Comparison of red–green equiluminance points in humans and macaques: evidence for different L:M cone ratios between species

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The human spectral luminosity function (V_λ) can be modeled as the linear sum of signals from long-wavelength-selective (L) and middle-wavelength-selective (M) cones, with L cones being weighted by a factor of ~2. This factor of ~2 is thought to reflect an approximate 2:1 ratio of L:M cones in the human retina, which has been supported by studies that allow for more direct counting of different cone types in the retina. In contrast to humans, several lines of retinally based evidence in macaques suggest an L:M ratio closer to 1:1. To investigate the consequences of differences in L:M cone ratios between humans and macaques, red–green equiluminance matches obtained psychophysically in humans ($n = 11$) were compared with those obtained electrophysiologically from single neurons in the extrastriate middle temporal visual area of macaques (*M. mulatta*, $n = 5$). Neurons in the middle temporal visual area were tested with sinusoidal red–green moving gratings across a range of luminance contrasts, with equiluminance being defined as the red–green contrast yielding a response minimum. Human subjects were tested under analogous conditions, by a minimally distinct motion technique, to establish psychophysical equiluminance. Although red–green equiluminance points in both humans and macaques were found to vary across individuals, the means across species differed significantly; compared with humans, macaque equiluminance points reflected relatively greater sensitivity to green. By means of a simple model based on equating the weighted sum of L and M cone signals, the observed red–green equiluminance points were found to be consistent with L:M cone ratios of approximately 2:1 in humans and 1:1 in macaques. These data thus support retinally based estimates of L:M cone ratios and further demonstrate that the information carried in the cone mosaic has functional consequences for red–green spectral sensitivity revealed perceptually and in the dorsal stream of visual cortex. © 2000 Optical Society of America [S0740-3232(90)00103-X]

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1. INTRODUCTION

In many respects, the color vision of macaque monkeys is extremely similar to that of humans. Both humans and macaques possess long-wavelength-selective (L), middle-wavelength-selective (M), and short-wavelength-selective (S) cone photoreceptors (with similar respective cone absorption spectra), and both species combine signals from the three cone types in very similar ways (see Ref. 1 for a review). Humans and macaques appear to differ, however, in the relative number of L to M cones (i.e., the L:M cone ratio) in the retinal mosaic. The perceptual consequences of these differences are the focus of this study.

Estimates of L:M ratios in humans and macaques have come from several lines of research. In humans these include estimates from retinally based methodologies, such as microspectrophotometry,[2,3] adaptive optics combined with retinal densitometry,[4] electroretinogram (ERG) flicker photometry,[5] and the quantification of pigment mRNA.[6,7] Although L:M ratios are found to be quite variable across human subjects, these studies generally support a mean L:M ratio of approximately 2:1. In addition to methods that directly count cones or quantify cone signals in the retina, human psychophysical techniques that measure the frequency of stimulating L versus M cones have also provided estimates of L:M cone ratios. The results from a variety of studies testing hyperacuity,[8] frequency of detection and stimulus size effects,[9,10] and two-point foveal thresholds[11,12] suggest an approximate 2:1 ratio of L to M cones in the human eye.

Decades before methodologies were developed to allow direct sampling of L and M cones in the eye, the L:M cone ratio of humans was estimated by modeling of the psychophysically derived spectral sensitivity curve (also referred to as the luminous efficiency function or the V_λ function) as a weighted sum of the psychophysically derived L and M cone fundamentals, with the weighting factor being thought to represent the L:M cone ratio. In other words, this model supposes that luminance is encoded by neural

mechanisms that compute a weighted sum of L and M cone excitations (Refs. 13–16; see Ref. 17 for review). Thus, when two lights are set to be equally luminous—referred to as equiluminance, the weighted sum of L and M cone excitation produced by one color ought to be equal to the weighted sum of L and M cone excitation produced by the other color. Based on this weighted-sums model of human spectral sensitivity, the L:M cone ratio for humans is calculated to be approximately 2:1 and thus in line with retinally based estimates.

By contrast to the situation in humans, macaque L:M cone ratios determined from retinally based techniques such as microspectrophotometry,[18] outersegment recordings,[19] photopigment-transmittance imaging,[20] ERG,[21] and anatomy of the cone pathways[22] support an L:M ratio near 1:1. Thus, despite the overall similarities of color vision between humans and macaques, the differences in L:M cone ratios between species predict differences in red–green spectral sensitivity. In fact, several psychophysical studies in macaques and humans have documented such differences between the two species. Results from experiments testing increment thresholds,[23–25] heterochromatic flicker photometry[26] (HFP), and spatial acuity[27,28] suggest that macaques, as compared with humans, are slightly more sensitive to short wavelengths and less sensitive to long wavelengths. Typically, these studies emphasized the similarity between the two species (e.g., Refs. 26 and 29), most likely to justify the use of macaques as a model for human color vision. For this reason these earlier studies did not attempt to model the L:M cone ratio of macaques on the basis of their spectral sensitivity.

To further investigate the functional consequences of differential L:M cone ratios between humans and macaques, we compared the relative sensitivity to red versus green lights in the two species. To this end, red–green equiluminance points were obtained in human ($n = 11$) and macaque (*M. mulatta*, $n = 5$) subjects. For our human subjects, equiluminance points were obtained psychophysically, by a minimally distinct motion technique. For our macaques, we used a neural metric of red–green equiluminance. Specifically, we obtained equiluminance points from individual neurons in the middle temporal visual area (area MT), which is part of the dorsal stream of extrastriate cortex. We chose to employ this neural metric from area MT for two reasons. First, area MT is known to be driven largely by activity originating in the magnocellular subcortical division of the visual system. Because magnocellular cells are known to receive additive (i.e., L + M) input, they (and the neurons they project to) are the likely substrate for the putative luminance mechanism. Second, in previous studies we have shown a close correspondence between an individual macaque's neural equiluminance in area MT and the behavioral equiluminance point determined for that macaque,[30] thus demonstrating that area-MT equiluminance can be used to infer behavioral equiluminance.

