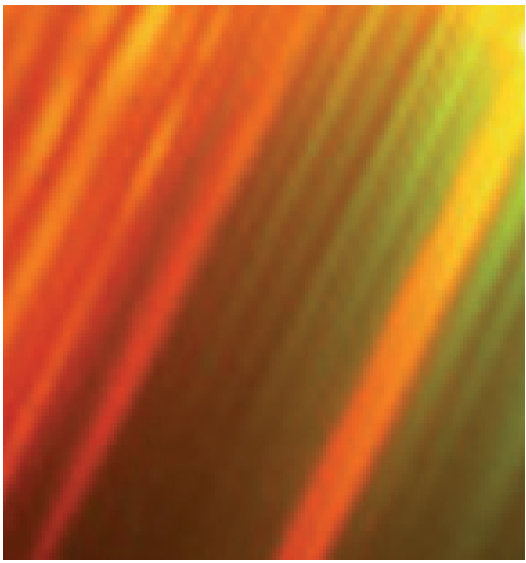
19th SYMPOSIUM of the INTERNATIONAL COLOUR VISION SOCIETY ABSTRACTS BOOK

BELÉM PARÁ BRAZIL
27-31 JULY 2007



luiz carlos l silveira
dora f ventura
barry b lee
[org]

19th SYMPOSIUM of the INTERNATIONAL COLOUR VISION SOCIETY ABSTRACTS BOOK

BELÉM PARÁ BRAZIL
27-31 JULY 2007

LUIZ CARLOS L SILVEIRA
DORA F VENTURA
BARRY B LEE
[ORG]

BELÉM: EDUFPA.
SÃO PAULO: IP/USP (NeC).

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QP 483

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19th Symposium of the ICVS Abstracts Book

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19th Symposium of the
International Colour Vision Society
Belém, 2007

Dear Colleagues,

This meeting is the first symposium of our Society to be held in a Latin American country, Brazil. A glance at the program reveals that the traditional interests of our Society are well represented this year, including contributions by physiologists, psychologists, physicists, geneticists, optometrists, ophthalmologists, and other related professionals who have a research interest in the many aspects of colour vision and colour vision deficiencies. One special session is dedicated to the Nagel Centennial, the anniversary of the introduction of the W.A. Nagel Anomaloscope in 1907.

Santa Maria de Belém do Grão Pará is Belém's official name. The city was founded in 1616 by the Portuguese Francisco Caldeira. It is located in a strategic position to guard the Amazon River delta to protect the Portuguese from invaders coming from the Atlantic Ocean. Belém's architecture reflects the Portuguese ability to adapt to new environments and different climates. The city has flourished with Amazon forest richness: Brazilian wood, rubber trees, and more recently gold and other minerals. The Amazonian forest biodiversity is high on the list of Brazilian interests. Belém is paved with mango trees, imported from India during the colonial period, which make arches on the main avenues. The mango tree shade is a nice refuge on sunny days and also in the rainy season. However, all the cars in Belém carry the marks of the mangos that fall from the trees! July in Belém is sunny and warm with temperatures of 35-40 ^{o}C. Humidity is relatively high, but not excessive compared to the central USA! There can be spectacular afternoon thunderstorms. Hotels and many restaurants usually have air conditioning.

The Federal University of Pará (UFPA) in Belém celebrates its 50 anniversary in 2007 with the centre of the festivities in July. The Rector and staff of the University welcome ICVS on this occasion and are pleased to acknowledge the 19th ICVS Symposium as part of the official University calendar. The Brazilian scientific community is proud to host the ICVS meeting.

We wish all participants a pleasant so journ in Belém and hope that they get the chance to enjoy the surrounding countryside. On behalf of the organising committee, we would like to thank the various organisations which have supported the meeting, and would also like to thank all the students and staff for their help in organising the meeting.

Luiz Carlos L. Silveira
Dora F. Ventura
Barry B. Lee

Program

19th Symposium of the
International
Colour Vision Society
27-31 July 2007
Belém Pará Brazil

Friday, 27th July 2007

Crowne Plaza Hotel

09:00
Welcome desk open

09:00 – 12:00
Directors' Committee Meeting

14:00 – 14:30
Opening of the Symposium

14:00 – 14:15
Dora F. Ventura
Organizing Committee Representative
Institute of Psychology,
University of São Paulo,
São Paulo, Brazil.

