements from the Eyes ROI. A paired samples t test reveals that there is not a significant difference in the SD between (A) photopic and (B) scotopic conditions [t (2) = −0.318, P = 0.781], indicating no difference in eye movements (Table S2). For comparison, C represents the BOLD variation in a task where subjects were required to make a series of eye saccades, which has significantly higher SD than in B [t (2) = −5.070, P = 0.037]. Note that a different scale is used for C than the other graphs; 20% BOLD modulation is indicated for scale comparison. Measurements for E–G are taken from (H) bilateral V1, which should not vary between conditions, even if eye movements did. A paired samples t test reveals no difference between (E) photopic and (F) scotopic conditions in the V1 ROI [t (2) = 0.574, P = 0.624] or (G) scotopic and eye saccade conditions [t (2) = −2.339, P = 0.144] (Table S2), ruling out task differences unrelated to eye movements between the eye saccade and scotopic conditions in (A–D) the Eyes ROI comparisons.
Fig. S5. Coherence under photopic and scotopic conditions. (A–E) Each graph displays coherence for photopic (dark gray lines with diamonds) and scotopic (light gray lines with squares) conditions in a single visual field map as a function of preferred eccentricity under photopic conditions averaged across subjects. (A) V1 coherence. (B) V2 coherence. (C) V3 coherence. (D) hV4 coherence. (E) VO-1 coherence. Note the relatively greater drop in coherence for scotopic relative to photopic conditions in the central eccentricities of each map. Error bars represent SEMs. (F–J) Each graph displays the coherence difference (scotopic – photopic) for each map for each individual subject. (F) V1 coherence difference. (G) V2 coherence difference. (H) V3 coherence difference. (I) hV4 coherence difference. (J) VO-1 coherence difference. The legend indicates the color and marker shape for each subject. Error bars represent SDs.

Fig. S6. Shifts in eccentricity representation across photopic and scotopic conditions. (A–E) Each graph displays eccentricity representation for photopic (dark gray lines with diamonds) and scotopic (light gray lines with squares) conditions in a single visual field map as a function of preferred eccentricity under photopic conditions averaged across subjects. (A) V1 pRF shifts. (B) V2 pRF shifts. (C) V3 pRF shifts. (D) hV4 pRF shifts. (E) VO-1 pRF shifts. Note that each map shows significant shifts outward from the rod scotoma in the central eccentricities. Error bars represent SEMs. (F–J) Each graph displays the ectopic eccentricity shift for each map for each individual subject. Positive numbers indicate shifts away from the scotoma (more eccentric from fixation). (F) V1 shift. (G) V2 shift. (H) V3 shift. (I) hV4 shift. (J) VO-1 shift. The legend indicates the color and marker shape for each subject. Error bars represent SDs.
Fig. S7. pRF size (σ) measurements across photopic and scotopic conditions. (A–E) Each graph displays pRF size for photopic (dark gray lines with diamonds) and scotopic (light gray lines with squares) conditions in a single visual field map as a function of preferred eccentricity under photopic conditions averaged across subjects. (A) V1 pRF sizes. (B) V2 pRF sizes. (C) V3 pRF sizes. (D) hV4 pRF sizes. (E) VO-1 pRF sizes. Error bars represent SEMs. (F–J) Each graph displays the pRF size (σ) percentage change for each map for each individual subject. (F) V1 pRF size change. (G) V2 pRF size change. (H) V3 pRF size change. (I) hV4 pRF size change. (J) VO-1 pRF size change. The legend indicates the color and marker shape for each subject. Error bars represent SDs.
### Table S1. Eye movement measurements

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<th>Subject</th>
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<td>Scotopic fixation</td>
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<tr>
<td>S1</td>
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<td>2.88</td>
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<td>1.67</td>
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<td>Average</td>
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<td>0.20</td>
<td>8.78</td>
<td>0.68</td>
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Rows for S1–S3 represent measurements of BOLD modulation from individual subjects. Average represents their average. Means are average SDs across scans. Data from the Eyes ROI (Fig. S4D) and the V1 ROI (Fig. S4H) are shown. Saccadic eye movement scans were not available for subject 2 for comparison here. In general, the more that the subjects moved their eyes, the higher the variations in BOLD as measured by the mean SDs (means) for measurements from the Eyes ROI. A paired samples t test reveals that there is not a significant difference in average SDs between photopic and scotopic conditions in the Eyes ROI \[ t(2) = -0.318, P = 0.781 \], indicating no difference in eye movements. For comparison, the average SD in the Eyes ROI is significantly higher for an eye saccade task than scotopic conditions \[ t(2) = -5.070, P = 0.037 \]. A paired samples t test reveals no difference between photopic and scotopic conditions in the V1 ROI \[ t(2) = 0.574, P = 0.624 \] or scotopic and eye saccade conditions \[ t(2) = -2.339, P = 0.144 \], ruling out task differences unrelated to eye movements between the eye saccade and scotopic conditions in the Eyes ROI comparisons.

### Table S2. Results of statistical analyses

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All F values and their associated P values reported are the results of multivariate ANOVAs with one hypothesis degree of freedom and three error degrees of freedom. Because one test was performed per hypothesis, no correction for multiple comparisons was necessary. Thus, the threshold for statistical significance was 0.05 in all cases. See Results for more details.