

DALTONIANA

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The bulletin of the International Colour Vision Society

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Daltoniana on the web

Welcome to the 12th 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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Message from the General Secretary - 29/01/03

Preparations for the meeting in Seattle this summer are well underway. The web site is now open for abstract submission and early registration. The address can be found later in this newsletter.

Don't forget to pay your dues and renew your membership. I am working on a venue for the next proceedings and expect to have a proposal from a reputable journal soon. The Proceedings of the previous meeting in Cambridge are in press now and are expected to be published in the Spring. The volume will be called "Normal and Defective Colour Vision", edited by John Mollon, Joel Pokorny and Ken Knoblauch, Oxford University Press.

Deliberations on the choice of the next Verriest Medalist or well under way, and there may be a decision as this newsletter goes to press.

We are all saddened on hearing of the death of Dick Cavonius. In addition to his many scientific contributions, Dick served on the Board of Directors of the ICVS for many years and edited or participated in the editing of several volumes of the Proceedings. He was elected to the status of Honorary Member at the last business meeting.

Obituary - Dick Cavonius

The death occurred on 20th January of Professor Carl Richard Cavonius, at the age of seventy. Professor Cavonius was an honorary member of ICVS. He contributed papers to several volumes of the Society's Proceedings and he gave the Society great service in editorial roles during the 1990's.

Having taken his first degree in physics, Dick Cavonius was a member of the distinguished group of visual scientists who were trained in Lorrin Riggs' laboratory at Brown University in the 1960's. He held research posts at the Universities of Maryland, Munich, Cambridge and Amsterdam before becoming a Director of the Institut für Arbeitsphysiologie at the University of Dortmund. There for twenty years he led an active Department of sensory scientists, whose work covered both fundamental visual processes and applied problems, such as the legibility of displays.

During his scientific career, Dick Cavonius himself made contributions on many topics, including spatial vision, chromatic discrimination, short-wave luminosity, binocular interaction, and the origin of the alpha rhythm. Amongst his particularly influential papers on colour vision are his demonstration, with R. Hilz, that luminance edges may enhance colour discrimination and his measurement, with O. Estévez, of the spatial contrast sensitivity functions of the individual cone mechanisms. He was one of the four founders of the European Vision Conference.

Born to Finnish parents who had emigrated to the United States, Dick Cavonius was a very private man, but to those who knew him well he extended a warm and generous friendship. He was fond of elaborate academic jokes, and once conspired successfully to secure the election of a fictitious candidate to a learned society that had grown lax in its admission procedures. And yet there was another side to him: He knew how to interact with officials and managers. As a young man he served as a pilot in the US Navy and he remained a reserve officer throughout much of his scientific career.

Dick Cavonius is survived by his wife Rita and his daughter Lillie.

John Mollon

Verriest medallist

We are pleased to inform you that as this issue went into press, it was announced that the Verriest Medal Committee has chosen André Roth as the Verriest medallist for 2003. More details in the next Daltoniana.

Next Symposium

The 17th Symposium of the International Color Vision Society will be held in Seattle July 11 - 15, 2003. The setting will be the beautiful campus of the University of Washington.

The meeting will follow the format of other recent ICVS meetings. A full social program will be included to foster informal interaction and to enjoy the physical beauty, history, and culture of Seattle and the Pacific Northwest.

Early meeting registration and abstract submission are now open. Both will close April 1, 2003.

Accommodations in either on-campus housing or nearby hotels can also now be reserved. On-campus housing deadline is also April 1. The reserved hotels will likely book up early.