14:15 – 14:30
Alex B. Fiúza de Mello
University Rector
Federal University of Pará,
Belém, Brazil.

14:30 – 15:30
David R. Williams
Invited speaker
Center for Visual Science,
University of Rochester,
Rochester, USA.
The limits of human vision.
D.R. Williams

15:30 – 16:00
Coffee break

16:00 – 17:00

Molecular biology of colour vision.

Jay Neitz

Chair

Department of Ophthalmology and Department of
Cell Biology, Neurobiology, & Anatomy,
Medical College of Wisconsin,
Milwaukee, USA.

16:00 – 16:15

Samir S. Deeb

Evolution of cone visual pigment genes.
S.S. Deeb, M. Anderson, F. Greutzner,
J.A. Marshall Graves, M. Wakefield

16:15 – 16:30

Maureen Neitz

How nucleotide polymorphisms upstream of the X-chromosome opsin gene array tune L:M cone ratio.
M. Neitz, K.L. Gunther, J. Neitz

16:30 – 16:45

Katie Mancuso

Welcome to the wonderful world of color: Gene therapy treatment for colorblindness.
K. Mancuso, T.B. Connor, M.C. Mauck,
J. Kuchenbecker, W.W. Hauswirth,
J. Neitz, M. Neitz

16:45 – 17:00

Matthew C. Mauck

Longitudinal evaluation of expression of virally delivered transgenes in gerbil cone photoreceptors.
M.C. Mauck, M. Neitz, J. Neitz

17:00 – 17:45

Analysis of normal colour vision

Steven L. Buck
Chair
Department of Psychology,
University of Washington,
Seattle, USA.

17:00 – 17:15
Marisa Rodríguez-Carmona

Sex-related differences in chromatic sensitivity.
M. Rodríguez-Carmona, J.A. Harlow,
L.T. Sharpe, J.L. Barbur

17:15 – 17:30
Neil R. A. Parry

Reaction time measures of adaptation to chromatic contrast.
N.R.A. Parry, I.J. Murray, D. McKeefry

17:30 – 17:45
Marcus Vinícius C. Baldo

A simple neural network model accounts for the visual decomposition of color in the flash-lag effect.
M.V.C. Baldo

18:30 – 18:50
Bus from Crowne Plaza Hotel to
Casa Feliz Lusitânia

19:00 – 21:00
Dinner
Casa Feliz Lusitânia

21:30 – 21:50
Bus from Casa Feliz Lusitânia to
Crowne Plaza Hotel

Saturday, 28th July 2007

Crowne Plaza Hotel

09:00 – 11:45

Photopigments, photorreceptors, and retinal mechanisms of colour vision.

Dora F. Ventura

Chair

Institute of Psychology,
University of São Paulo,
São Paulo, Brazil.

09:00 – 09:30

James K. Bowmaker

Invited speaker

Colour vision: phylogeny and ontogeny.
J.K. Bowmaker, J.W.L. Parry, K.L. Carleton, T. Spady, D.M. Hunt, G. Jeffery

09:30 – 10:00

Ellis R. Loew

Invited speaker

Oil droplet distribution in three species of anoline lizard: Implications for colour vision.
E.R. Loew, D. Campbell.

10:00 – 10:30

Russell D. Hamer

Invited speaker

New knockout and overexpression data challenge our understanding of the 'front-end' reactions in vertebrate rod phototransduction.
R.D. Hamer, D. Tranchina, S.C. Nicholas, T.D. Lamb.

10:30 – 11:00

Coffee break

11:00 – 11:30
Heinz Wässle
Invited speaker

The primordial, blue-cone color system of the mouse retina.
H. Wässle

11:30 – 11:45
Kenkichi Fukurotani

Spectral responses of horizontal cells in the retina of chracinid fishes.
K. Fukurotani

11:45 – 12:15
Cone signal processing
Neil R. A. Parry
Chair
Vision Science Centre,
Manchester Royal Eye Hospital,
Manchester, England, UK.

