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Do magnocellular and parvocellular ganglion cells avoid short-wavelength cone input?

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Abstract

We recently developed a new technique to measure cone inputs to visual neurons and used this technique to seek short-wavelength-sensitive (S) cone inputs to parasol, magnocellular (MC) and midget, parvocellular (PC) ganglion cells. Here, we compare our physiological measurements of S-cone weights to those predicted by a random wiring model that assumes cells' receptive fields receive input from mixed cone types. The random wiring model predicts the average weights of S-cone input to be similar to the total percentage of S-cones but with considerable scatter, and the S-cone input polarity to be consistent with that of PC cells' surround and of MC cells' center. This is not consistent with our physiological measurements. We suggest that the ganglion cells' receptive fields may have a mechanism to avoid S-cone inputs, as is the case in the H1 horizontal cells. Previous reports of S-cone inputs, in particular substantial input to MC cells, are likely to reflect variation in prereceptoral filtering and/or the failure to correct for variation in macular pigment.

Keywords: Random wiring, S-cone weight, S-cone polarity, Receptive field

Introduction

In the primate visual system, the outputs of the three types of cones (long- (L), middle- (M), and short- (S) wavelength sensitive) are combined to give additive and opponent cone signals (L+M, L−M, and S−(L+M)), before being transmitted to the higher centers of the brain. The specificity of the combination of the cone signals is relevant to retinal development, to retinal circuitry, and to the efficiency of visual information transmission. In this paper, we consider whether the lack of S-cone input to midget, parvocellular (PC) and parasol, magnocellular (MC) ganglion cells that we measured (Sun et al., 2006) can be explained by a random wiring model, or whether it requires a process in which connections from S cones to these cells are avoided during retinal development.

In physiological measurements of lateral geniculate nucleus (LGN) neurons, Derrington et al. (1984) estimated cone inputs by finding cells' null planes in an S-, M-, L-cone space. The null planes of PC- and MC-LGN cells scattered around the M-, L-cone plane. This scatter could be due to real S-cone input or to measurement noise. In other studies, Reid and Shapley (2002) estimated cone weights of LGN neurons by measuring a cell's response to L-, M-, and S-cone isolating modulation and found negligible S-cone input to PC and MC cells. However, Chatterjee and Callaway (2002) estimated ~7% S-cone input to MC cells in the LGN with S-cone isolating stimuli. Using a new technique involving measurement of response phase to stimuli modulated around the circumference of cone space, we recently measured cone inputs to ganglion cells (Sun et al., 2006), and found little S-cone input to PC and MC cells. We argued that the new technique permits rapid and precise measurement of cone weights.

The possible absence of S-cone input to ganglion cells has implications for understanding the specificity of retinal wiring, that is, whether ganglion cells receive random or cone-specific input. For midget (PC) ganglion cells, the center must be either M- or L-cone specific since it is derived from a single cone (Polyak, 1941). In theory, these ganglion cells can derive surround inputs randomly from the cone mosaic (Lennie et al., 1991; Mullen & Kingdom, 1996), but experimental evidence suggests surrounds may be cone specific (Lee et al., 1998; Reid & Shapley, 1992, 2002). S cones make up 8–10% of the cone population in the parafovea (Martin & Grünert, 1999). If the random wiring scheme is true, we should expect a mean S-cone input of 8–10% with the same sign as the surround (assuming the center and surround weights are balanced). For parasol (MC) ganglion cells, random cone input would also be conceivable. The center dominates the flicker response, so the average S-cone input estimates derived from physiological recordings are expected to match the polarity of the center.

In this study, we compared our physiological measurements of S-cone inputs to PC and MC cells (Sun et al., 2006) with predic-

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tions from a random wiring model. The signs and weights of S-cone inputs derived from the physiological measurements are not consistent with the model's predictions, which suggests that MC and PC cells' receptive fields may have a mechanism to avoid S-cone input.