The human and macaque equiluminance points obtained in the present study were used to derive estimates of L:M cone ratios in the two species. The values obtained from this analysis support a significantly higher L:M cone ratio in humans as compared with macaques and are quantitatively in agreement with retinally based estimates. These data thus demonstrate that, for both humans and macaques, the relative number of L to M cones in the eye has functional consequences for red–green spectral sensitivity revealed perceptually and in extrastriate area MT.

2. METHODS

A. Subjects

Five rhesus monkeys (Macaca mulatta) provided single-unit neurophysiological data for this study {mean age, 10.8 years (yr) ±4.0 [standard deviation (SD)]}. Three of the macaques were obtained from the University of Massachusetts Primate Center. The other two were obtained from the University of California, Davis, Primate Center. All but one was male. The neurons from which we recorded were studied during the course of other experiments, aimed at investigating the strength of chromatic input to motion processing in area MT.[31,32] Protocols for all the experiments were approved by the Salk Institute Animal Care and Use Committee and conformed to U.S. Department of Agriculture regulations and National Institutes of Health guidelines for the humane care and use of laboratory animals. Eleven human subjects (7 females, 4 males) provided psychophysical data for this study [mean age, 30.7 yr ±6.7 (SD)]. Human subjects reported no known color abnormalities in themselves or in their family histories. All the human subjects passed the Ishihara color plate test, ensuring that they were not red–green dichromats (i.e., they had functioning L and M cones).

B. Apparatus

Visual stimuli were generated with a Sgt. Pepper Graphics board (Number Nine Computer Corp.: 640 × 480 pixel resolution, analog RGB output, 8 bits/gun, 60-Hz frame rate) residing in a Pentium-based or AT-class PC. For all the human subjects and two of our macaques (Teiresias and Kimball), stimuli were displayed on a 50.8-cm (20-in.) Sony monitor (Model GDM 2000TC, analog RGB, noninterlaced). The stimuli in these experiments were generated under the charge of CORTEX 5.7 (Laboratory of Neuropsychology, National Institute of Mental Health), which was also used for data acquisition and behavioral control. For three macaques tested in an older study (Lefty, Tutu, and Frisbee), stimuli were displayed on a 50.8-cm (20-in.) Phillips monitor (Model C2064-AS, analog RGB, noninterlaced). Here stimulus generation, data acquisition, and behavioral control operated under the charge of a PDP 11/73 computer. The CIE chromaticity coordinates of the Phillips monitor were as follows: red (0.618, 0.350), green (0.280, 0.605), and blue (0.152, 0.067). For the Sony monitor, the CIE coordinates were red (0.623, 0.343), green (0.285, 0.605), and blue (0.150, 0.065). For both monitors, the voltage–luminance relationship was linearized independently for each of the three guns in the display[33] by means of a PR-650 SpectraColorimeter (PhotoResearch). The PR-650 SpectraColorimeter was also used for spectroradiometric measurements to compute L and M cone excitations produced by our stimuli.

C. Stimuli

Red–green sinusoidal gratings were produced by summing of sinusoidal luminance modulations of the red and the green phosphors, of identical spatial frequency and orientation but 180° out of phase with each other. Rendered in this manner, luminance contrast of the resultant red–green grating is dependent on the mean luminances and modulation depths of the red and the green sinusoids. In these experiments modulation depth was held constant (and identical for the red and the green sinusoids), and luminance contrast in the grating was varied by differential adjustment of the mean luminances of the red and the green sinusoids such that the mean luminance of the resultant red–green grating was held constant. Luminance contrast of the red–green grating is expressed as Modulation Depth $\times$ $[(G_{\mathrm{mean}} - R_{\mathrm{mean}})/(G_{\mathrm{mean}} + R_{\mathrm{mean}})]$. With this metric, luminance contrast can be either positive or negative, depending on which of the two colors is more luminous. By our convention, positive (+) contrast refers to the case in which the green phase of the grating is more luminous than the red. Likewise, negative (−) contrast refers to the case in which red is more luminous than green. Although we did not attempt to precisely isolate the L − M/L + M plane, i.e., the plane that produces no variation in S cone activity, spectroradiometric measurements revealed that our red–green stimuli produced less than 10% modulation and negligible overall activation in S cone photoreceptors (s = ~0.12 units in MacLeod–Boynton chromaticity space, normalized to s = 1.0 for equal-energy white[34]). Because this amount of S cone activation is small, and because S cones are thought not to contribute to luminance (see, e.g., Refs. 35–37, but compare Ref. 38), we assume that S cones are not a factor in our experiments.

Slight differences in color parameters existed between the two studies from which these data were obtained. For experiments conducted on the Sony monitor (in all the human subjects and in two macaques), heterochromatic gratings were set at a mean luminance of 24 candelas per square meter (cd/m^2) and were presented on a yellow background of the same luminance, and the red and the green sinusoids had a modulation depth of 100%. For older experiments conducted on the Phillips monitor (in three macaques), heterochromatic gratings were set at a mean luminance of 10 cd/m^2 and were presented on a black background, and the red and the green sinusoids had a modulation depth of 90%. The results from pilot experiments in our human subjects confirmed that equiluminance settings are not affected by these slight differences in stimulus conditions.

D. Procedures

1. Neurophysiology

Our general procedures for recording action potentials from isolated area-MT neurons of awake fixating macaques have been described in detail previously.[31] Briefly, animals fixated a small (0.3°-diameter) spot of light on the video monitor in the presence of moving stimuli on the display while single-unit responses were recorded from area MT. Receptive-field size, position relative to sulci, and degree of selectivity for direction of motion were all criteria used to establish that our recordings were from area MT. For each isolated area-MT neuron, receptive field was mapped out, and best direction was determined with a high-contrast luminance-defined bar. All subsequently presented stimuli were centered on the geometric center of the receptive field.