11:45 – 12:00
Jan Kremers

Cone signal processing in the asymmetrical on- and off-electroretinograms.
J. Kremers

12:00 – 12:15
Ian J. Murray

High luminance L- & M-cone isolating ERGs: LED vs CRT stimulation
I.J. Murray, J. Kremers, N.R.A. Parry

12:30 – 13:30
Lunch
Crowne Plaza Hotel

14:00 – 17:00

The colour vision of primates: retinal organization and visual pathways.

John D. Mollon
Chair

Department of Experimental Psychology,
University of Cambridge,
Cambridge, England, UK.

14:00 – 14:30
Gerald H. Jacobs
Invited speaker

New World monkeys and color.
G.H. Jacobs

14:30 – 15:00
Barbara L. Finlay
Invited speaker

Developmental programs coordinating size and niche variations in the primate eye and retina.
B.L. Finlay, M.A. Dyer, M. da Silva Filho, J.A.P.C. Muniz, L.C.L. Silveira

15:00 – 15:15
Luiz Carlos L. Silveira

Physiological properties of photoreceptors and retinal ganglion cells from a thrichromatic platyrrhine: the howler monkey, *Alouatta sp*.
L.C.L. Silveira, C.A. Saito, M. da Silva Filho, J.K. Bowmaker, J.Kremers, B.B. Lee

15:15 – 15:30
Hao Sun

Perceived vernier phase shift due to contrast gain control.
H. Sun, B.B. Lee, R.C. Baraas

15:30 – 16:00
Coffee break

16:00 – 16:15
Valdir F. Pessoa

Colour vision perception in howler monkeys (*Alouatta caraya*).
A.C. Araújo Jr, U.R. Gomes, J.J. Didonet, C.S. Araújo, P. Saletti, V.F. Pessoa

16:15 – 16:30
Brice Chaix de Lavarène

Model of adaptive processing for reconstructing chromatic information from the random mosaic of cones.
B. Chaix de Lavarène, J. Hérault, D. Alleysson

16:30 – 16:45
Marina V. Danilova

Estimation of relative L-cone and M-cone sensitivities from a performance measure and from a phenomenological measure.
M.V. Danilova, T.V. Demchenko

16:45 – 17:00
Mikhail Vorobyev

Sensitivity to luminance and chromaticity of the parvocellular pathway: an ideal observer model.
M. Vorobyev

17:00 – 18:00
Verriest Medal
Barry B. Lee
Verriest Medalist

Psychophysical models, physiological reality and the specificity of retinal signals.
B.B. Lee

SUNY
College of Optometry,
State University of
New York,
New York, USA.

18:30 – 18:50

Bus from Crowne Plaza Hotel to
Igreja de Santo Alexandre

19:00 – 21:00

Reception

Igreja de Santo Alexandre and Galeria Fidanza
Reception offered by the Governor of the State of Pará, talk about the Amazon, music, and cocktails.
Free time to visit the Old City, Castle Fort, House of the Eleven Windows, Carmo College Square, and the surroundings.

21:30 – 21:50

Bus from Igreja de Santo Alexandre to
Crowne Plaza Hotel (optional)

Sunday, 29th July 2007
Crowne Plaza Hotel

09:00 – 12:15
Colour and reality
Qasim Zaidi
Chair
SUNY College of Optometry,
State University of New York,
New York, USA.

09:00 – 09:30
Shin'ya Nishida
Invited speaker
The perception of reflectance properties of natural surfaces using image statistics.
S. Nishida, I. Motoyoshi, L. Sharan, Y. Li, E.H. Adelson

09:30 – 10:00
David H. Brainard
Invited speaker
Color, gloss, and 3D objects.
D.H. Brainard, B. Xiao

10:00 – 10:15
João Manuel M. Linhares
The effects of colored lenses on the number of discernible colors perceived by dichromats in natural scenes.
J.M.M. Linhares, P.D. Pinto, S.M.C. Nascimento

10:15 – 10:30
Vasco Miguel N. de Almeida
Color constancy of real 3-D objects and the roles of spatial and temporal mechanisms.
V.M.N. de Almeida, P.T. Fiadeiro, M. Teixeira, S.M.C. Nascimento, Q. Zaidi