Materials and methods

Stimulus and rationale

A detailed description of the apparatus, calibration, and stimuli is given in Sun et al. (2006) to which the reader is referred for a mathematical description of the stimulus, the mode of analysis, and assorted control observations. Briefly, the stimulus was a uniform field, the chromaticity of which was modulated around the circumference of a color circle in a counterclockwise (CCW) or clockwise (CW) direction in one of three color planes: the equiluminant plane, the L- *vs.* M-cone plane, or the L+M *vs.* S-cone plane (Fig. 1). We measured macaque retinal ganglion cells' response amplitude and phase to such stimuli at different temporal frequencies, and estimated each ganglion cell's preferred vector by averaging the CCW and CW response phases (Fig. 1). S-cone inputs to PC cells were estimated from the preferred vector projections in the equiluminant plane, and S-cone inputs to MC cells were estimated from the preferred vector projections in the L+M *vs.* S-cone plane. L- and M-cone input ratios could be estimated from the preferred vector projections in the L- *vs.* M-cone plane.

Model simulation

We simulated S-cone inputs to MC and PC ganglion cells between 4 deg and 8 deg eccentricity using a random wiring model (Fig. 2). The model comprised two stages. In the first stage, 1500 cones formed a jittered hexagonal array with cone–cone distance of about 2 arcmin, as in parafovea. Each cone was randomly assigned to be L-, M-, or S-cone type with the probability of each cone type being proportional to its cone ratio. We kept the total number of S cones at 10% (Martin & Grünert, 1999) but varied the ratio of L and M cones from 1:1, 2:1, to 4:1. The second stage of the model consisted of an array of ganglion cells, with the receptive field of each ganglion cell centered on a cone. Each ganglion cell received mixed cone inputs indiscriminately from all cone types. Its receptive field was simulated by a difference of Gaussian functions for center and surround. To calculate the S-, M-, and L-cone inputs to each ganglion cell, we first multiplied the S-, M-, and L-cone distribution with the cell's two-dimensional (2-D) receptive field to get the weighted cone distribution, and then computed the sum of each weighted cone distribution to get the total S-, M-, and L-cone input. Finally, we normalized the sum of L-, M-, and S-cone inputs to 1.

For PC cells, the model assumed a single cone input to the receptive field center, which is consistent with the anatomical evidence that, in the central 10 deg of retina, a single L or M cone connects to a single midget bipolar cell, which in turn connects to a single midget ganglion cell (Polyak, 1941). The surround Gaussian radius was varied from 1 to 8 arcmin, which included the range of 3–8 arcmin that might be encountered in macaque parafovea based on physiological estimates (Lee et al., 1998). We also assumed balanced center-surround weights, which would produce balanced M- and L-cone opponent inputs, as found in physiological measurements (Derrington et al., 1984; Reid & Shapley, 2002; Sun et al., 2006).

For MC cells, both the center and surround Gaussian radii and their relative weights were variable. Instead of varying the three

