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Peripheral Color Vision and Motion Processing

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Abstract

A demonstration of the vividness of peripheral color vision is provided by arrays of multicolored disks scaled with eccentricity. These demonstrations are designed to correct the widespread misconception that peripheral color vision is weak or non-existent. In fact, both small and large disks of color scaled with eccentricity demonstrate that color perception is just as strong in throughout the periphery as in the fovea, under appropriate viewing conditions. Moreover, further demonstrations with cone-isolating motion stimuli indicate that motion perception is undiminished with rod activation silenced by the choice of colors with equal activation strengths for the rod spectral sensitivity.

Introduction

In designing next-generation visual displays for entertainment and commercial applications, it is important to have a good understanding of the full capabilities of human visual processing. There is a widespread misconception even among vision scientists, and hence the population in general, that the high cone density in the fovea implies that color vision is restricted to the fovea, and conversely that the high density of rods in the periphery implies a lack of color vision in the periphery. For example, the Wikipedia article on peripheral vision says: “rod cells are unable to distinguish color and are predominant at the periphery, while cone cells are concentrated mostly in the center of the retina, the fovea.” (https://en.wikipedia.org/wiki/Peripheral_vision).

Eccentricity Scaling

In fact, however, both historical [1] and more recent [2,3] measurements of photoreceptor densities indicate otherwise. Despite the high concentration of cones in the fovea, even the central 5° of the retina contains only about 1% of the con population, about 50,000 cones, while the remainder of the total cone population of about 5 million cones are distributed throughout the peripheral retina with an average density of about 4,000 cones/mm^2 (beyond about 10° eccentricity). Since the cone inner segments act as their light-catching apertures, and since their inner segment diameter is about 9 mm, this density in the periphery implies that the light-catching area of the cones is about 0.32 mm^2 per mm^2 of peripheral retina, while the rod light-catching area accounts for most of the rest. Thus, about 1/3 of the peripheral retina should be considered to support color vision [4], with an area of about half the light-catching area of the rods.

The mapping from retina to cortex can be approximated as a linear scaling from the fovea to the periphery, particularly for the cortical mappings of V2 and V3 [5]. To project from the retina to equal regions of early visual cortex, therefore, the stimuli should be scaled in proportion to eccentricity, and studies of peripheral color processing should use such scaling in order to assess the cortical capabilities of color processing. Indeed, with suitable areal scaling, color discrimination can be equated at all eccentricities [6].

