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# DALTONIANA

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**The bulletin of the International Colour Vision Society**

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## Daltoniana on the web

Welcome to the sixth edition of the web based **Daltoniana**. This edition will be transmitted by email and mailed to members from locations in North America, Europe and Australasia.

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## Officers and Committee

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## General Secretary's report

The editing of the proceedings is finished and all of the accepted papers have been transmitted to Color Research & Application. I expect that galley proofs will go out over the next few months. For the 71 submitted papers, only 7% were rejected as not meeting minimum standards for publication. We expect the proceedings to be published as the first issue of CRA of 2001, if all continues to go smoothly. I want to take this opportunity to thank the other three editors, Dick Cavonius, Barry Lee and Joel Pokorny for their rigor, care and efficiency in getting this job done.

The 200 for 2000 drive was a great success. The possibility that the dues should be paid two years at a time seems to be the best solution to the difficulties encountered in collection during years in which there is no meeting.

The next meeting to be held in Cambridge in 2001 is being organized by John Mollon. First details can be found below. The coincidence of the site in Cambridge and the bicentenary of Thomas Young's address on trichromacy give this meeting a special significance.

We are sad to report the death of A. J. L. G. Pinckers who was an active contributor to the society from its inception. An obituary by Marion Marré will appear in the next Daltoniana.

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## Next Symposium

Friday July 13th to Tuesday July 17th, 2000 in Cambridge, UK.

John Mollon will be the recipient of OSA's Tillyer award for the year 2000

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## ICVS WEBNEWS

The web server was off the air for a while, in September - Apologies. This was due initially to a move of buildings and then to a delay in reconfiguring within an upgraded server environment. The server is now running Mac System 8.6 and Appleshare IP which seems to be far more stable than the previous system which froze 2 or 3 times a week for no apparent reason. To date we have had no problems with the new system. In the next edition of Daltoniana we will announce associate arrangements with Amazon.co.uk and Amazon.de to add to Amazon.com. If Amazon operates in any other country, please let [Stephen Dain](#) know and they will be added.

# **Abstracts of colour vision papers. Compiled by Joel Pokorny**

## **Abstracts of colour vision papers. Compiled by Joel Pokorny**

Authors and titles of the Feature Issue on

### **CHROMATIC TOPOGRAPHY OF THE RETINA**

Journal of the Optical Society of America A Vol.17 - Issue 3 - 2000

Joseph Carroll , Carrie McMahon , Maureen Neitz , Jay Neitz. Flicker-photometric ERG estimates of L:M cone photoreceptor ratio in men with photopigment spectra derived from genetics p. 499 - 509

John Krauskopf. Relative number of long- and middle-wavelength-sensitive cones in the human fovea p. 510 - 516

Jan Kremers , Hendrik P. N. Scholl , Holger Knau , Tos T. J. M. Berendschot , Tomoaki Usui , Lindsay T. Sharpe. L/M cone ratios in human trichomats assessed by psychophysics, electroretinography and retinal densitometry p. 517 - 526

Stephanie A. Hagstrom , Maureen Neitz , Jay Neitz. Cone pigment gene expression in individual photoreceptors and the chromatic topography of the retina p. 527 - 537

Samir S. Deeb , Lisa Diller , David Williams , Dennis Dacey. Interindividual and topographical variation of red and green cone ratios in monkey retinæ p. 538 - 544

Karen R. Dobkins , Alex Thiele , Thomas D. Albright. Comparison of red/green equiluminance points in humans and macaques: evidence for different L:M cone ratios between species p. 545 - 556

Paul R. Martin , Ulrike Grunert , Tricia L. Chan , Keely Bumsted. Spatial order in short-wavelength sensitive cone photoreceptors: a comparative study of the primate retina p. 557 - 567

Agoston Szel , Akos Lukats , Tibor Fekete , Zsuzsanna Szepessy , Pal Rohlich. Photoreceptor distribution in the retina of subprimate species p. 568 - 579

Peter Kurt Ahnelt , Eduardo Fernandez , Oscar Martinez , Jose Angel Bolea , Anna Kubber-Heiss. Irregular S-cone mosaics in felid retinas. Spatial interaction with axonless horizontal cells revealed by cross correlation. p. 580 - 588

Dennis M. Dacey , Lisa C. Diller , David R. Williams. Physiology of L- and M-cone inputs to H1 horizontal cells in primate retina p. 589 - 596

David J. Calkins. The Representation of Cone Signals in the Primate Retina p. 597 - 606

David H. Brainard , Austin Roorda , Yasuki Yamauchi , Jack B. Calderone , Andrew Metha , Maureen Neitz , Jay Neitz , David R. Williams, Gerald H. Jacobs. Functional consequences of

the relative numbers of L and M cones p. 607 - 614

Shiro Otake , Carol M. Cicerone. L and M cone relative numerosity and red-green opponency from fovea to mid-periphery in human retina p. 615 - 627.