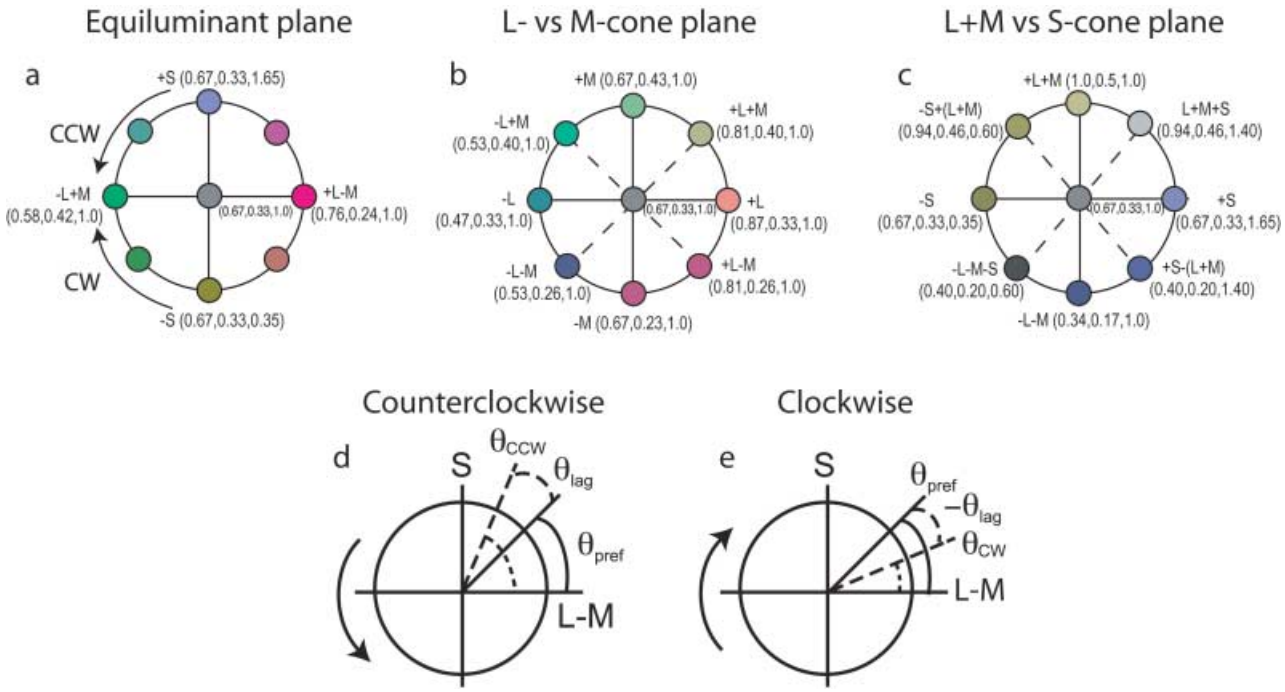

Fig. 1. (a–c) The chromaticity of a uniform field was modulated around a color circle in CW or CCW directions in three color planes. (d–e) A cell's response phase equals the sum of the cell's preferred vector θ_{pref} and a phase delay θ_{lag}. θ_{pref} does not change from CW to CCW modulation, while θ_{lag} changes its sign. Averaging CW and CCW response phases cancels θ_{lag} to reveal the cell's preferred vector θ_{pref}.

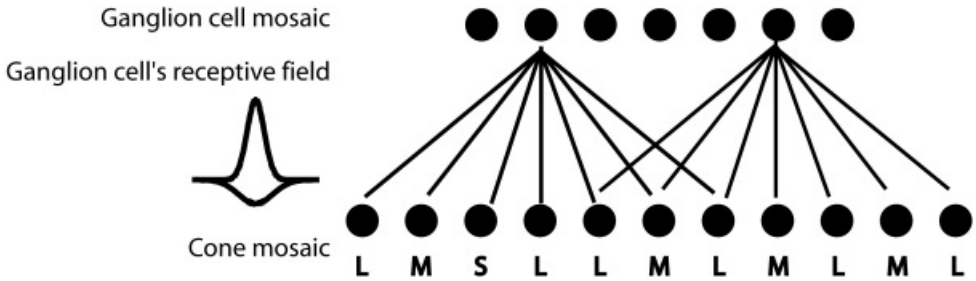

Fig. 2. A 1-D illustration of the random wiring model. Ganglion cells receive mixed L-, M-, and S-cone inputs. Ganglion cell's receptive field is modeled as a difference of two Gaussian functions.

parameters individually, we chose estimates of MC cells' receptive fields and center-surround weights from area summation experiments (Kunken et al., 2005). The center radius varied between 4 and 14 arcmin, the surround radius varied between 12 and 60 arcmin, and the ratio of center-surround weights varied between 4 and 20.

Results

We first summarize our physiological estimates of preferred vectors and our subsequent derivation of S-cone inputs to PC and MC cells. We then show the S-cone inputs to ganglion cells that are predicted by the random wiring model and compare the two. The physiological sample consisted of 44 MC cells and 62 PC cells from the parafovea.

Figs. 3a and b show the distribution of cells' preferred vectors from Sun et al. (Sun et al., 2006). A PC cell that receives only L−M opponent cone input should have a preferred vector at either 0 or 180 deg in the equiluminant plane, while an MC cell that receives only L+M additive cone input should have a preferred vector at either +90 or −90 deg in the L+M *vs.* S-cone plane. The preferred vectors of PC and MC cells cluster around these numbers. S-cone inputs to PC and MC cells, after taking the variation in prereceptoral filtering into account, are shown in Figs. 3c and 3d. The x-axis represents S-cone inputs relative to the polarity of the receptive field center; that is, positive input means the S-cone input has the same sign as the center, and negative input means the S-cone input has the same sign as the surround. S-cone input is specified as the ratio of S/(S+M+L). Both MC and PC cells show negligible S-cone input with the distribution of S-cone weight centered around zero, and signs not specifically related to the center or surround. The S-cone input to PC cells showed a much narrower distribution than that of the MC cells. Since MC cells give only weak responses at low temporal frequencies, the increased scatter in the MC data may be largely due to increased measurement uncertainty rather than a difference in underlying specificity.