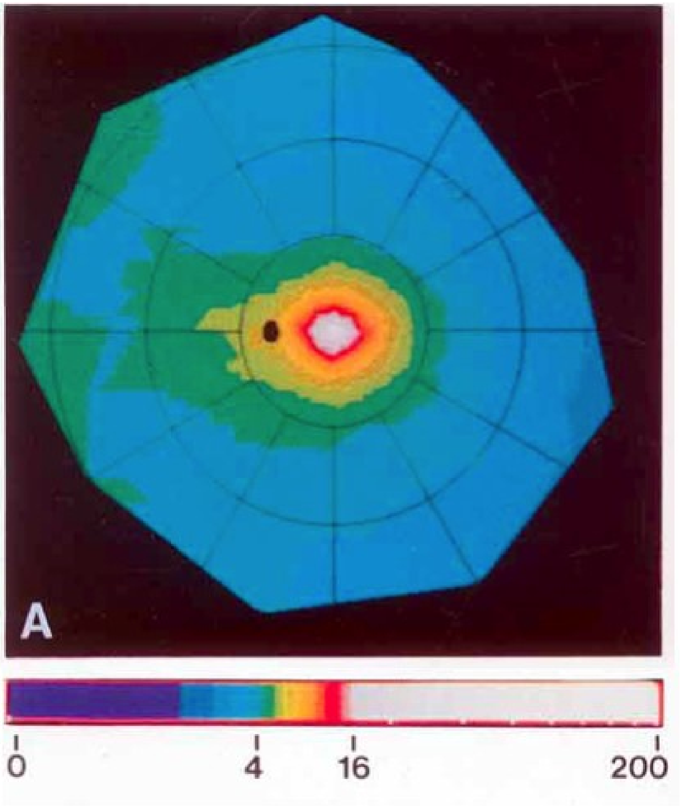

Figure 1. *Map of the retinal distribution of the cones in the human eye (in thousands/mm2; see color bar). Note extensive regions of peripheral retina colored in blue out to the far periphery, indicating cone densities of the order of 4000/mm^2 throughout the retina. From Curcio et al. (1990), with permission.*

Demonstration Images

These properties are indicated by the demonstration image of Fig. 2, which should be viewed at a distance of about 3 inches, so that the outer rim of the figure projects to about 45° eccentricity. This figure shows an array of multi-colored ‘balloons’ scaled to stimulate about 1 cm^2 of visual cortex at each eccentricity. If peripheral color vision had weaker color vision, the colors when viewing Fig. 2 should appear desaturated in the periphery relative to those in the center, but inspection with fixation at the central point verifies that they do not when the stimuli are scaled in proportion to eccentricity, although the colors become much less salient when the size is held constant (horizontal line of dots in Fig. 2). The key factor in the displays is scaling the size of the colored patches in proportion with eccentricity, which is a good approximation to a uniform cortical scaling such that each color patch projects to a roughly equal area of primary visual cortex.

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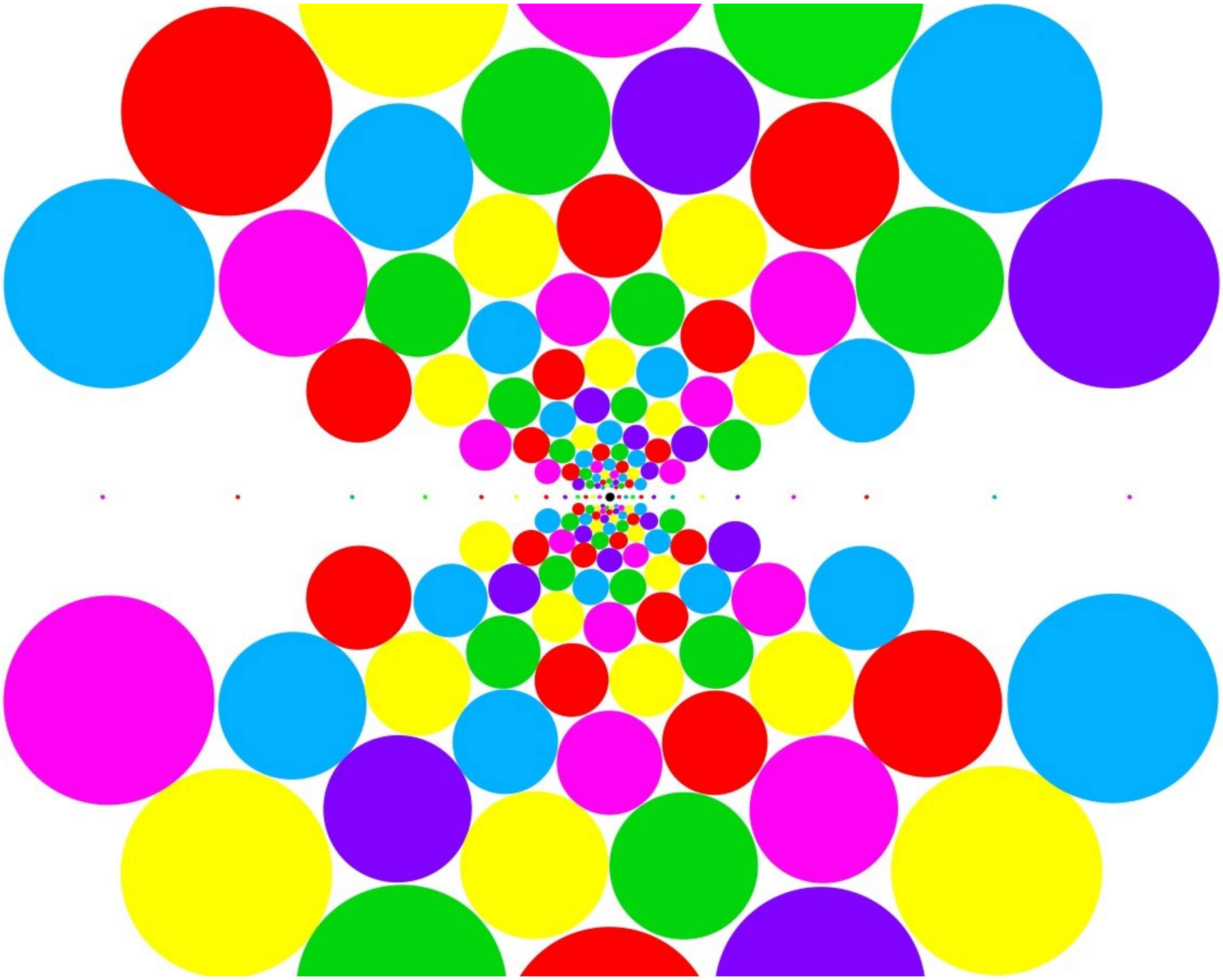