Vicki J. Volbrecht , Janice L. Nerger , Sheila M. Imhoff , Corey J. Ayde. The effect of the short-wavelength-sensitive-cone mosaic and rods on the locus of unique green p. 628 - 634

Andrew Hsu , Robert Smith , Gershon Buchsbaum , Peter Sterling. Cost of cone coupling to trichromacy in primate fovea p. 635 - 640

Vicki J. Volbrecht , Erin E. Shrago , Brooke E. Scheffrin , John S. Werner. Spatial summation in human cone mechanisms from 0 to 20 in the superior retina p. 641 - 650

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## **ANATOMY AND PHYSIOLOGY**

Dacey, D. M. (2000). "Parallel pathways for spectral coding in primate retina." *Annual Review of Neuroscience* 23: 743-75.

The primate retina is an exciting focus in neuroscience, where recent data from molecular genetics, adaptive optics, anatomy, and physiology, together with measures of human visual performance, are converging to provide new insights into the retinal origins of color vision. Trichromatic color vision begins when the image is sampled by short- (S), middle- (M) and long- (L) wavelength-sensitive cone photoreceptors. Diverse retinal cell types combine the cone signals to create separate luminance, red-green, and blue-yellow pathways. Each pathway is associated with distinctive retinal architectures. Thus a blue-yellow pathway originates in a bistratified ganglion cell type and associated interneurons that combine excitation from S cones and inhibition from L and M cones. By contrast, a red-green pathway, in which signals from L and M cones are opposed, is associated with the specialized anatomy of the primate fovea, in which the "midget" ganglion cells receive dominant excitatory input from a single L or M cone.

Hanazawa, A., H. Komatsu and I. Murakami (2000). "Neural selectivity for hue and saturation of colour in the primary visual cortex of the monkey." *European Journal of Neuroscience* 12: 1753-63.

In the inferior temporal (IT) cortex of monkeys, which has been shown to play a critical role in colour discrimination, there are neurons sensitive to a narrow range of hues and saturation. By contrast, neurons in the retina and the parvocellular layer of the lateral geniculate nucleus (pLGN) encode colours in a way that does not provide explicit representation of hue or saturation, and the process by which hue- and saturation-selectivity is elaborated remains unknown. We therefore tested the colour-selectivity of neurons in the primary visual cortex (V1) and compared it with those of pLGN and IT neurons. Quantitative analysis was performed using a standard set of colours, systematically distributed within the CIE (Commission Internationale de l'Eclairage)-xy chromaticity diagram. Selectivity for hue and saturation was characterized by analysing response contours reflecting the overall distribution of responses across the chromaticity diagram. We found that the response contours of almost all pLGN neurons were linear and broadly tuned for hue. Many V1 neurons behaved similarly; nonetheless, a

considerable number of V1 neurons had clearly curved response contours and were selective for a narrow range of hues or saturation. The relative frequencies of neurons exhibiting various selectivities for hue and saturation were remarkably similar in the V1 and IT cortex, but were clearly different in the pLGN. Thus, V1 apparently plays a very important role in the conversion of colour signals necessary for generating the elaborate colour selectivity observed in the IT cortex.

Bumsted, K. and A. Hendrickson (1999). "Distribution and development of short-wavelength cones differ between Macaca monkey and human fovea." *Journal of Comparative Neurology* 403: 502-516.