2. Determining Neural Equiluminance in Macaque Area-MT Neurons

The methods for determining equiluminance in individual area-MT neurons, including information about the recording procedures and parameters, are described in detail in our previous studies.[30–32] Briefly, each area-MT neuron was presented with heterochromatic red–green gratings moving in preferred (P) and nonpreferred (NP) directions (stimulus duration, 1.0 or 1.5 s). Neural responses were obtained for several (typically eight) different luminance contrasts of the heterochromatic grating, varied from red-more-luminous-than-green to green-more-luminous-than-red contrast. For each red–green pair, a direction index (DI) was determined from the mean responses (spikes/s, averaged across the duration of the stimulus) to motion in P and NP directions: DI = (P − NP)/(P + NP). A Gaussian curve was fitted to the resulting DI versus red–green luminance contrast data, and the luminance contrast yielding the minimum in the curve was provisionally defined as the neural equiluminance point (see Fig. 1 below). Note that, for two macaques (Teiresias and Kimball), neural equiluminance was determined directly from minima in P motion responses rather than from DI's. This difference was a consequence of a slightly different experimental design for the study in which these macaques were tested[32] as compared with our earlier study.[31] This difference should not affect our results, as the two methods for defining neural equiluminance yield equivalent results.

Tables 1 and 2 present the conditions under which equiluminance points were obtained for each macaque, including the different spatial frequencies [cycles/degree (cpd)] and temporal frequencies (cycles/second, or hertz) employed. Also shown are the stimulus size and the mean stimulus eccentricity (based on the mean receptive-field eccentricity of area-MT neurons) for each animal. In Table 3 we present the number of area-MT neurons tested at each spatiotemporal frequency and the resulting mean red–green equiluminance points obtained under that condition. To obtain an overall mean equiluminance point for each macaque, equiluminance points across all the neurons were averaged.

3. Determining Equiluminance in Human Subjects

Red–green equiluminance points were determined in human subjects by use of the minimally distinct motion method (see, e.g., Refs. 39 and 40). Subjects adjusted the luminance contrast in a moving heterochromatic (red–green) grating until the percept of motion was least salient. Equiluminance points were determined from the mean of 20 trials. Subjects were tested across a range of stimulus conditions chosen to overlap with those employed for macaques. These conditions are presented in Tables 1 and 2. As for macaque data, mean equiluminance points in humans were determined separately for

Table 1. Stimulus Parameters Employed for Macaque Subjects ($n=5$)[a]

Macaque	SF	TF	Size (°)	Mean Eccentricity (°)
1. Teiresias	0.4, 0.7, or 1.4	1, 2, 4, or 8	5	3.5 (SD, 1.3; parafoveal)
2. Kimball	0.4, 0.7, or 1.4	1, 2, 4, or 8	5	4.1 (SD, 1.9; parafoveal)
3. Lefty	0.5	2, 8, or 13	10	8.0 (SD, 2.5; peripheral)
4. Tutu	0.5	2, 8, or 13	10	7.7 (SD, 2.5; peripheral)
5. Frisbee	0.5	2, 8, or 13	10	8.4 (SD, 2.9; peripheral)

[a] SF, spatial frequency (cycles/degree). TF, temporal frequency (cycles/second, or hertz). Size (°), stimulus size. Eccentricity (°), stimulus eccentricity. For macaques, mean stimulus eccentricities are shown (based on the mean receptive-field eccentricities of area-MT neurons). Note that, while we use the term parafoveal to refer to eccentricities relatively close to the fovea (2.5°–4.1°), "peripheral" is used to refer to stimuli placed farther out (~8°).

Table 2. Stimulus Parameters Employed for Human Subjects ($n=11$)[a]

Stimulus	SF	TF	Size (°)	Eccentricity (°)
1	0.7	8	5	2.5 (parafoveal)
2	0.7	4	5	2.5 (parafoveal)
3	1.4	8	5	2.5 (parafoveal)
4	1.4	4	5	2.5 (parafoveal)
5	0.7	8	10	8 (peripheral)
6	0.7	13	10	8 (peripheral)

[a] See Table 1 footnote. For humans, stimuli were centered at one of two eccentricities (2.5° and 8°). The parafoveal stimuli used for humans (i.e., 2.5°) were slightly closer to the fovea than those for macaques (i.e., mean for two macaques, 3.7°), for the following reason: The stimulus eccentricity chosen for humans was guided by the mean receptive-field eccentricity of the sampled area-MT neurons in Teiresias and Kimball, which at the time was close to 2.5°. The mean eccentricity for area-MT neurons moved more peripherally as more neurons were added to the sample. We do not expect this small difference of ~1.0° between macaques and humans to affect any of our comparisons. Also, note that human subjects were not tested under all the spatiotemporal conditions employed in the macaque experiments.

the different spatiotemporal frequency conditions. To yield an overall mean equiluminance point for each human subject, equiluminance points across different spatiotemporal frequencies were averaged, separately for stimuli presented at 2.5° and 8° eccentric to fixation.

E. Estimating L:M Cone Ratios from Red–Green Equiluminance Points

For human subjects, estimates of L:M cone ratios were calculated based on psychophysically determined red–green equiluminance points. For macaques, estimates of L:M cone ratios were calculated based on the mean neural equiluminance point across area-MT neurons. Estimates of L:M cone ratios were derived in the following manner: First, we determined the L and M cone excitations produced by the red and the green peaks of heterochromatic gratings set to be equiluminant (either for a given human subject or for the average area-MT neuron). This involved using the PR-650 SpectraColorimeter to obtain the spectral output function of the red and the green peaks of the grating (from 380–780 nm, in 4-nm intervals). These spectral functions were then cross multiplied with the L and M cone fundamentals reported for 2° stimuli by Stockman *et al.*,[41] and the resultant function was inte-

Table 3. Number of Area-MT Neurons Tested at Each Spatiotemporal Frequency, and the Mean Red–Green Equiluminance Point for Those Neurons[a]