Figure 2. *Array of multicolored disks scaled with eccentricity, with a line of unscaled dots along the horizontal meridian. Fixate the central black dot while viewing from a (close) distance of about 3 inches. The unscaled dots lose their color appearance in peripheral view, while the scaled dots retain their color vividness throughout the field. Modified from [7].*

1 and 25 cortical hypercolumn units at all eccentricities the demo image. (A hypercolumn unit is the minimal area of primary visual cortex encompassing a complete cycle of orientations, ocular dominances and other stimulus properties such as spatial frequency and color selectivity. The geometric organization of the cortex is irregular, so there are no discrete regions corresponding to this notional unit, but it expresses the distance metric of the cortical organization. Each hypercolumn unit encompasses approximately 10,000 neurons in the 6-12 cortical layers. In humans, the natural units of cortical processing characterized by the concept of the 'hypercolumn' are of the order of 2 mm wide in human visual cortex, the disks in Fig. 2 should each stimulate about 25 such units.

If anything the color perception is ***more*** vivid in the periphery, as might be expected from the fact that the cone density decreases at a slower rate than linear reciprocity with eccentricity. In fact, the cone density scales with approximately the -2/3 power of eccentricity out to 20° [8]. Thus, the linear scaling of the disk sizes should result in the stimulation of about 5 times [$(10^{2/3}/10^1)^2$] more cones in areal

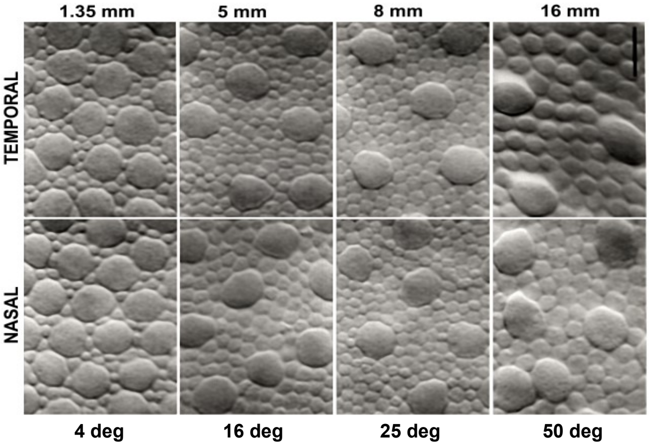

Figure 3. *Electronmicrographs of the rod and cones inner segments at four representative eccentricities. Note that the cone densities are similar beyond 16 °°° eccentricity, and account for up to 1/3 of the peripheral light capture area of the photoreceptors. (from [2] with permission).*

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terms by 20° than 2°, giving scope for cortical processing to account for the extra vividness that is perceptually observed.