Macaca monkey and humans have three cone types containing either long- wavelength (L), medium-wavelength (M), or short-wavelength (S)-specific opsin. The highest cone density is found in the fovea, which mediates high visual acuity. Most studies agree that the adult human fovea has a small S cone-free area, but data are conflicting concerning S-cone numbers in the adult Macaca monkey fovea, and little evidence exists for how either primate fovea develops its characteristic cone pattern. Single- and double-label in situ hybridization and immunocytochemistry have been used to determine the pattern of foveal S cones in both the fetal and adult Macaca and human. Both labels find a clear difference at all ages between monkey and human. Adult humans have a distinct but variable central zone about 100 microm wide that lacks S cones and is surrounded by a ring in which the S-cone density is 8%. This S cone- free zone is detectable at fetal week 15.5 (Fwk15.5), shortly after S opsin is expressed, and is similar to the adult by Fwk20.5. Adult monkey foveas have an overall S-cone foveal density of 10%, with several areas lacking a few S cones that are not coincident with the area of highest cone density. A surrounding zone at 200-microm eccentricity has an S-cone density averaging 25%, but, by 800 microm, this has decreased to 11%. Fetal day 77-135 monkeys all have a distribution and density of foveal S cones similar to adults, although the high-density ring is not obvious in fetal retinas. Estimates of the numbers of S cones missing in the fetal human fovea range from 234 to 328, whereas no more than 40 are missing in the fetal monkey. These results show that, in these two trichromatic primates, S-cone distribution and the developmental mechanisms determining S-cone topography are markedly different from the time that S cones are first detected.

Lee, B. B., D. M. Dacey, V. C. Smith and J. Pokorny. (1999). "Horizontal cells reveal cone type-specific adaptation in primate retina." *Proceedings of the National Academy of Sciences of the United States of America* 96: 14611-14616.

The human cone visual system maintains contrast sensitivity over a wide range of ambient illumination, a property known as light adaptation. The first stage in light adaptation is believed to take place at the first neural step in vision, within the long, middle, and short wavelength sensitive cone photoreceptors. To determine the properties of adaptation in primate outer retina, we measured cone signals in second-order interneurons, the horizontal cells, of the macaque monkey. Horizontal cells provide a unique site for studying early adaptational mechanisms; they are but one synapse away from the photoreceptors, and each horizontal cell receives excitatory inputs from many cones. Light adaptation occurred over the entire range of light levels evaluated, a luminance range of 15-1,850 trolands. Adaptation was demonstrated to be independent in each cone type and to be spatially restricted. Thus, in primates, a major source of sensitivity regulation occurs before summation of cone signals in the horizontal cell.

Silveira, L. C., B. B. Lee, E. S. Yamada, J. Kremers, D.M. Hunt, P.R. Martin, and

F.L. Gomes (1999). "Ganglion cells of a short-wavelength-sensitive cone pathway in New World monkeys: morphology and physiology." *Visual Neuroscience* 16: 333-343.

We have studied the morphology and physiology of retinal ganglion cells of a short-wavelength-sensitive cone (SWS-cone) pathway in dichromatic and trichromatic New World anthropoids, the capuchin monkey (*Cebus apella*) and tufted-ear marmoset (*Callithrix jacchus*). In Old World anthropoids, in which males and females are both trichromats, blue-ON/yellow-OFF retinal ganglion cells have excitatory SWS-cone and inhibitory middle- and long-wavelength-sensitive (MWS- and LWS-) cone inputs, and have been anatomically identified as small-field bistratified ganglion cells (SB-cells) (Dacey & Lee, 1994). Among retinal ganglion cells of New World monkeys, we find SB-cells which have very similar morphology to such cells in macaque and human; for example, the inner dendritic tree is larger and denser than the outer dendritic tree. We also find blue-on retinal ganglion cells of the capuchin to have physiological responses strongly resembling such cells of the macaque monkey retina; for example, responses were more sustained, with a gentler low frequency roll-off than MC-cells, and no evidence of contrast gain control. There was no difference between dichromatic and trichromatic individuals. The results support the view that SWS-cone pathways are similarly organized in New and Old World primates, consistent with the hypothesis that these pathways form a phylogenetically ancient color system.

## **PSYCHOPHYSICS**

Stromeyer, I. C., P. D. Gowdy, A. Chaparro, et al. (2000). "Colour adaptation modifies the temporal properties of the long- and middle-wave cone signals in the human luminance mechanism." *Journal of Physiology (London)* 526: 177-194.