SF	TF	Number of Cells	Mean Equiluminance Point
Macaque 1:	Teiresias		
0.4	1	0	–
0.4	2	6	−7.77%
0.4	4	5	−3.53%
0.4	8	4	−5.46%
0.7	1	4	−10.81%
0.7	2	6	−7.57%
0.7	4	9	−8.51%
0.7	8	1	−10.27%
1.4	1	0	–
1.4	2	3	−7.48%
1.4	4	12	−10.35%
1.4	8	5	−10.81%
Macaque 2:	Kimball		
0.4	1	0	–
0.4	2	2	−3.21%
0.4	4	4	−5.38%
0.4	8	8	−3.82%
0.7	1	0	–
0.7	2	1	−8.54%
0.7	4	7	−4.58%
0.7	8	10	−4.32%
1.4	1	0	–
1.4	2	1	−8.58%
1.4	4	1	−7.51%
1.4	8	3	−6.80%
Macaque 3:	Lefty		
0.5	2	12	−8.30%
0.5	7.5	10	−8.40%
0.5	13	14	−0.39%
Macaque 4:	Tutu		
0.5	2	23	−13.61%
0.5	7.5	64	−11.89%
0.5	13	31	−9.09%
Macaque 5:	Frisbee		
0.5	2	26	−14.26%
0.5	7.5	58	−8.33%
0.5	13	31	−4.62%

[a] SF, spatial frequency (cycles/degree). TF, temporal frequency (cycles/second, or hertz).

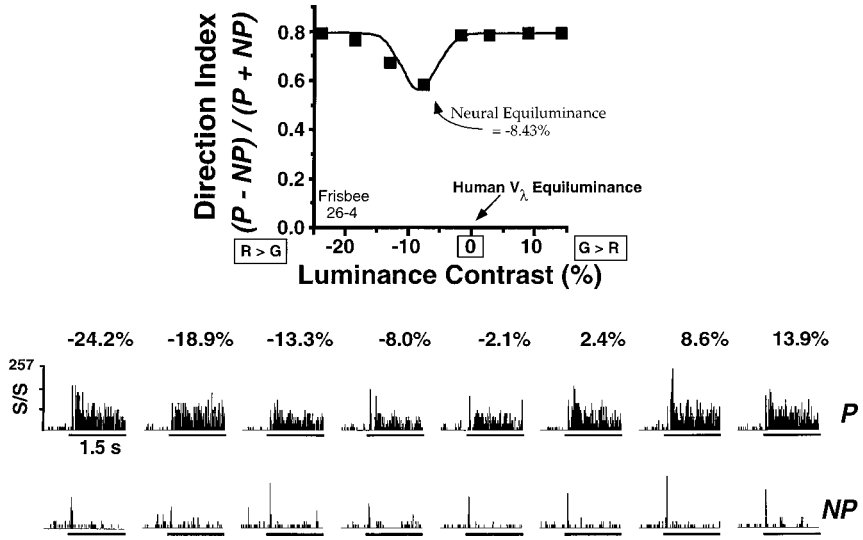

Fig. 1. Example data from an area-MT neuron presented with heterochromatic (red–green) gratings. The neuron was tested with eight different red–green luminance contrasts ranging in equal intervals (5.48%) from −24.2% to 13.9%, moving in both preferred (P) and nonpreferred (NP) directions (stimulus duration, 1.5 s). Bottom: Post-stimulus-time histograms [spikes/s (S/S)] are plotted as a function of luminance contrast in the red–green grating. Top: Corresponding DI = (P − NP)/P + NP) for each red–green pair. 0% luminance contrast denotes standard CIE (1924) human V_λ equiluminance (as measured by our PR-650 SpectraColorimeter). Neural equiluminance is defined as the luminance contrast yielding the minimal DI of a Gaussian curve fitted to the mean data, which was determined to be −8.43% for this neuron.

grated, to yield L and M cone excitations produced by the red and the green peaks.

L:M cone ratios were then calculated by determination of the weighting factor (F) for the L cones necessary to equate the sum of L and M cone excitation for the red and the green peaks of the heterochromatic grating:

$$F(L_r) + M_r = F(L_g) + M_g, \tag{1}$$

where L_g and M_g refer to the cone excitations produced by the green peak, L_r and M_r refer to the cone excitations produced by the red peak, and the weighting factor (F) is an approximation of the L:M cone ratio. Thus the L:M ratio is calculated as follows:

$$\text{L:M RATIO} = (M_g - M_r)/(L_r - L_g). \tag{2}$$

Note that our model relies on human cone fundamentals for the standard observer (as determined by Stockman *et al.*[41]) to compute L and M cone excitations. Because cone fundamentals are expected to differ somewhat across individuals (based on differences in λ_{max} and photopigment optical density, as well as in lens and macular pigment, across subjects), there will be some error in L:M derivations associated with using a standard set of cone fundamentals for all the subjects (see Ref. 42 for further discussion). For the purpose of comparing human and macaque L:M cone ratios, a potentially greater concern regards our use of human cone fundamentals to estimate L:M ratios in macaques. As addressed further in Section 4, we believe that the use of human cone fundamentals as a close approximation to macaque cone fundamentals is justified because evidence supports similar optics, screening factors, and λ_{max} between the two species.

Another assumption of our model is that the weighting factor (F) represents the relative number of L to M cones, as opposed to some postreceptoral synaptic weighting of L to M cones. We believe that this is a reasonable assumption inasmuch as there exists empirical evidence, within individual human subjects, demonstrating that spectral sensitivity is closely tied to the relative number of L to M cones (see, e.g., Refs. 11, 12, 43, and 44).