Peripheral Motion Processing

A further misconception that is also often held is that peripheral motion processing is mediated by the rod photoreceptors. The first aspect of this misconception is to consider the relative distribution of rods and cones across the retina. This is illustrated in en face electronmicrograph views of the retina from [2] at the level of the inner segments, which are the light-catching elements mechanism for the photoreceptors (Fig. 3).

These images illustrate that the cone inner segments are much larger than the rod inner segments at all peripheral eccentricities, with a diameter of about 9 mm. This means that their light capture area is about 25% of the retinal area, or 1/3rd of that of the rods at the minimum cone density of $4000/\text{mm}^2$, and as much as 33% of the retinal area over large regions of the periphery, or up to ½ of the light capture area may be expected to contribute a large proportion of the signal to motion processing under mesopic lighting conditions, when both rods and cones are active, and the whole of the motion processing signal under photopic conditions, when the rods are saturated or suppressed and no longer contributing any significant differential signals to the cortex.

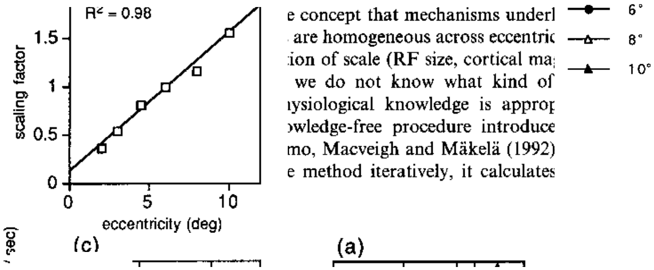

Figure 4. Strength of the motion aftereffect as a function of eccentricity (from [9], with permission). Left panel: cancellation velocities for the motion aftereffect as a function of stimulus size at each of the eccentricities coded at right. Left panel: rescaling the same data to a uniform estimated cortical size in proportion to eccentricity aligns them to a single function.