For all details, abstract submission, registration, and accommodations for ICVS 2003 Seattle, please visit the conference web site at

<http://depts.washington.edu/icvs2003/>

TENTATIVE SESSION TOPICS

- Color appearance and constancies
- Spatial and temporal aspects of color vision
- Color vision outside the fovea
- Retinal and cortical color processing
- Photopigments and genetics of color vision
- Comparative color vision, evolution, and ecology
- Development and aging of color vision
- Color-vision deficiencies, testing, and standards
- Applied issues in color display and recognition

FEATURED SPEAKERS (more to be announced)

- Dennis Dacey, University of Washington
- Anita Hendrickson, University of Washington
- Brian Wandell, Stanford University
- Shozo Yokoyama, Syracuse University

SOCIAL PROGRAM (included in the meeting registration fee)

- Group lunches and receptions to foster informal scientific and social interaction.
- A reception/dinner and guided visit to the Burke Museum of Natural History and Culture of the Pacific Northwest on the UW campus.
- A visit to the vibrant and historic Pike Place Market and the Seattle waterfront.
- An evening cruise of Puget Sound and Seattle waterways with views of downtown Seattle, Mount Rainier, and the Olympic Mountain Range.
- A visit to Blake Island featuring a re-creation of a Northwest Native American village and traditional alder-smoked salmon dinner.
- A formal conference banquet at the UW Faculty Club with sweeping views of Lake Washington and the Cascade Mountain Range.

ACCOMPANYING PERSONS

Seattle is a truly great place to visit and accompanying persons, including families, are most welcome. The conference web site notes accommodations particularly suited for families. The registration fee for accompanying persons will include all evening social events (receptions/dinners on Friday, Saturday, and Monday) and the Sunday excursion, as described above.

CONFERENCE ORGANIZERS:

Steve Buck Samir Deeb

<http://depts.washington.edu/icvs2003/> or contact Steve Buck, sbuck@u.washington.edu.

Membership 2002/3

To apply for membership for 2002/3, fill out the accompanying form, noting the appropriate method of payment, and return it to Anne Kurtenbach (e-mail: anne.kurtenbach@uni-tuebingen.de; Fax: + 49 7071 295038). Subscriptions are payable in EUROS only. Regular/new members are required to pay 120 EURO (students/retired 25 EURO). Please check that all bank charges are pre-paid and that the credit card supplement is added to your dues, to ensure that we receive the full amount.

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Thank you.

Anne Kurtenbach Lindsay T. Sharpe

(Membership Secretary) (Treasurer)

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Abstracts of color vision papers. Compiled by Joel Pokorny

Color in the cortex

Shapley, R. & M. Hawken (2002). "Neural mechanisms for color perception in the primary visual cortex." Current Opinion in Neurobiology 12(4): 426-432.

New neurophysiological results show the existence of multiple transformations of color signals in the primary visual cortex (V1) in macaque monkey. These different color mechanisms may contribute separately to the perception of color boundaries and colored regions. Many cells in V1 respond to color and to black-white (luminance) patterns. These neurons are spatially selective and could provide signals about boundaries between differently colored regions. Other V1 neurons that prefer color over luminance respond without much spatial selectivity to colored stimuli, and could be the neural basis for the response to local color modulation within a region. How these different types of color cells combine inputs from cone photoreceptors is what gives them their different spatial selectivities for color.

Dow, B. M. (2002). "Orientation and color columns in monkey visual cortex." *Cerebral Cortex* **12**(10): 1005-1015.

The literature on orientation and color columns in monkey visual cortex is reviewed. The orientation column model most consistent with existing data is one containing 'stripes' of alternating positive and negative orientation 'singularities' (cytochrome oxidase blobs) which run along the centers of ocular dominance (OD) columns, with horizontal and vertical orientations alternating at interblob centers. Evidence is summarized suggesting that color is mapped continuously across the monkey's primary visual cortex, with the ends of the spectrum located at 'red' and 'blue' cytochrome oxidase blobs and extra-spectral purple located between adjacent red and blue blobs in the same OD column. In the orientation column model, the 'linear zones' of Obermayer and Blasdel have the appearance of the lines on a pumpkin. A pinwheel model of color columns, consistent with existing data, includes spectral and extra-spectral colors as spokes. Spectral iso-color lines run across iso-orientation lines in linear zones, while extra-spectral iso-color lines occupy the 'saddle points' of Obermayer and Blasdel. The color column model accounts for closure of the perceptual color circle, as proposed by Isaac Newton in 1704, but does not account for color opponency.