Simulated S-cone inputs to ganglion cells from the random wiring model are also shown in Figs. 3c and d. Each curve represents a simulation with different sets of parameters. The results shown are for L-, M-cone ratios of 2:1. Similar results were obtained for other L-, M-cone ratios (1:1 and 4:1) as would be expected, since the S-cone weights should not vary with the relative L- and M-cone ratio. For PC cells, the average S-cone input weight was 10% for all sets of parameters. When the surround radius is small, the distribution of S-cone input tends to peak around zero with large variation (standard deviation (S.D.) $>$ 0.2), while when the surround radius is large, the distribution of S-cone input tends to peak at 10% with smaller variation (S.D. $<$ 0.02). This is because with a small surround radius, a PC cell's receptive field is less likely to cover any S cones, but when it does so, the S-cone weight can be large depending on the location of the S cone(s) relative to the cell's receptive field; while with a large surround radius, the PC cell's receptive field covers many more cones, and the mean S-cone weight tends to be closer to the population average. The polarity of S-cone input is always the same as that of the surround, since the model assumes a single cone input to a PC cell's center and S cones can only be included in the surround. The dark curves in Fig. 3c indicate model simulations with surround radii (4 and 8 arcmin) that are similar to our physiological estimates using area summation. For PC cells, the S-cone inputs predicted by the random wiring model are not consistent with the physiological measurements, which show a distribution of S-cone inputs centered around zero with both positive and negative polarities (same and different signs from the center).

The model simulation for MC cells shows an average S-cone input weight of about 10% for all sets of parameters that we tested. Again, the distribution of S-cone inputs showed large variation (S.D. $>$ 0.07) when the center and surround receptive fields are small, and smaller variation when the center and surround receptive field are big (S.D. $<$ 0.02). The polarity of S-cone input is consistent with that of the center with a few exceptions. For MC cells, the S-cone inputs predicted by the random wiring model are not consistent with the physiological measurements, which center around zero.

Discussion

We measured S-cone inputs to retinal ganglion cells with a novel technique and found negligible S-cone input to MC and PC ganglion cells. This is in contrast with Chatterjee and Callaway's finding of 7% S-cone input to the MC cells in the LGN (Chatterjee & Callaway, 2002). A potential discrepancy between the two studies concerns the calculation of S-cone isolating stimuli. Chatterjee et al. calculated their stimuli based on foveal color matching functions (Stockman et al., 1993*a*; Stockman et al., 1993*b*). As they correctly pointed out, these may not be appropriate for the parafoveal cells of the macaque that were analyzed. However, they suggested that these fundamentals were as good as other fundamentals, since the macaque fundamentals are unknown. This is not the case. The factors that could cause cone fundamentals of human and macaque to differ include the cone spectra themselves, and macular pigment and preretinal absorption differences. Sequences