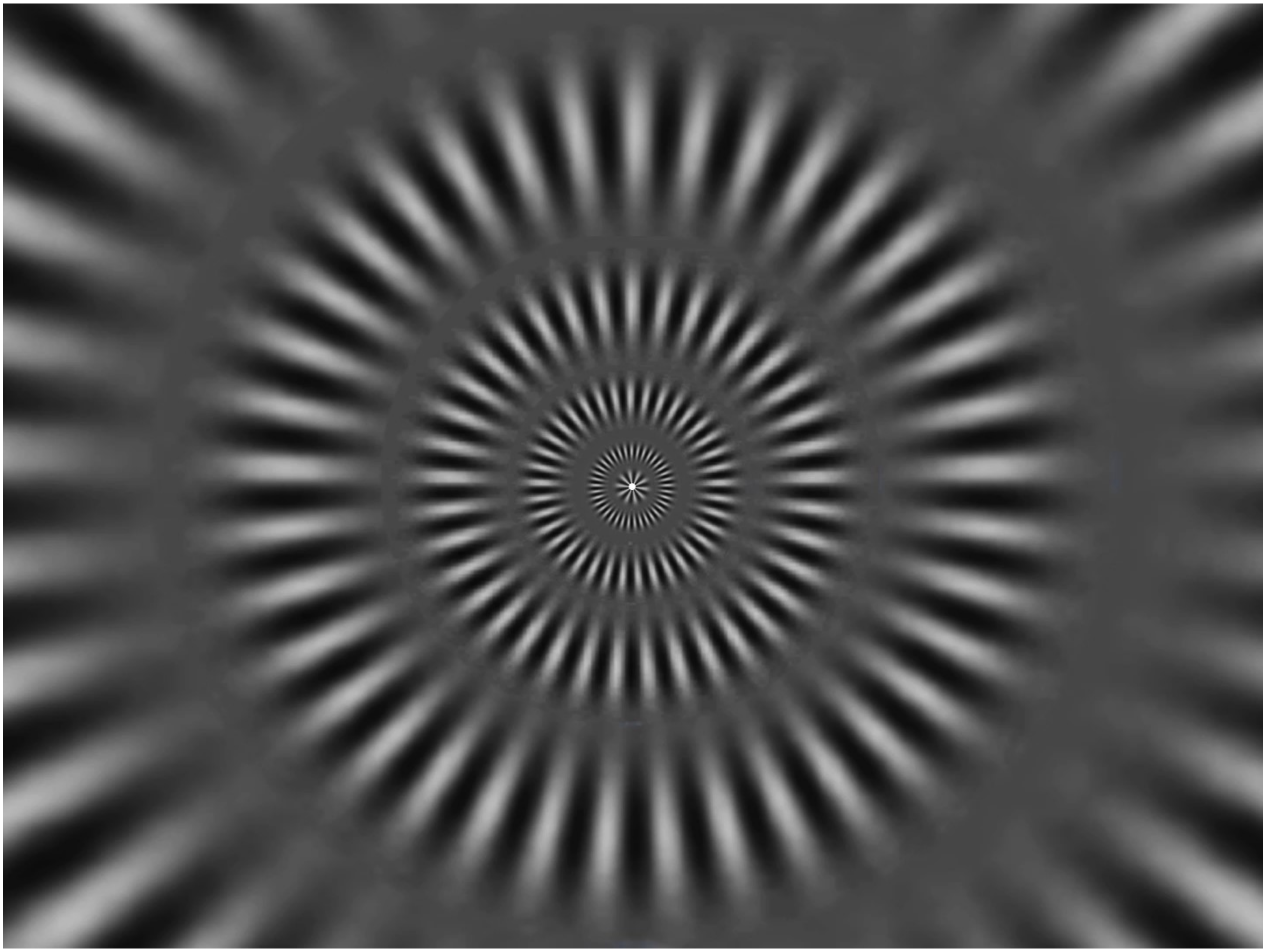

Figure 5. *Demonstration movie illustrating the uniformity of the motion aftereffect for stimuli scaled with eccentricity. Fixate at the center to develop a motion aftereffect, then maintain fixation at the center of the blank field to observe the motion aftereffect on the blank field and then on the static stimuli when they reappear.*