Conway, B. R., D. H. Hubel, & M. S. Livingstone (2002). "Color contrast in macaque V1." *Cerebral Cortex* **12(9): 915-925.**

We explored the neural basis for spatial color contrast (red looks redder surrounded by green) and temporal color contrast (red looks redder if preceded by green) in primary visual cortex (V1) of the alert macaque. Using pairs of stimuli, we found a subset of neurons that gave stronger responses to sequences of red and green spots and stronger responses to adjacent red and green spots. These cells combined their cone inputs linearly: for a red-ON-center cell, the sum of the OFF response to green and the ON response to red predicted the peak response to red preceded by green. These 'color' cells, which could underlie hue discrimination because they show cone opponency, could mediate spatial and temporal color contrast. In contrast, the majority of cortical cells, which do not show overt cone opponency but which are often orientation tuned and/or direction selective, are by themselves incapable of mediating hue discrimination. The remarkable degree of specialization shown by cells in V1, especially that of the double-opponent color cells, is discussed.

Landisman, C. E. & D. Y. Ts'o (2002). "Color processing in macaque striate cortex: relationships to ocular dominance, cytochrome oxidase, and orientation." *Journal of Neurophysiology* **87(6): 3126-3137.**

We located clusters of color-selective neurons in macaque striate cortex, as mapped with optical

imaging and confirmed with electrophysiological recordings. By comparing responses to an equiluminant red/green stimulus versus a high-contrast luminance stimulus, we were able to reveal a patchy distribution of color selectivity. Other color imaging protocols, when compared with electrophysiological data, did not reliably indicate the location of functional structures. The imaged color patches were compared with other known functional subdivisions of striate cortex. There was a high degree of overlap of the color patches with the cytochrome-oxidase (CO) blobs. The patches were often larger than a single blob in size, however, and in some instances spanned two neighboring blobs. More than one-half (56%) of the color-selective patches seen in optical imaging were not confined to one ocular dominance (OD) column. Almost one-quarter of color patches (23%) extended across OD columns to encompass two blobs of different eye preference. We also compared optical images of orientation selectivity to maps of color selectivity. Results indicate that the layout of orientation and color selectivity are not directly related. Specifically, despite having similar scales and distributions, the maps of orientation and color selectivity were not in consistent alignment or registration. Further, we find that the maps of color selectivity and of orientation are each only loosely related to maps of OD. This description stands in contrast to a common depiction of color-selective regions as identical to CO blobs, appearing as pegs in the centers of OD columns in the classical "ice cube" model. These results concerning the pattern of color selectivity in V1 support the view (put forth in previous imaging studies of the organization of orientation and ocular dominance) that there is not a fundamental registration of functional hypercolumns in V1.

Landisman, C. E. & D. Y. Ts'o (2002). "Color processing in macaque striate cortex: electrophysiological properties." *Neurophysiology* 87(6): 3138-3151.

We have shown in the accompanying paper that optical imaging of macaque striate cortex reveals patches that are preferentially activated by equiluminant chromatic gratings compared with luminance gratings. These imaged color patches are highly correlated, although not always in one-to-one correspondence, with the cytochrome-oxidase (CO) blobs. In the present study, we have investigated the electrophysiological properties of neurons in the imaged color patches and the CO blobs. Our results indicate that individual blobs tend to contain cells of only one type of color opponency: either red/green or blue/yellow. Individual imaged color patches, however, can bridge blobs of similar opponency or differing opponency. When imaged color patches contain two blobs of differing opponency, the cells in the bridge region exhibit mixed color properties that are not opponent along the two cardinal color axes (either red/green or blue/yellow). Two blobs within a single imaged color patch receive input from the same eye or from different eyes. In the latter case, the bridge region between blobs contains binocular cells that are color selective. Because the cells recorded in imaged color patches were more color selective and unoriented than cells outside of color patches, color properties appear to be organized in a clustered and segregated fashion in primate V1.