10:30 – 11:00
Coffee break

11:00 – 11:15
Hannah E. Smithson
Keeping track of colour contexts.
H. Smithson, R. Lee

11:15 – 11:30
Qasim Zaidi
Color-based identification of real 3-D objects.
Q. Zaidi, M. Bostic

11:30 – 11:45
John D. Mollon
The caerulean line and the unique hues.
J.D. Mollon, R. Lee

11:45 – 12:15
Discussion

12:30 – 12:50
Bus from Crowne Plaza Hotel to
Estação das Docas

13:00 – 18:00
River boat trip
Departure from Estação das Docas, lunch in the boat, a bit of music, stop in Mosqueiro Island to explore the village, back to Estação das Docas.

19:00 – 21:00
Dinner
Restaurante Pomme d'Or

21:30 – 21:50
Bus from Estação das Docas to
Crowne Plaza Hotel

Monday, 30th July 2007

Crowne Plaza Hotel

09:00 – 10:30

Rods and colour discrimination

Stephen J. Dain

Chair

School of Optometry and Vision Science,
University of New South Wales,
Sydney, Australia.

09:00 – 09:15

Joel Pokorny

Surface color perception of color defective observers under dim illuminations.

J. Pokorny, M. Lutze, D. Cao, A.J. Zele

09:15 – 09:30

Steven L. Buck

Modeling rod influence on hue perception.

S.L. Buck, C.R. Connor

09:30 – 09:45

Ding Cai Cao

Chromatic discrimination with rod contrast.

D. Cao, J. Pokorny, A.J. Zele

09:45 – 10:00

Alex J. Shepherd

Colour induction and rod-cone interactions.

A.J. Shepherd, G. Wyatt

10:00 – 10:15

Laura P. Thomas

Time-course of rod influences on hue perception.

L.P. Thomas, S.L. Buck, C.R. Connor,
K.B. Green, T.Y. Quintana

10:15 – 10:45

Coffee break

10:45 – 11:00

Chromatic discrimination

Joel Pokorny

Chair

Department of Ophthalmology and Visual Science,
The University of Chicago, Chicago, USA.

11:00 – 11:15

Andrew J. Zele

The role of spatial and temporal chromatic contrast for S-cone chromatic discrimination.

A.J. Zele, D. Cao, V.C. Smith, J. Pokorny

11:15 – 11:30

Barbara Y. Ling

Performance of the Lanthony New Color Test by young children.

B.Y. Ling, S.J. Dain

11:30 – 11:45

Rigmor C. Baraas

Mass screening for color-vision deficiencies in Norwegian children.

R.C. Baraas

11:45 – 12:00

Balazs Vince Nagy

Color deficiency correction – methodology and experiment report.

B.V. Nagy, Gy. Ábrahám

12:00 – 12:15

Valdir F. Pessoa

Influence of color on Müller-Lyer illusion in dichromats and trichromats.

C.Y. Simon, M.C.H. Tavares, V.F. Pessoa

12:15 – 12:30

Stephen J. Dain

Colour and luminance increment thresholds in poor readers.

S.J. Dain, R. Floyd, R.T. Elliot

12:30 – 13:30
Lunch
Crowne Plaza Hotel

14:00 – 16:00
Higher cortical mechanisms of colour vision
Ricardo Gattass
Chair
Biophysics Institute,
Federal University of Rio de Janeiro,
Rio de Janeiro, Brazil.

14:00 – 14:15
Steven K. Shevell
Does color misbind to form in afterimages?
S.K. Shevell, R. St. Clair, S.W. Hong

14:15 – 14:30
Anthony D. D'Antona
Object segmentation influences perceived temporal variation of brightness.
A.D. D'Antona, S.K. Shevell

14:30 – 14:45
Sang Wook Hong
Binocular rivalry between identical retinal stimuli with an induced color difference.
S.W. Hong, S.K. Shevell

14:45 – 15:00
Para Kang
The role of luminance edges in misbinding of color to form.
P. Kang, S.K. Shevell