The human luminance mechanism (LUM) detects rapid flicker and motion, summing the neurally integrated L' and M' 'contrast' signals from the long- and middle-wave cones, respectively. We previously observed large temporal phase shifts between the L' and M' signals in LUM, which were maximal and of reversed sign on green versus orange background fields and which were accompanied by large variations in the relative L' and M' contrast weights. The effects were modelled with phasic magnocellular retinal ganglion cells. The changing L' versus M' contrast weights in the model predict that the temporal dynamics of the L' and M' luminance signals will differ on green and orange fields. This is assessed with several protocols. Motion thresholds for 1 cycle deg<sup>-1</sup> drifting gratings or static pulsed gratings on the orange field show that the M' signal is more temporally bandpass than the L' signal; this reverses on the green field. Strong motion due to the different dynamics of the L' and M' signals is even seen with a pair of L' and M' gratings pulsed simultaneously. Impulse response functions were measured with gratings pulsed spatially in phase or antiphase. The impulse response was clearly biphasic for the M' signal on the orange field and L' signal on the green field, while the other signals were more sustained. The impulse responses predicted the motion seen with gratings pulsed in spatial quadrature.

Smith VC, Pokorny J. and Sun, H. (2000) "Chromatic contrast discrimination: Data and prediction for stimuli varying in L and M cone excitation." *Color Research and Application* 25: 105-115.

Chromatic discrimination data are presented for pulsed and steady stimuli as a function of surround chromaticity and structure. All stimuli and surrounds were at equiluminance and at a constant level of short-wavelength-sensitive cone excitation. The test stimulus was a square array of four 1 degree squares. A 0.07 degree crosshair of the same chromaticity as the surround separated the squares. Both the test stimuli and the surrounds varied in relative excitation of the long-wavelength and middle-wavelength sensitive cones. When stimuli briefly replaced a portion of a steadily viewed background (the Pulse Paradigm), the discriminations were optimal at the background chromaticity and degraded for chromaticities away from the background. The discrimination steps were independent of the background size, which varied from a spatially extensive display to one matching exactly the appearance of the test array. Discrimination was determined only by the spatio-temporal chromatic contrast of the stimulus relative to the background. When the stimuli were presented continuously within a surround (the Pedestal Paradigm), discrimination was still determined by the surround chromaticity, independent of the surround size. Even a narrow 0.07 degree crosshair was sufficient to establish optimal discrimination at the crosshair chromaticity. With the surround and crosshair dark, spectral opponent channels maintained an intrinsic normalization near equal energy while. There was little indication of adaptation to the test stimuli. The data were fit by a model of spectral opponency linking detection and discrimination as a function of both retinal illuminance level and chromaticity. The model is explicitly based on observations of the behavior of retinal ganglion cells of the Macaque retina. The model incorporates well-accepted psychophysical concepts that adaptation in cone spectral-opponent channels occurs at multiple sites both before and after spectral opponency.

Tsujimura, S., S. Shioiri, Y. Hirai and Yaguchi, H. (1999). "Selective cone suppression by the L-M- and M-L-cone-opponent mechanisms in the luminance pathway." *Journal of the Optical Society of America A* 16: 1217-1228.

We investigated how transient changes of background color influence the L- and M- (long- and middle-wavelength-sensitive-) cone signals in the luminance pathway. Motion identification thresholds were measured for a drifting sinusoidal grating (1 cycle/deg) modulated along different vector directions in L- and M-cone contrast space. The color of a central 4-degree diameter region was briefly altered (500 ms) by incrementing or decrementing either L- or M-cone excitation. Incrementing L-cone and decrementing M-cone excitation produced a field that appeared reddish relative to the yellow surround. Likewise, incrementing M-cone and decrementing L-cone produced a field that appeared greenish. Motion identification thresholds were obtained on the yellow field following the brief color transitions. The results show that the threshold for the L-cone direction was selectively elevated by the background substitution of incrementing L-cone and decrementing M-cone excitation (shift toward reddish color). The same substitution, however, did not affect the threshold in the M-cone direction. Similarly, the threshold for the M-cone direction was selectively elevated by the background substitution of incrementing M-cone, decrementing L-cone excitation (shift toward greenish) without affecting the threshold in the L-cone direction. Experiments using the motion quadrature paradigm confirmed that these effects occur within the luminance mechanisms. These results indicate that the activation of L-on plus M-off signals suppresses the L-cone signal and that the activation of L-off plus M-on signals suppresses the M-cone signals in the luminance pathway. We propose a retinal model based on the experimental results.

## WHAT IS COLOR FOR?

Sumner, P. and J. D. Mollon (2000). "Catarrhine photopigments are optimized for detecting targets against a foliage background." *Journal of Experimental Biology* 203: 1963-1986.