Xiao, Y., Y. Wang & D.J. Felleman (2003). "A spatially organized representation of colour in macaque cortical area V2." *Nature* 421(6922): 535-539.

Neurons responding selectively to different colours have been found in various cortical areas in macaque monkeys; however, little is known about whether and how the representation of colour is spatially organized in any cortical area. Cortical area V2 contains modules that respond preferentially to chromatic modulation, which are located in thin cytochrome oxidase stripes. Here we show that within and beyond these modules, gratings of different colours produce activations that peak at different locations. Optical recording of intrinsic signals revealed that the peak regions of the responses to different colours were spatially organized in the same order as colour stimuli are arranged in the DIN (German standard colour chart) colour system. Nearby regions represented colours of a similar hue. We found that the set of colour-specific regions formed 0.07-0.32-mm-wide and approximately 1.3-mm long bands that varied in shape from linear to nearly circular. Our finding suggests that thin stripes in V2 contain functional maps where the colour of a stimulus is represented by the location of its response activation peak.

Shipp, S. & S. Zeki (2002). "The functional organization of area V2, I: specialization across stripes and layers." *Visual Neuroscience* 19(2): 187-210.

We used qualitative tests to assess the sensitivity of 1043 V2 neurons (predominantly multiunits) in anesthetised macaque monkeys to direction, length, orientation, and color of moving bar stimuli. Spectral sensitivity was additionally tested by noting ON or OFF responses to flashed stimuli of varied size and color. The location of 649 units was identified with respect to cycles of cytochrome oxidase stripes (thick-inter-thin-inter) and cortical layer. We used an initial 8-way stripe classification (4 stripes, and 4 "marginal" zones at interstripes boundaries), and a 9-way layer classification (5 standard layers (2-6), and 4 "marginal" strata at layer boundaries). These classes were collapsed differently for particular analyses of functional distribution; the main stripe-by-layer analysis was performed on 18 compartments (3 stripes x 6 layers). We found direction sensitivity only within thick stripes, orientation sensitivity mainly in thick stripes and

interstripes, and spectral sensitivity mainly in thin stripes. Positive length summation was relatively more frequent in thick stripes and interstripes, and negative length/size summation in thin stripes. All these "majority" characteristics of stripes were most prominent in layers 3A and 3B. By contrast, "minority" characteristics (e.g. spectral sensitivity in thick stripes; positive size summation in thin stripes) tended to be most frequent in the outer layers, that is, layers 2 and 6. In consequence, going by the four functions tested, the distinctions between stripes were maximal in layer 3, moderate in layer 2, and minimal in layer 6. Pooling all layers, there was some indication of asymmetry in the stripe cycle, in that thin stripe characteristics (spectral sensitivity, orientation insensitivity, and negative size summation) were also evident in the marginal zone and interstripe immediately lateral to a thin stripe, but less so medially. Within thin stripes, spectral and orientation selectivities were negatively correlated; this was still more accentuated amongst the minority spectrally tuned cells of thick stripes, but absent from interstripes, where these two properties were randomly assorted. Directional and spectral sensitivities were each coupled to negative size summation, but not to each other. We conclude that these functional characteristics of stripes are consistent with segregated, specialized pathways ascending through their middle layers, whilst the outer layers, 1, 2, and 6, utilize feedback from higher areas to adopt a more integrative role.

Receptor input and color in the cortex

Baseler, H. A., A. A. Brewer, L.T. Sharpe, A.B. Morland, H. Jagle & B.A. Wandell (2002). "Reorganization of human cortical maps caused by inherited photoreceptor abnormalities." *Nature Neuroscience* 5(4): 364-370.