15:00 – 15:15
Ken Knoblauch
Local and global integration of color and orientation in form perception.
K. Knoblauch, E. Mahler, M. Dojat

15:15 – 15:30
Baingio Pinna
Amodal completion of chromatic and achromatic colors.
B. Pinna

15:30 – 15:45
M. Tanca
The object-hole effect in the watercolor illusion.
M. Tanca, B. Pinna

15:45 – 16:15
Stimulus correlates of object colour

15:45 – 16:00
Alexander D. Logvinenko
Stimulus correlates of object colour.
A.D. Logvienko

16:00 – 16:15
Rumi Tokunaga
Perceived dissimilarity of yellow-blue surfaces under neutral light sources differing in intensity: separate contributions of light intensity and chroma.
R. Tokunaga, A.D. Logvinenko, L.T. Maloney

16:15 – 16:30
Coffee break

16:15 – 17:00
Poster session
Posters should be placed in the appropriate locations from Friday 15:30 until Tuesday 10:45. Thus, additional discussion about results exhibited in the posters will be possible at other times during the Symposium.

17:00 – 17:30
Business Meeting

18:30 – 18:50
Bus from Crowne Plaza Hotel to
Parque da Residência

19:00 – 21:00
Banquet
Parque da Residência

21:30 – 21:50
Bus from Parque da Residência to
Crowne Plaza Hotel

Tuesday, 31st July 2007

Crowne Plaza Hotel

09:00 – 10:45

Acquired colour deficiency

Luiz Carlos L. Silveira

Chair

Tropical Medicine Institute and
Department of Physiology,
Biological Sciences Institute,
Federal University of Pará,
Belém, Pará, Brazil.

09:00 – 09:30

John L. Barbur

Invited speaker

Colour vision assessment in patients with acquired loss of chromatic sensitivity.

J.L. Barbur

09:30 – 10:00

Gordon T. Plant

Invited speaker

Colour in disorders of the visual cortex.

G.T. Plant

10:00 – 10:15

Dora F. Ventura

Color vision losses in Duchenne Muscular Dystrophy.

D.F. Ventura, M.F. Costa, M. Zatz, A.G.F. Oliveira, C. Feitosa-Santana

10:15 – 10:45

Coffee break

10:45 – 11:45

The Nagel Centennial

Barry B. Lee
Chair
SUNY College of Optometry,
State University of New York,
New York, USA.

10:45 – 11:00
John D. Mollon

The Nagel anomaloscope 1907-2007.
J.D. Mollon

11:00 – 11:15
Jennifer Birch

Failure of the Farnsworth D15 test and the Nagel anomaloscope matching range in anomalous trichromatism.
J. Birch

11:15 – 11:30
John L. Barbur

A study of the variables that can affect the parameters of the yellow match.
J.L. Barbur, M. Rodríguez-Carmona, J.A. Harlow, K. Mancuso, J. Neitz, M. Neitz

11:30 – 11:45
Donald McPherson

Anomoloscope design with tunable primaries.
D. McPherson, A. Schmeder, J.S. Werner, K. Knoblauch, G. Haegerstrom-Portnoy

11:45 – 12:00
Yang Sun

The contribution to Rayleigh matches of the third red-green photopigment of color-defect carriers.
Y. Sun, S.K. Shevell

12:00 – 12:15

Closing of the meeting

Luiz Carlos L. Silveira
Organizing Committee
President

Tropical Medicine Institute and Department of
Physiology, Biological Sciences Institute,
Federal University of Pará,
Belém, Brazil.

12:30 – 13:00

Bus from Crowne Plaza Hotel to
Churrascaria Pavan

13:00 – 15:00

Churrasco

Optional (by booking)

15:00 – 15:30

Bus from Churrascaria Pavan to
Crowne Plaza Hotel

Verriest Medal Winner 2007

Prof. Barry Lee, PhD

The International Colour Vision Society is pleased to announce that the Verriest Medal will be awarded to Barry B. Lee, Professor of Biological Sciences at the State University of New York, College of Optometry, New York, NY, USA.