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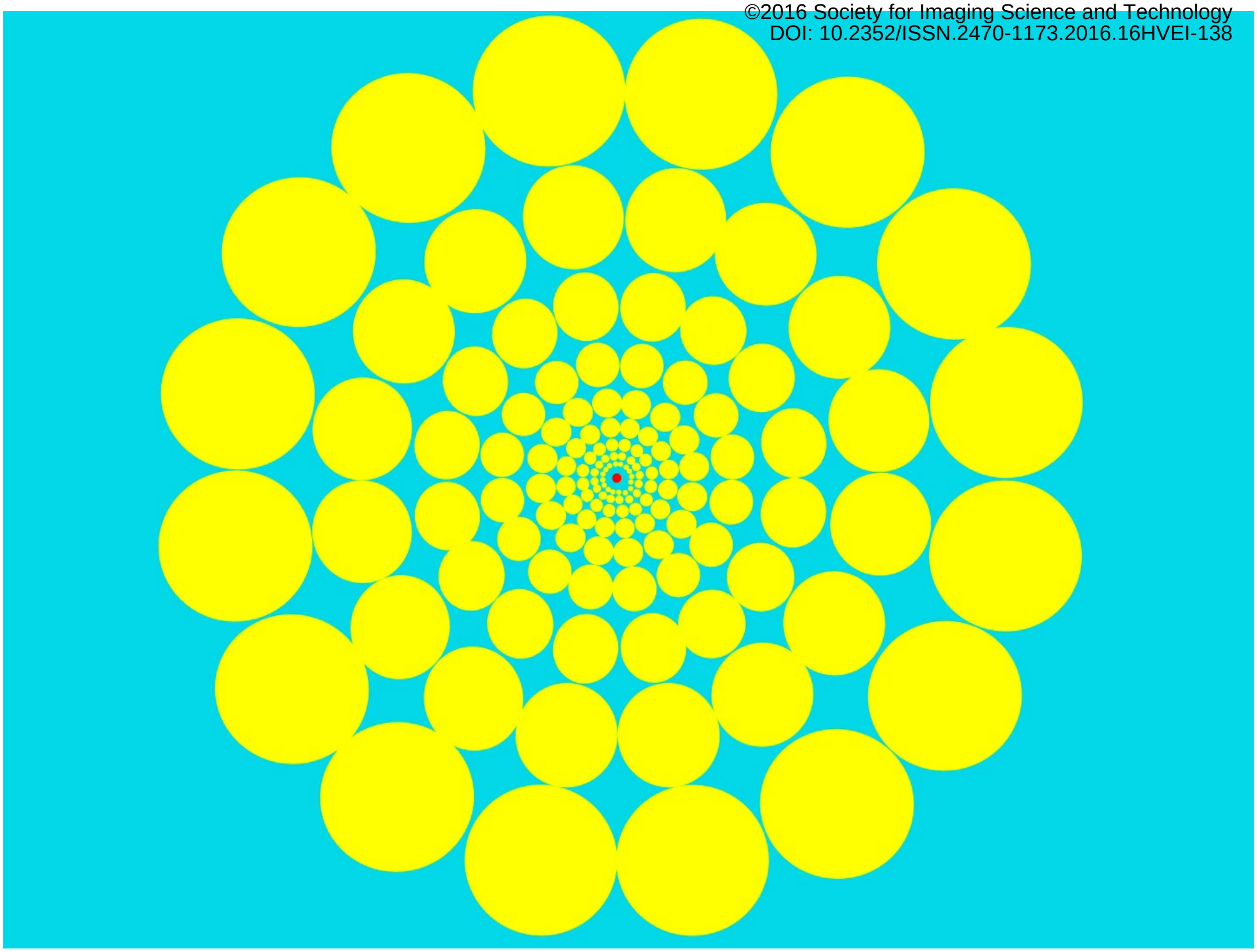

Figure 6. *Demonstration movie illustrating the non-uniformity of the motion aftereffect for equiluminant stimuli scaled with eccentricity. As for Figure 5,f ixate at the center to develop a motion aftereffect, then maintain fixation at the center of the static test field to view the motion aftereffect, which now seems more pronounced at the center. View through a dark filter to verify that the colors contrast is invisible under scotopic (rod-mediated) conditions.*

Motion Aftereffects

The motion aftereffect is a well-established measure of motion-specific processing in the visual system, since the perception of motion may be mediated by a variety of mechanisms, such as change in position, or eye-movement or attentional tracking, but the perception of motion from static stimuli is immune to all these mechanisms and can only be attributed to the perception of motion per se. To assess the relative rod-cone contribution, it needs to be assessed as a function of luminance and eccentricity. Few studies appear to have been conducted on this issue, but Murakami & Shimojo [9] used a cancellation technique to show that the motion aftereffect at photopic retinal illumination levels falls on a uniform function when stimulus size is scaled with eccentricity (Figure 4). This result implies that the motion processing is fully operational under conditions of rod saturation, which is also supported by [10,11].

To demonstrate the uniformity of the motion aftereffect with eccentricity over a wider range than Murakami & Shimojo [9], Figure 5 provides a stimulus of eccentricity-scaled annular targets over an eccentricity range of 8:1. This stimulus may be viewed at the requisite viewing distance to achieve any desired eccentricity range. For example, if viewed at a distance of half the width of the outer moving annulus, it will stimulate out to 45° eccentricity. The first epoch of the video is designed to develop a motion aftereffect, which is first observed on the subsequent blank field and then on the static stimuli when they reappear. Note that the motion aftereffect appears equally strong across multiple eccentricities, although it tends to fluctuate on the static background stimuli, being most noticeable on the ring attended at any given time. (it may also be weaker on the central ring due to optical limitations in reproducing the grating structure.) On a high intensity screen, the images are being viewed under photopic conditions when the rods should be inactivated by rod saturation and cone inhibition.