We describe a compelling demonstration of large-scale developmental reorganization in the human visual pathways. The developmental reorganization was observed in rod monochromats, a rare group of congenitally colorblind individuals who virtually lack cone photoreceptor function. Normal controls had a cortical region, spanning several square centimeters, that responded to signals initiated in the all-cone foveola but was inactive under rod viewing conditions; in rod monochromats this cortical region responded powerfully to rod-initiated signals. The measurements trace a causal pathway that begins with a genetic anomaly that directly influences sensory cells and ultimately results in a substantial central reorganization.

Solomon, S. G. (2002). "Striate cortex in dichromatic and trichromatic marmosets: neurochemical compartmentalization and geniculate input." *Journal of Comparative Neurology* 450(4): 366-381.

The superficial layers of primate striate cortex (V1) contain a regular pattern of dense staining for cytochrome oxidase (CO) reactivity ("blobs") that receive direct input from the koniocellular layers of the lateral geniculate nucleus. It has been suggested that the blob regions are dedicated to processing color information. Here, the neurochemical compartmentalization of blobs and their input from the lateral geniculate nucleus (LGN) was measured in marmosets (*Callithrix jacchus*) identified as having either dichromatic or trichromatic color vision. In all animals, layer III of V1 showed a patchy distribution of CO. The spatial density of CO blobs (mean, 4.6 blobs/mm²; range, 3.9-5.5), blob diameter, and the proportion of cortical area within blobs was not significantly different in dichromats and trichromats. The LGN input was studied by injecting retrograde tracer into V1. The koniocellular layers of the LGN contribute 11% of all relay cells, and form the only geniculate input to upper layer III of V1. Only half of all relay cells

in the KC layers express calbindin. There is no obvious difference between dichromats and trichromats in the pattern of the geniculate projection to V1. It is concluded that the trichromatic phenotype is not associated with changes in the gross anatomy, neurochemistry, or organization of the geniculate afferents to the superficial layers of V1.

Shostak, Y., Y. Ding, J. Mavity-Hudson, & V.A. Casagrande (2002). Cortical synaptic arrangements of the third visual pathway in three primate species: *Macaca mulatta*, *Saimiri sciureus*, and *Aotus trivirgatus*. *Journal of Neuroscience* 22(7): 2885-2993.

The koniocellular (K) pathway is one of three pathways from the lateral geniculate nucleus (LGN) to primate visual cortex (V1). K pathway projections to the cytochrome oxidase (CO) blobs of V1 suggest involvement in chromatic processing given reports that the CO blobs in diurnal primates contain cells selective for color. K LGN layers and CO blobs, however, are also well developed in nocturnal primates such as owl monkeys, which are likely to be color blind. Thus, the K pathway plays either different roles in different species or some as yet unidentified common role(s). Because synaptic arrangements underlie functional mechanisms, the purpose of this investigation was to compare the synaptic circuitry related to the K pathway within the CO blobs of two diurnal primates (macaque monkeys and squirrel monkeys) and one nocturnal primate (owl monkey). Presynaptic K axons were labeled with wheat germ agglutinin-HRP, and presynaptic and postsynaptic profiles in CO blobs were identified with post-embedding immunocytochemistry for GABA and glutamate. In all three species, K axon terminals are glutamatergic and larger than local axon terminals, suggesting that they have a greater impact on postsynaptic CO blob targets than signals arriving via layer IV from the P or M pathways. A greater proportion of K axons, however, synapse with larger glutamatergic shafts in the diurnal monkeys than in the nocturnal owl monkey, perhaps reflecting the importance of color within the K pathway of these diurnal species. Alternatively, the loss of color vision in the owl monkey could impact K pathway circuitry earlier in the pathway. The basic similarities between K axon circuitry within the CO blobs of the three primate species examined also could indicate that this pathway plays some common role or roles across species.