This award is bestowed by the Society to honor long-term contributions to the field of color vision. Professor Lee is an innovative multidisciplinary scientist who has an extraordinary record of productivity. He has made significant contributions to our understanding of basic coding mechanisms in visual processing and is recognized for his efforts at bridging the gap between psychophysics and physiology.

In addition, through collaborative efforts, he has been at the center of the great advances that have been made in the last 20 years in unraveling the relations between structure and visual function in the retina.

Finally, the Society recognizes his long-term service to the society, as member of the board of directors, meeting organizer and proceedings editor.

Kenji Kitahara
Ken Knoblauch
Jay Neitz
Janice Nerger
Joel Pokorny
André Roth

Abstracts
Oral Presentation

19th Symposium of the
International
Colour Vision Society
27-31 July 2007
Belém Pará Brazil

Evolution of cone visual pigment genes

S.S. Deeb [1]
M. Anderson [1]
F. Greutzner [2]
J.A. Marshall Graves [2]
M. Wakefield [3]

[1] Departments of Medicine and Genome Sciences,
University of Washington,
Seattle, Washington, USA.

[2] Research School of Biological Sciences,
Australian National University,
Canberra, Australia.

[3] Bioinformatics Division,
The Walter and Eliza Hall Institute,
Parkville, Australia.

We have determined the sequence and structure of the cone visual pigment genes of the platypus (*Ornithorhynchus anatinus*) and the echidna (*Tachyglossus aculeatus*), and inferred their spectral properties and evolutionary pathways. We prepared platypus and echidna retinal RNA and used primers of the middle-wave-sensitive (MWS), long-wave-sensitive (LWS) and short-wave sensitive (SWS1) pigments, corresponding to coding sequences that are highly conserved among mammals, to PCR amplify the corresponding pigment sequences. Amplification from the retinal RNA revealed the expression of LWS pigment mRNA that is homologous in sequence and spectral properties to the primate LWS visual pigments. However, we were unable to amplify the mammalian SWS1 pigment from these two species. Subsequently, when the platypus genome sequence became available, we found that the X-chromosome has an LWS pigment gene that resembles the primate pigment, but, surprisingly we found an adjacent (~ 20 kb) SWS2 pigment gene within this region of conserved synteny. We obtained the same result after sequencing the echidna genes. The encoded SWS2 pigment is predicted to have a

wavelength of maximal absorption of about 440 nm, and is paralogous to SWS pigments typically found in birds, fish and reptiles but not in mammals. In conclusion, a duplication event of an ancestral cone visual pigment gene on the X-chromosome, followed by sequence divergence and selection gave rise to the LWS and SWS2 visual pigments. So far, the echidna and platypus are the only mammals that share the gene structure of the LWS-SWS2 pigment gene complex with birds, fishes or reptiles.

How nucleotide polymorphisms upstream of the X-chromosome opsin gene array tune L:M cone ratio

M. Neitz
K.L. Gunther
J. Neitz

Department of Ophthalmology and Department of Cell Biology, Neurobiology, & Anatomy, Medical College of Wisconsin, Milwaukee, Wisconsin, USA.

Spectral sensitivity functions from the flicker photometric electroretinogram (ERG) corrected for genetic-based variation have been used to characterize the tremendous variation in the ratio of L:M cones among males with normal color vision. We hypothesized that polymorphisms in the region of the L and M photopigment genes are responsible for individual differences in cone ratio. Since it is probable that the L:M cone ratio is subtly tuned by cumulative effects of several individual polymorphisms, testing the hypothesis requires precise estimates of the L:M cone ratio. These were obtained by adjusting for differences in the relative contribution of L versus M cones to the ERG signal using a correction factor obtained by the direct comparison of results from the ERG to those from adaptive optics combined with retinal densitometry. Evidence has accumulated in support of the hypothesis that L and M cones represent a single cell type, differing only in the stochastic choice of which opsin gene is expressed. Under this hypothesis, L:M cone ratio would be tuned by polymorphisms that subtly influence the stochastic choice mechanism. Here we examined nucleotide polymorphisms in the DNA upstream of the opsin gene array between two known cis-regulatory elements, the locus control region (LCR) and the L gene promoter at the 5′ end of the opsin gene array. The polymerase chain reaction and direct DNA sequencing were used to identify nucleotide polymorphisms in 67 Caucasian males. Eleven