3. RESULTS

A typical example of neural equiluminance in a single area-MT neuron is shown in Fig. 1. This neuron preferred leftward motion and had a receptive field located in the upper contralateral quadrant, centered 7.5° eccentric from the center of gaze. The neuron was presented with eight different red–green luminance contrasts ranging in equal intervals (5.48%) from −24.2% to 13.9%, moving in both P and NP directions (stimulus duration, 1.5 s). In this example the neuron was tested with a 0.5-cpd grating moving at 7.5 Hz. The resulting post-stimulus-time histograms as a function of luminance contrast in the heterochromatic grating are shown in the bottom half of Fig. 1, and the corresponding DI [DI = (P − NP)/(P + NP)] for each red–green pair is plotted in the top half. Neural equiluminance was estimated by determination of the luminance contrast yielding the minimal DI of a Gaussian curve fitted to the mean data. For this neuron, the equiluminance point was determined to be −8.43% with respect to human V_λ equiluminance.

A. Human and Macaque Equiluminance Points

Red–green equiluminance points for humans (n = 11) and macaques (n = 5) are shown in Fig. 2(a). For each macaque, we obtained an individual mean red–green equiluminance point by averaging equiluminance points across all area-MT neurons (open symbols). Note that two of the macaques were tested at mean eccentricities of 3.5° and 4.1° (referred to as parafoveal; open circles), while the other three were tested at ~8° (referred to as

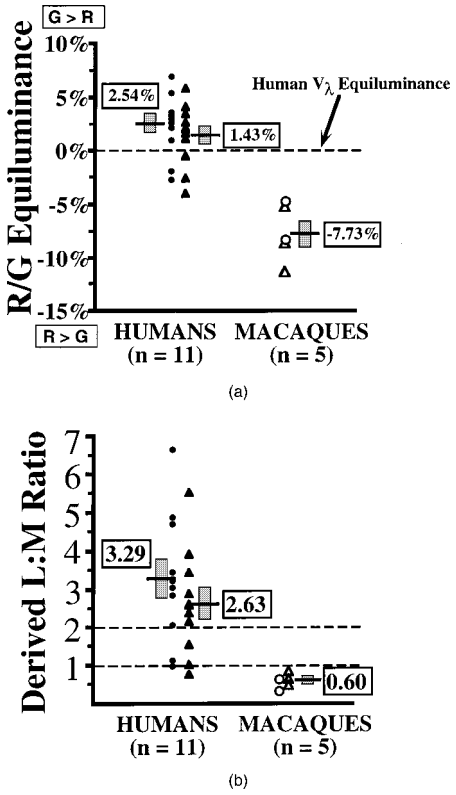

Fig. 2. (a) Red–green equiluminance points for humans (n = 11, filled symbols) and macaques (n = 5, open symbols), obtained by averaging data across spatiotemporal frequency conditions. Circles and triangles represent data obtained from parafoveal and peripheral locations, respectively (see text and Tables 1 and 2). Group mean equiluminance points and standard errors are depicted by horizontal lines and shaded rectangles (height = ±1 standard error of the mean), respectively. For both parafoveal and peripheral stimuli, there is a clear and significant difference between human and macaque data points. (b) L:M cone ratios for humans and macaques, derived from red–green equiluminance points shown in (a). Dashed horizontal lines represent the approximate L:M ratios of humans and macaques as determined from direct retinally based methods. [Symbols are same as in (a).]

peripheral; open triangles). For each human, we obtained a mean equiluminance point by averaging across spatiotemporal frequency conditions, separately for stimuli presented at 2.5° (parafoveal; filled circles) and 8° (peripheral; filled triangles) eccentric to fixation.

Group mean equiluminance points and standard errors for humans and macaques are depicted by horizontal lines and shaded rectangles (height = ±1 standard error of the mean), respectively. For macaques, the group mean equiluminance point was −7.73% with respect to human V_λ equiluminance. For humans, group mean equiluminance points were 2.54% and 1.43% for parafoveal and peripheral stimuli, respectively. Thus these data demonstrate a clear and significant separation between human and macaque red–green equiluminance points [$F(1, 14) = 40.7$, $p < 0.0001$].

B. Derived L:M Cone Ratios

As described in Section 2, red–green equiluminance points were used to derive estimates of L:M cone ratios. Individual L:M ratios, determined from red–green equiluminance points [presented in Fig. 2(a)], are plotted in Fig. 2(b). As for red–green equiluminance points, there exists a clear separation between derived L:M ratios for humans and macaques. For humans, the group mean L:M ratio was determined to be 3.29 and 2.63 for parafoveal and peripheral stimuli, respectively. For macaques, the group mean L:M ratio was 0.60. We should acknowledge, however, that the low number of macaque subjects may produce somewhat biased estimates, and for this reason the exact values should be interpreted with some caution. Nonetheless, our derived L:M ratios for humans and macaques fall quite close to those determined from retinally based methods [dashed horizontal lines in Fig. 2(b)].

C. Effects of Temporal and Spatial Frequency

In Fig. 3 we have plotted the equiluminance points of humans (filled symbols) and macaques (open symbols) as a function of temporal frequency (2–13 Hz, top plot) and

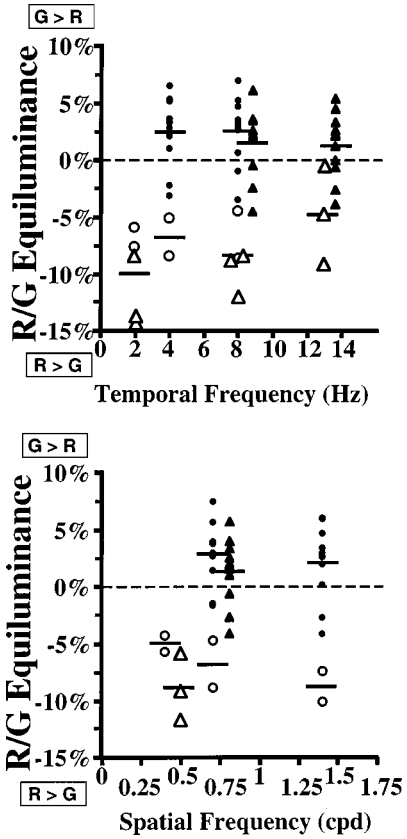

Fig. 3. Red–green equiluminance as a function of temporal frequency (2–13 Hz, top plot) and spatial frequency (0.4–1.4 cpd, bottom plot). Note that temporal frequency data are collapsed across spatial frequencies. Likewise, spatial frequency data are collapsed over temporal frequency. Combining data in this fashion was necessary because, for macaques, there was an insufficient number of neurons to allow investigation of each combination of spatial and temporal frequency. A two-factor analysis of variance conducted on the human data revealed no significant effects of spatial or temporal frequency (and no significant interaction between the two). Single-factor analysis of variance in macaques revealed no significant effect of spatial frequency, yet a significant effect of temporal frequency, on equiluminance points. At higher temporal frequencies macaques needed more green to match the red. (Symbols are same as in Fig. 2.)