The colour vision of many primates is trichromatic, whereas that of all other mammals is thought to be dichromatic or monochromatic. Moreover, the triplets of cone pigments in different catarrhines (Old World apes and monkeys) are strikingly similar in their spectral positions. We ask whether the selective advantage of trichromacy lies in an enhanced ability to find edible leaves or fruit. Further, we ask whether any factor in these two search tasks has constrained the particular set of cone spectral sensitivities observed in all catarrhines. We measured the spectral properties of the natural environments of six primate species in Uganda: *Pan troglodytes*, *Cercopithecus mitis*, *Cercopithecus ascanius*, *Lophocebus albigena*, *Colobus guereza* and *Colobus badius*. We concentrated on the fruit and leaves in their diets and the leaves of the trees that make up the background against which these diet items must be found. We plotted these measured stimuli in colour spaces appropriate for each primate species, and found that both frugivory and folivory are facilitated by the extra dimension of colour vision found in catarrhines but lacking in most other mammals. Furthermore, by treating the task of searching for food as a signal-detection task, we show that, of all possible combinations of cone sensitivities, the spectral positions of the actual primate pigments are optimal for finding fruit or young leaves against the background of mature leaves. This is because the variance of the chromaticities of the mature leaves is minimised in one channel of the primate's colour vision, so allowing anything that is not a mature leaf to stand out.

Purves, D., B. Lotto and T. Polger (2000). "Color vision and the four-color-map problem." *Journal of Cognitive Neuroscience* 12: 233-237.

Four different colors are needed to make maps that avoid adjacent countries of the same color. Because the retinal image is two dimensional, like a map, four dimensions of chromatic experience would also be needed to optimally distinguish regions returning spectrally different light to the eye. We therefore suggest that the organization of human color vision according to four-color classes (reds, greens, blues, and yellows) has arisen as a solution to this logical requirement in topology.

Loop, M. S. and D. K. Crossman (2000). "High color-vision sensitivity in macaque and humans." *Visual Neuroscience* 17: 119-25.

Psychophysical (behavioral) detection thresholds and color-discrimination thresholds were determined in a macaque using a two-alternative forced-choice procedure. On a white background, detection thresholds were determined for a white increment and three spectral increments: 618, 516, and 456 nm. Intermixed with detection threshold determinations, color-discrimination thresholds were determined by presenting the white increment, and one of the spectral increments, at 1.0 log units above their respective detection thresholds and dimming both until discrimination performance fell to threshold. The monkey could discriminate the color of the increments at detection threshold because the average color-discrimination threshold was  $0.98 \pm 0.14$  log attenuation. Because the monkey was much more sensitive to the spectral increments than the white increment, we performed an unconventional experiment. We determined the monkey's detection threshold for the white increment alone, and with broadband

color filters in the white light path without adjusting the light's intensity. Insertion of several color filters in the light path lowered detection thresholds of both the macaque and six human trichromats. We believe that this improvement in detection thresholds produced by simply inserting color filters in a white light path is a threshold manifestation of the Helmholtz-Kohlrausch effect and suggests that one of color vision's important evolutionary advantages may be improved detection sensitivity.

## **CLINICAL STUDIES AND TESTING**

Sankeralli, M. J., J. C. Chen, A. B. Metha, et al. (2000). "Evidence for mild blue-yellow colour vision deficits immediately following fluorescein angiography." *Ophthalmic and Physiological Optics* 20: 137-141.

**AIMS:** We have investigated the short term effects of fluorescein angiography on the blue-yellow, red-green, and luminance contrast sensitivity of patients with early age-related macular degeneration (ARMD). **METHODS:** Nine ARMD patients with no exudative complications and a visual acuity of 20/60 or better in the tested eye were selected. Cardinal colour directions for the isolation of the red-green, blue- yellow and achromatic (luminance) visual mechanisms were determined for each patient. Contrast sensitivity was measured in each cardinal colour direction immediately before and 20 min after standard 20-flash fluorescein angiography. **RESULTS:** A significant, albeit mild, reduction for blue-yellow contrast sensitivity following angiography was observed (ANOVA,  $\alpha = 0.05$ ). Fluorescein angiographic exposure had no significant effect on red-green or luminance contrast sensitivity. **CONCLUSION:** Our results show that fluorescein angiography causes at least a short term deficit selective to blue-yellow contrast sensitivity in our patient group.