positions were found to be polymorphic, but only two occurred at relatively high frequency. The two high frequency polymorphic positions defined three haplotypes: 11 males had CA, 5 males had TA, and 51 had CG. A comparison of the mean percentage of L cones revealed a significant difference between groups. We propose that these nucleotide differences influence chromatin structure and subtly alter the balance between mechanisms of gene silencing versus mechanisms for promoting transcription of the opsin genes, thereby biasing the stochastic mechanism responsible for choosing an L versus an M opsin gene for expression. Although 11 other polymorphisms occurred at too low a frequency to be useful in our statistical analysis, they nonetheless are also likely to contribute to variation in cone ratio.

Supported by

The National Eye Institute and Research to Prevent Blindness.

Welcome to the wonderful world of color: Gene therapy treatment for colorblindness

K. Mancuso [1]
T.B. Connor [1]
M.C. Mauck [1]
J. Kuchenbecker [1]
W.W. Hauswirth [2]
J. Neitz [1]
M. Neitz [1]

[1] Department of Ophthalmology, Medical College of Wisconsin, Milwaukee, Wisconsin, USA.

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Current evidence indicates that the long- (L) and middle- (M) wavelength-sensitive cone photoreceptors are identical except for expression of an L- or M- photopigment gene, making it unlikely that chromatically selective connections are made by postsynaptic neurons. This suggests that during evolution, L/M opponent cells, the substrate for red-green color vision, could have arisen by random wiring to a newly introduced mosaic of L and M cones. However, while it may be possible to explain how the color circuits arose at the level of the retina, understanding how the cortical circuits for color vision might have arisen from random connections has been difficult. For this project, a gene therapy approach to investigate cortical circuitry for color was developed. Gene therapy was performed on adult dichromatic squirrel monkeys that had only short- (S) and M cones, with the intent of adding a new sensory capacity, red-green color vision. An adeno-associated viral vector containing the human L-opsin gene was injected subretinally. The goal was to take advantage of the capricious nature of viral infection to transduce only a subset of the cones near the injection site, producing a retinal

region with two randomly interspersed cone types absorbing in the middle-to-long wavelengths, analogous to the normal human retina. The time course of expression and function of the introduced photopigment was measured in the retinas of treated animals using the RetCam II digital imaging system and a custom built wide-field color multi-focal electroretinogram system. The behavioral effects of adding a third population of cone were assessed using a computer-based test of color vision that was modified for use with animals. Before treatment, the dichromatic monkeys' color discrimination was highly reliable and they always failed to make "red-green" color discriminations, as predicted from their known cone complement. After treatment, the monkeys showed marked improvement in red-green color vision. The finding that the introduction of a third cone pigment by gene therapy in an adult is sufficient to transform a dichromatic animal into one with trichromatic color vision has implications for understanding the cortical circuitry for color vision and plasticity of the adult primate visual system.

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Longitudinal evaluation of expression of virally delivered transgenes in gerbil cone photoreceptors

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Delivery of foreign opsin genes to cone photoreceptors using recombinant adeno-associated virus (rAAV) is a potential tool for studying the basic mechanisms underlying color vision and for treating color vision defects. It is important to understand the details of transgene expression for these methods to be useful. We used an *in vivo* retinal imaging system to monitor, over time, expression of virally-delivered genes targeted to cone photoreceptors in the Mongolian gerbil (*Meriones unguiculatus*). Gerbils have a well-developed photopic visual system, with 11-14% of their photoreceptors being cones. We used replication deficient serotype 5 rAAV to deliver a gene for green fluorescent protein (GFP). In an effort to direct expression of the gene specifically to either S or M cones, the transgene was under the control of either the human X-chromosome opsin gene regulatory elements, i.e., an enhancer termed the Locus Control Region (LCR) and L promoter or the human S-opsin promoter. Longitudinal fluorescence images reveal that gene expression is first detectable about 14 days post-injection, reaches a peak after about 3 months, and is observed more than a year post-injection if the initial viral concentration is sufficiently high. The regulatory elements are able to direct expression to a subpopulation of cones while excluding expression in rods and non-photoreceptor retinal cells. The specificity of the transgene

expression promises to allow experiments to dissect the circuitry underlying color perception by introducing novel opsins into a subset of either S- or M-cones in dichromatic mammals.