spatial frequency (0.4–1.4 cpd, bottom plot). Horizontal bars denote group means. (Note that standard errors are not plotted because some means are from only two subjects.) The number of neurons included in each condition can be found in Table 3. As for equiluminance points averaged across all the spatiotemporal frequencies [Fig. 2(a)], the data shown in Fig. 3 demonstrate a clear separation between human and macaque data at all the spatial and temporal frequencies. Although there exists some overlap between human and macaque equiluminance points at the highest temporal frequency tested (13 Hz), the difference between species was nonetheless significant at this temporal frequency [$F(1, 12) = 8.62$, $p = 0.01$].

When statistical tests were applied to evaluate the influence of spatial and temporal frequency (separately for macaque and human data), the only significant effect was that of temporal frequency on macaque equiluminance points [$F(2, 2) = 10.4$, $p = 0.026$], with more green needed to match the red at higher temporal frequencies. The effects of temporal frequency observed in macaques but not humans is likely to reflect the fact that, relative to macaques, humans were tested over a restricted range of temporal frequencies. That human red–green equiluminance points are, in fact, affected by temporal frequency is supported by several previous psychophysical studies (see, e.g., Refs. 34 and 45–49). It is perhaps important to point out that such effects indicate that the relative number of L to M cones in the eye cannot be the sole factor underlying red–green equiluminance. Other factors, such as changes in the weights or relative phases (see, e.g., Refs. 45 and 49) of L and M cones must also play a role.

D. Effects of Eccentricity

The extent to which red–green equiluminance points and/or L:M ratios vary with eccentricity is still an unsettled matter (see, e.g., Refs. 6, 9, 50, and 51). To investigate the effects of eccentricity, statistical analyses were applied to the data. For human subjects, we used equiluminance data for 8-Hz, 0.7-cpd gratings, obtained at both 2.5° (parafoveal) and 8° (peripheral) eccentric to fixation. As might be expected by comparison of parafoveal with peripheral data points in Figs. 2(a) and 3, human subjects exhibited significantly lower equiluminance points (i.e., more red needed to match the green) for 8°, as compared with 2.5°, stimuli [$F(1, 10) = 20.6$, $p = 0.001$]. The effect was rather small, however, with equiluminance points lowered (on average) by 1.5%. This effect of eccentricity on equiluminance points may be accounted for by several factors, including the known decrease in macular pigment with increasing eccentricity, a lower L:M cone ratio in the periphery, or differential cone weightings as a function of eccentricity.

In macaques, regression analysis was employed to investigate the effect of area-MT receptive-field eccentricity on equiluminance points, separately for each animal. The results of this analysis revealed a negative regression slope for four of five animals. Although the effect was not significant for any of the animals, the general tendency for lower equiluminance points (i.e., needing more red to match the green) with increasing eccentricity is a pattern similar to that observed in human subjects.

4. DISCUSSION

The results of these studies demonstrate a significant difference in red–green equiluminance points between macaque and human subjects. When these red–green equiluminance values are used to derive estimates of L:M cone ratios, human and macaque values appear fairly close to those determined from direct retinally based methods[2–7,19–22] and from psychophysical techniques that selectively stimulate L and M cones.[8–12] Thus these data add to the mounting evidence that the relative number of L to M cones in the eye has predictable consequences for red–green spectral sensitivity. Furthermore, the fact that macaque L:M estimates were based on equiluminance measures in area MT suggests that the dorsal stream of visual cortex provides the substrate for the luminance mechanism, which computes a weighted sum of L and M cone excitations.

In our discussion of these findings, first we discuss evidence that area MT provides the neural substrate for red–green equiluminance revealed behaviorally. Second, we address the potential for factors other than differences in L:M cone ratios to contribute to the differences that we observed. Third, we discuss our results within the context of previous studies that have measured spectral sensitivity in macaques. Finally, we speculate about the potential benefits of higher versus lower L:M ratios and why differences in L:M ratios across species may have evolved.

A. Does Area MT Provide the Neural Substrate for Behavioral Equiluminance?

Before we proceed with a discussion of the results, it is perhaps important to establish that equiluminance determined for area-MT neurons reflects behavioral equiluminance. In previous experiments[30] we used an oculomotor technique to measure behavioral equiluminance in two of the macaques (Lefty and Tutu) included in the present study. The stimulus in these experiments consisted of a field of moving black dots superimposed upon a temporally modulated heterochromatic red–green grating (0.5 cpd, 13 Hz). When the red–green grating is set to be equiluminant the overall flicker in the grating is minimized, thus revealing the motion of the overlying black dots. This motion elicits smooth tracking eye movements. Under nonequiluminant conditions motion of the black dots is masked by luminance flicker, and eye movements are consequently of smaller amplitude. Using this paradigm, we measured macaques' oculomotor responses at different luminance contrasts in the red–green grating, with behavioral equiluminance being defined as the luminance contrast yielding the largest eye movement amplitude. The results of this experiment revealed an extremely tight correspondence between the behavioral equiluminance points of our two macaques and the mean equiluminance points of their area-MT neurons (obtained at the same spatiotemporal frequency). Such results

suggest that area-MT equiluminance can be used to infer behavioral equiluminance.