However, to address the issue of rod saturation more directly, the motion may also be generated with a color combination that is equiluminant to the rods. Figure 6 provides such a demonstration. It should be verified that, if viewed with sufficient neutral density filtering (2.0 log units) to eliminate the color contrast, the stimulus motion is no longer visible. Thus, under the classical duplex interpretation, this condition forms a null stimulus for the rod system, and all motion can only be seen by the cone system. Viewing the

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stimulus under high intensity conditions reveals that the motion aftereffect is now strongest at the center, decreasing with eccentricity. Thus, on the static test field array, the central ring seems to twist more rapidly than the peripheral regions, even though they were subject to the same rotational adaptation stimulus. This decrease toward the periphery under pure color stimulation is consistent with the cone distribution across the retina (see Figure 1), supporting the concept that peripheral motion is adequately mediated by the cone photoreceptor system rather than by the rods (although a rods contribution to the effect from Figure 5 cannot be ruled out if the viewing intensity is in the mesopic range). Taken together, these analyses and demonstrations of Figures 5 & 6 restore the legitimate roles of peripheral cones in both the perception and processing of color and motion out to the far periphery of the visual field.

Acknowledgements

Some of this material has been published in *iPerception* [7].

References

1. Østerberg G.A. Topography of the layer of rods and cones in the human retina. Acta Ophthalmol 13 (Supp. 6) 1-97, 1935.
2. Curcio C.A., Sloan K.R., Kalina R.E., Hendrickson A.E., Human photoreceptor topography. J Comp Neurol 292, 497-523, 1990.
3. Song H., Chui T.Y., Zhong Z., Elsner A.E., Burns S.A. Variation of cone photoreceptor packing density with retinal eccentricity and age. Invest Ophthalmol Vis Sci, 52(10):7376-84, 2011.
4. Williams R.W. The human retina has a cone-enriched rim. Visual Neurosci 6:403–406, 1991.
5. Schira M.M., Tyler C.W., Breakspear M., Spehar B. The foveal confluence in human visual cortex. J Neurosci. 29:9050-8, 2009.
6. Noorlander C., Koenderink J.J., den Ouden R.J., Edens B.W. Sensitivity to spatiotemporal colour contrast in the peripheral visual field. Vision Res. 23:1-11, 1991.
7. Tyler C.W. Peripheral colour demo. i-Perception 6 (6), 2041669515613671, 2015.
8. Tyler C.W. Analysis of human receptor density. In Basic and Clinical Applications of Vision Science. Lakshminarayanan V. (ed.) Doc. Ophthal Proc. 60:63-71, 1987.
9. Murakami I., Shimojo S. Modulation of motion aftereffect by surround motion and its dependence on stimulus size and eccentricity. Vision Res. 35(13):1835-44. 1995.
10. Gegenfurtner K.R., Mayser H.M., Sharpe L.T. Motion perception at scotopic light levels. J Opt Soc Am A Opt Image Sci Vis. 17(9):1505-1, 2000.
11. Vaziri-Pashkam, M., & Cavanagh, P. (2008). Apparent speed increases at low luminance. J Vision, 8(16), 9.1–912. http://doi.org/10.1167/8.16.9.

Author Biography

Christopher Tyler received his undergraduate and graduate training in England and has taught at Northeastern University, Boston, UCLA, UC Santa Barbara and UC Berkeley. He is the author of over 250 publications in visual psychophysics, visual neuroscience and the perceptual analysis of art. He developed the Sweep VEP for estimating infant visual acuity, the flicker visuogram to assess ocular processing deficits in ophthalmic diseases and the corrugation frequency approach to the analysis of stereoscopic processing.