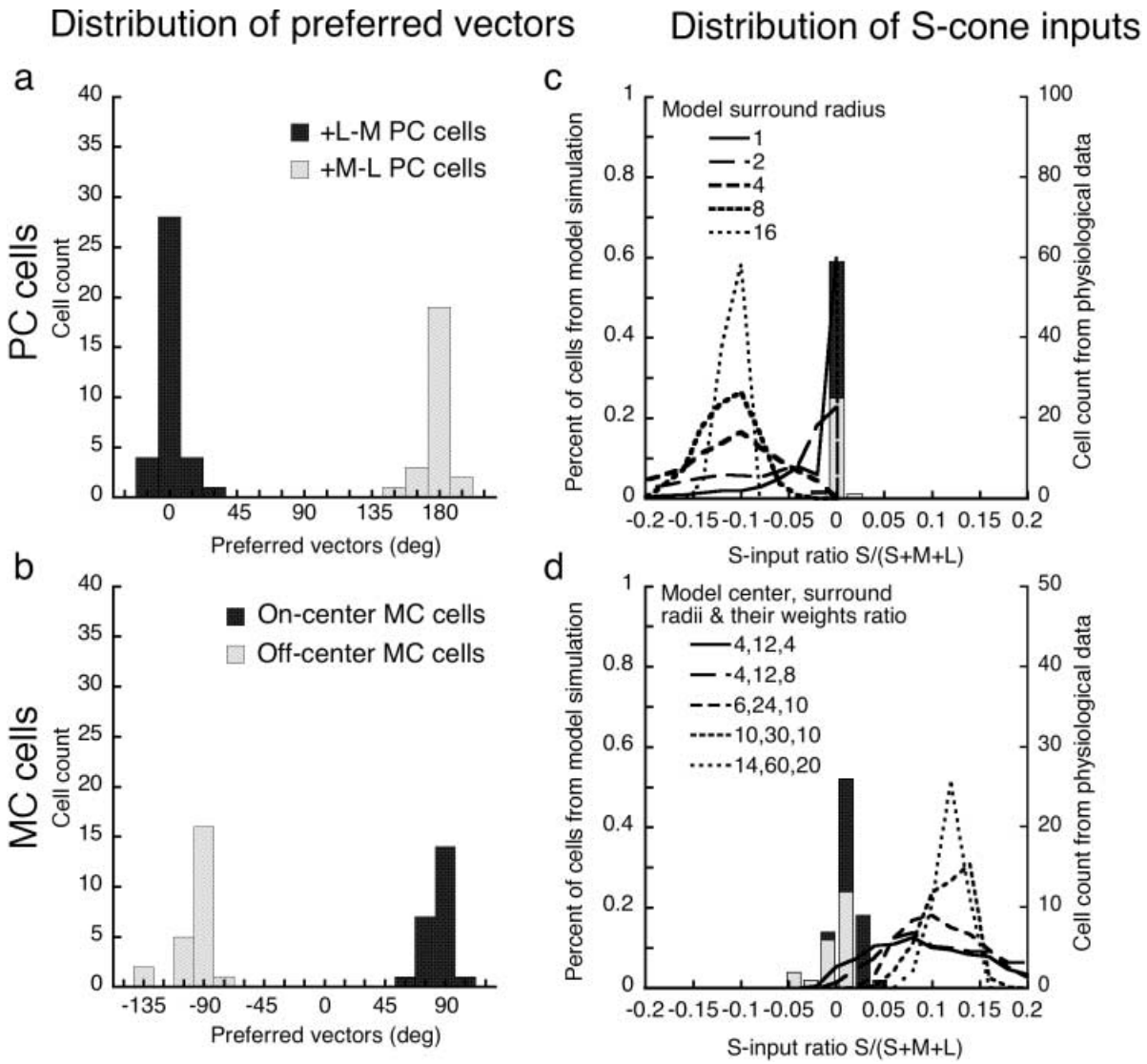

Fig. 3. The distribution of PC and MC cells' preferred vectors (a, b) and the distribution of S-cone input from physiological estimation compared to predictions of random wiring model (c, d). The dark and gray bars represent the physiological data for +L−M and +M−L PC cells (a, c), or On-center and Off-center MC cells (b, d). Lines represent model simulation (L- to M-cone ratio is 2:1). For PC cells (c), the dark thick lines represent model simulation with Gaussian radii similar to the physiological measurements. For MC cells (d), all parameters are consistent with physiological measurements.

of human and macaque opsins are very similar (Ibbotson et al., 1992), and the similarity of macaque cone spectra to human cone fundamentals has been confirmed by suction electrode measurements (Baylor et al., 1987). The macular pigments in human and macaque also have similar spectra (Snodderly et al., 1984). The major factor that could lead to an inappropriate stimulus is their lack of correction for the absence of macular pigment in parafovea. For a regular cathode ray tube (CRT) monitor, we calculated that the failure to correct for lack of macular pigment would lead to a residual ~6% luminance contrast in the putative S-cone isolating stimulus in a direction consistent with center polarity (i.e., non-opponent), as reported by the authors. We also carried out a series of measurements using stimuli calibrated with the foveal cone fundamentals, and these resulted in a spurious S-cone weighting of 6%. Further, the adolescent macaque eye lens is expected to be more transparent at shorter wavelengths (Gaillard et al., 2000) than the lens of a human observer represented by the foveal color matching functions, and this will further increase residual luminance contrast.

In the model, we assumed a random S-cone distribution. There is considerable interspecies variability in the regularity of the S-cone mosaic (Martin et al., 2000). However, outside the foveola the S-cone mosaic in the macaque is quite regular (deMonasterio et al., 1981), with an average spacing of around 5–7 arcmin. For the random wiring model, we tested if the weight of S-cone inputs would be affected by assuming a regular rather than a random array for selected conditions. Mean S-cone weight was little affected, but there was a slight decrease in the width of the distributions.