In addition to this direct approach, one could also argue that a link between area-MT and behavioral equiluminance is predicted by the responses of (and projections from) neurons at earlier stages of visual processing. It has long been known that, while neurons of the magnocellular subcortical pathway receive primarily additive, i.e., L + M, input, neurons of the parvocellular pathway receive primarily opponent, i.e., L − M, input (see Ref. 52 for review, but compare Ref. 53). Based on the pattern of input to these two neuronal types, it is perhaps not surprising to learn that magnocellular, but not parvocellular, retinal ganglion cells yield spectral sensitivity (V_λ) curves similar to those obtained psychophysically.[54–56] Because area MT appears to receive predominantly magnocellular-driven input,[57] these previous experiments conducted in the retina predict that a correlation between neural and behavioral equiluminance should also be found in area MT.

B. Other Potential Factors Underlying Differences between Macaques and Humans

1. Stimulus Conditions

Several previous human psychophysical studies have demonstrated that stimulus factors such as spatial and temporal frequency, as well as adaptation state, can alter equiluminance measures (see, e.g., Refs. 35, 48, 49, 58, and 59). Because we expect that the equiluminance points observed in our study were likewise influenced by such factors, our derived L:M ratios are expected to be an approximation. However, these derived L:M values are, in fact, reasonably close to those predicted by retinal studies, which suggests that any error associated with our particular choice of stimulus conditions is rather small. More importantly, we believe that stimulus factors (should they have affected our derived measures) cannot explain the differences that we observed between species, since humans and macaques were tested under nearly identical stimulus conditions.

2. Age

Because of the yellowing of the lens with age, older animals are expected to be relatively less sensitive to green as compared with younger animals (see, e.g., Refs. 60 and 61). Because our human subjects were older than our macaques [mean human yr, 30.7 ± 6.7 (SD), mean macaque yr, 10.8 ± 4.0 (SD)], one could argue that the differences in equiluminance points observed in our study are a mere consequence of age differences. We believe, however, that it is more appropriate to use adjusted age (by threefold) for our macaques, to reflect the difference in life span between the species.[62] When we use adjusted age for our macaques, the mean macaque age [32.4 yr ± 11.9 (SD)] was indistinguishable from that of our human subjects ($t = 0.3$, p, not significant). Our use of adjusted age is justified on several grounds. First, macaques develop presbyopia and senile cataracts at the same adjusted ages as humans, which suggests that changes such as lens yellowing are also likely to be tied to adjusted age. This prediction is, in fact, supported by previous experiments demonstrating that the lens absorption of a 5-yr-old macaque is similar to that of a 20-yr-old human.[63] A second issue concerns the possibility that lens yellowing is the result of accumulative UV exposure (see, e.g., Ref. 64) rather than part of the natural aging processes. If this is true, it might be inappropriate to use adjusted age for our macaque subjects. The lens changes associated with aging appear to be similar for macaques maintained in cages all their lives (i.e., with little UV exposure) and those who live in outdoor colonies,[65] which argues against this possibility. For these reasons, we believe that differences in lens yellowing associated with aging cannot explain the differences in equiluminance points observed between humans and macaques.

3. Rods

Because the stimuli used in our experiment were not bright enough to completely saturate rods, it is possible that rod activity may have contributed to equiluminance measurements. In general, this would have the effect of biasing red–green equiluminance points toward V'_λ equiluminance (i.e., a shift toward relatively greater sensitivity to green). Thus it is possible that the shifted equiluminance points observed in macaques reflect a larger rod contribution in macaques as compared with humans. Such a situation could arise if rod signals were more dominant in macaques than in humans. However, this possibility is not supported by psychophysical comparisons of human versus macaque rod vision (see, e.g., Ref. 24) and is therefore unlikely to account for the differences observed in this study.

4. Cone Fundamentals

In our derivations of L:M cone estimates from red–green equiluminance points, we used human cone fundamentals reported by Stockman *et al.*[41] These cone fundamentals represent functions for the standard observer, obtained from a mean across several subjects. Individual differences in cone fundamentals exist across subjects, however, arising from differences in λ_{max} and photopigment optical density, as well as in macular and lens pigment. Thus it is reasonable to assume that the standard cone fundamentals used in our derivation of L:M ratios were not perfect for each subject, resulting in some expected error in our estimates. While this is not in itself of particular concern, our use of human cone fundamentals to calculate macaque L:M ratios potentially could be important. Although we might have attempted to model cone fundamentals for macaques, we believe that using human functions is a close enough approximation, since cone optical density,[20] lens density,[25,63] and macular pigment[25,66] are thought to be comparable between the two species.

However, with regard to the absorption spectra of human and macaque cone photoreceptors, there is reason to believe that the λ_{max} of L and M cones in the macaque may be shifted toward longer wavelengths (by as much as 4 nm), as compared with human cones (although the issue is still a matter of some debate; see Ref. 1 or 21 for a review). To address the possibility that differences in λ_{max} might explain the differences observed in our study, we

recalculated macaque L:M cone ratios, using a shifted set of cone fundamentals (i.e., by shifting the human L and M cone fundamentals to higher wavelengths by 4 nm). With these shifted functions, macaque L:M ratios were even lower than our original estimates and thus even more different from those calculated for humans. For this reason it seems highly unlikely that differences in λ_{max} can account for our results.

5. Contribution of Luminance versus Brightness Mechanisms

Despite our assumption that equiluminance judgments rely on a mechanism that computes a weighted sum of L and M cone signals (i.e., an L + M, or luminance, mechanism), it is possible that an opponent cone mechanism (i.e., an L − M, or chromatic, mechanism) may also contribute. The relative weighting of L + M versus L − M mechanisms may depend partially on stimulus parameters such as spatial and temporal frequency. In addition, the relative weighting may be task dependent, leading subjects to selectively monitor activity in L + M versus L − M pathways. For example, it is known that red–green matches based on HFP are discrepant from red–green matches based on heterochromatic brightness matching.[67] Such differences have typically been explained by the assumption that while HFP relies solely on L + M mechanisms, heterochromatic brightness matching relies on both L + M and L − M mechanisms (e.g., Refs. 68 and 69). Thus, in principle, the differences that we observed in red–green equiluminance matches between humans and macaques could have arisen if our human subjects employed a brightness matching strategy, which would allow a greater contribution of L − M mechanisms in humans as compared with macaques. We consider this explanation unlikely, however, since the majority (i.e., 9 out of 11) of our subjects were naïve to issues of brightness matching and were simply told to minimize the motion in the stimulus (without any mention of brightness whatsoever).

C. Spectral Sensitivity in Humans and Macaques: Relation to Previous Studies

1. Psychophysical Evidence

Several previous psychophysical studies have found differences in spectral sensitivity between humans and macaques. The results from experiments testing increment thresholds,[23–25] HFP,[26] and spatial acuity[27,28] indicate that macaques are slightly more sensitive to short wavelengths yet less sensitive to long wavelengths as compared with humans. In general, these small differences went unnoticed and were therefore not attributed to differences in L:M cone ratios between species. This is perhaps not surprising, since retinally based estimates of L:M cone ratios had not been reported (for either humans or macaques) at the time that these experiments were conducted.

2. Spectral Sensitivity Revealed by Retinal Electrophysiology

In a recent study, Jacobs and Deegan[21] used ERG flicker photometry (31 Hz) to obtain spectral sensitivity functions in macaques (both *M. mulatta* and *M. fascicularis*) and in humans. Consistent with previous psychophysical findings, they found small but systematic differences between the two species. Compared with humans, the ERG response of macaques reflected slightly greater sensitivity to short wavelengths (<520 nm) and slightly lower sensitivity to wavelengths longer than this value. As in the present study, they modeled their results in terms of L:M cone ratios and concluded that the difference between human and macaque data reflects differences in the relative proportions of L and M cones in the retinas of the two species. Thus our data (obtained from a cortical metric) serve to confirm those of Jacobs and Deegan (obtained from a retinal metric). Unlike the results of Jacobs and Deegan, however, the variability of L:M ratios across our macaques was extremely low [see Fig. 2(b)]. Note that this low variability may be an artifact of the low number of subjects in our study, i.e., low n can produce biased estimates of variability. Other possible reasons for differences in variability between studies include the fact that, while Jacobs and Deegan combined data from two macaque species (*M. mulatta* and *M. fascicularis*), which may differ from each other, we tested only one (*M. mulatta*). In addition, the low variability in our study may have arisen from potential genetic similarity among our five macaques (three macaques were obtained from one colony, and two were obtained from another colony).

It is also interesting that, unlike the present study, in which cortical recordings necessarily reflect postreceptoral processing of L and M cone signals, the degree to which the ERG reflects receptoral versus postreceptoral processes is still uncertain. Because the ERG spectral sensitivity data of Jacobs and Deegan can be well modeled by a simple summing of L and M cone signals, it is reasonable to assume that the ERG signal at high flicker rates reflects solely additive (L + M) responses. One way in which this could occur is if the ERG reflects signals originating exclusively from cone photoreceptors such that the summing of L and M cone responses occurs at the level of the recording device. However, because there is reason to believe that the fast-flicker ERG contains signals from postreceptoral cells as well as from cone photoreceptors,[70] Jacobs and Deegan suggest that the postreceptoral contribution to the ERG signal arises selectively from retinal cells that receive additive (L + M), rather than opponent (L − M), cone input. Although it is difficult to imagine how L − M signals would be excluded from the ERG signal, the fact remains that their ERG spectral sensitivity data can be modeled by a simple summing of L and M cone fundamentals (see also Ref. 5).

Also relevant to the present study is that of Dacey *et al.*,[71] who recently reported estimates of L:M ratios in macaques, based on the strength of L and M cone input to H1 horizontal cells in the retina. Dacey *et al.*, like Jacobs and Deegan,[21] found greater variability in their L:M estimates as compared with the present study. The greater variability in the study by Dacey *et al.* may be due to the fact that they combined data from three different macaque species (*M. nemestrina, M. fascicularis,* and *M. pabio anubis*). In addition, differences between studies

may simply reflect the existence of less variability at higher stages of visual processing. Based on convergence in the visual pathway, the variability of L versus M cone input across individual cortical neurons should be far less than that observed across retinal cells.

D. Potential Benefits of High versus Low L:M Cone Ratios

On a final note, it is tempting to speculate as to why differences in L:M cone ratios between humans and macaques may exist. To address this, we might ask whether any benefit can be expected from possessing a higher versus a lower L:M cone ratio. In a recent human psychophysical study, we found that subjects' red–green equiluminance points (which presumably reflect their L:M cone ratios) were correlated with their contrast sensitivity for luminance-defined and chromatically defined gratings.[48] Specifically, at high temporal frequencies, subjects who exhibited relatively greater sensitivity to red than to green (i.e., indicative of higher L:M cone ratios) tended to exhibit higher-than-average luminance contrast sensitivity. By contrast, at low temporal frequencies, these subjects tended to exhibit lower-than-average chromatic contrast sensitivity. Thus this pattern of results suggests that the relative number of L to M cones in the eye may place constraints on luminance and chromatic contrast sensitivity. Consequently, macaques might be expected to exhibit higher chromatic, yet lower luminance, contrast sensitivity as compared with humans. Thus differences in L:M ratio may have evolved to accommodate different needs for greater chromatic sensitivity versus greater luminance sensitivity. For example, in macaques, greater chromatic contrast sensitivity afforded by a lower L:M ratio may have been necessary to distinguish red fruit against green foliage.[72] By contrast, in humans, greater luminance contrast sensitivity afforded by a higher L:M cone ratio may have been relatively more important for high-precision tasks such as vernier alignment, which is known to be highly dependent on luminance contrast.[73]

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