The minimal S-cone input to PC and MC ganglion cells is relevant to studies of retinal connectivity. In the central 10 deg of retina, the receptive field center of each midget ganglion cell is

thought to be derived from a single cone input (Polyak, 1941), although in reality the situation may be more complex (McMahon et al., 2000). This could lead to the prediction that any S-cone input to PC cells would be from the surround. If the random wiring scheme were implemented as described in Lennie et al. (1991), one might expect a mean surround S-cone input of 8–10%, but we found negligible S-cone input with no association of its polarity with the surround. For MC cells, the center dominates the cell's response to a uniform field flicker, and so physiological estimates of S-cone input to these cells would be expected to be of the same polarity as the center. Our measurements of S-cone inputs to MC cells again are inconsistent with this prediction. The lack of demonstrable S-cone input to both ganglion cell types implies some underlying connectional specificity, and there is a precedent for such selective avoidance of S-cone input in the H1 horizontal cell (Dacey et al., 1996). We do not imply, however, that S-cone input is totally absent—even the H1 horizontal cell makes occasional S-cone contacts—but that it is functionally undetectable or negligible under our measurement conditions.

Our results suggest that the wiring mechanisms for MC and PC ganglion cells may deliberately avoid S-cone inputs. It is unclear however how ganglion cells may derive such cone selectivity. At the photoreceptor level, the electrotonic interreceptor pathway seems to circumvent S-cone pedicles as they have almost no telodendrial gap-junctional connections to neighboring M and L cones (Ahnelt et al., 1990; Hornstein et al., 2004; Li & DeVries, 2004). Beyond the photoreceptor level, the S-cone specific bipolar cells (Mariani, 1984) appear to occupy most of the invaginating synapses of S-cones (Kolb et al., 1997; Kouyama & Marshak, 1997), and they feed into specific nonmidget ganglion cells, primarily the small bistratified cell (Dacey & Lee, 1994). Midget S-cone bipolar cells have not been found. Hence midget (PC) ganglion cells with S-cone centers are unlikely. Parasol (MC) ganglion cells construct their centers from diffuse bipolar cells, of which there are six types (Boycott & Wässle, 1991). Cone selectivity has only been studied anatomically for one type, the DB6 (Lee et al., 2004), which shows no selectivity. It is unknown whether the other types avoid S-cone inputs. If they do, this might account for the lack of S-cone input to the MC cell center, which is likely to be fed by the diffuse bipolar system. Additionally, it has been proposed that the surround of MC cells derives from H1 horizontal cells (McMahon et al., 2000). Both these factors would be consistent with minimal or no S-cone input for this cell type. The lack of S-cone input to PC cells' surround argues against the indiscriminate model of Lennie et al. (1991). However, it could be possible to consider a random wiring scheme by which the surround were derived solely from M and L cones. Such a surround, theoretically, could be derived from H1 horizontal cells, but the widely different surround sizes of MC and PC cells (B.B. Lee and H. Sun, unpublished observations) make such a common surround mechanism for both MC and PC cells less feasible. It is interesting though that physiological evidence suggests that the H1 cells do demonstrate some degree of wiring specificity (Lee et al., 1998; Reid & Shapley, 1992, 2002), although this need not be complete (Lee, 2004). The mechanism by which S-cone input might be avoided during development is unknown. S-cone opsin expression seems to follow a different time course from the long-wavelength opsins, but the developmental situation is complex (Cornish et al., 2004). In any event, the results suggest a more complex picture than predicted by random wiring models.

Why would the MC and PC systems try to avoid S-cone input? What is the potential benefit for the visual system? From the viewpoint of information processing, the absence of S-cone input to the L+M and the L−M systems leads to the least possible correlation with the S−(L+M) system, and linear operators with the least possible correlation form an efficient information transmission system (Buchsbaum & Gottschalk, 1983). From the viewpoint of visual ecology, isolating the L−M system from S-cone inputs may also be helpful for the visual system to detect reddish-yellowish fruit from the greenish foliage background (Parraga et al., 2002). In a single scene, the color of leaves varies along the yellowish-bluish color axis between sunlight and skylight (Taylor & Kerr, 1941), and thus absence of S-cone input means that such variation does not provide distracting noise to the L−M system. In addition, S-cone signals can be spatially degraded due to chromatic aberration at short wavelengths, which may make such inputs disadvantageous for high spatial frequency systems.

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