Sex-related differences in chromatic sensitivity

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It is often assumed that women have superior colour vision on average compared to men; being more expert in their use of colour names. However, if both X-chromosome linked colour blind males (c. 8%) and females (<1%) as well as heterozygote female carriers (c. 15%) are excluded from comparisons, then no significant differences between men and women in red-green colour discrimination have been reported (e.g., Pickford, 1951; Hood *et al*., 2006). We re-examined this question by assessing the performance of 147 males and 151 females on the Colour Assessment and Diagnosis (CAD) test (Rodriguez-Carmona *et al*., 2005). This test employs direction-specific, moving, chromatic stimuli embedded in a background of random, dynamic, luminance contrast noise. It uses a four-alternative, forced-choice procedure to measure the subject's chromatic displacement thresholds for colour signals in 16 interleaved directions in colour space, while ensuring that the subject cannot make use of any residual luminance contrast signals. In addition, we measured the Rayleigh anomaloscope (Type 1) equation in a subgroup of 61 males and 65 females. The age-matched males (31.0 ± 9.7) and females (26.7 ± 8.8) had normal colour vision according to standard colour vision tests. Females with known colour-blind relatives were eliminated from the study. Non-parametric comparisons (Mann-Whitney tests) between the male and female groups revealed no significant differences in anomaloscope midpoints

(p= 0.898) and matching ranges (p= 0.2), although females tended on average to have a larger mean range (4.22) than males (3.85). However, females had significantly higher CAD thresholds than males along the red-green discrimination axis (p= 0.0002), but not along the yellow-blue. The differences between males and females in discriminating along the red-green axis may be related to X-chromosome inactivation and polymorphic variations in long-wavelength cone sensitivity.

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Reaction time measures of adaptation to chromatic contrast

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There is a very robust relationship between reaction time and contrast that we have previously exploited to obtain an RT measure of sensitivity. We have been interested in what this can tell us about the spatio-temporal and retinotopic properties of the chromatic visual system. In the present study, we have exploited this relationship to obtain a rapid index of chromatic adaptation. Conventional psychophysics usually requires some time to build up a measure of sensitivity, and is thus not well-suited to measuring rapid changes in sensitivity following adaptation. Despite their trial-by-trial variability, RTs have the potential to give high temporal resolution in the adaptation domain. RTs were measured to brief temporally blurred (total 570ms) Gaussian isoluminant chromatic patches (s.d. 0.5deg) whose chromaticities lay along the cardinal chromatic axes (0, 90, 180 and 270deg in MBDKL colour space). Bipolar adapting stimuli were employed (0 vs. 180deg or 90 vs. 270deg). These were larger Gaussian blobs (s.d. 1deg), modulating sinusoidally between the two hues at 1Hz. Throughout the background was illuminant "C". In a single run, 64 stimuli were presented without adaptation,

followed by 64 stimuli each of which was preceded by 3s of adaptation, either along the same or the orthogonal chromatic axis. Finally, 192 RTs were recorded to measure the "washout" of any adaptation. Both adapting and test stimuli were presented at fixed supra-threshold contrasts. The effect of adaptation was seen as a lengthening of the reaction time. This occurred in the first few seconds of the adaptation period. During washout, there was an initial rapid recovery from adaptation (of the order of seconds) although full recovery took several minutes. Adaptation gain functions suggested that the blue-yellow system was less prone to adaptation than red-green.

A simple neural network model accounts for the visual decomposition of color in the flash-lag effect

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In the flash-lag effect (FLE), a stationary, abrupt-onset stimulus is perceived as lagging behind a moving object, when they happen to be physically aligned in both space and time. This visual illusion was rediscovered in its present form by Romi Nijhawan (1994). Nijhawan also showed that a physically yellow stimulus resulting from the combination of a red stationary flash superimposed on a green moving object is perceptually decomposed into a red stimulus that spatially lags behind a moving green one. Despite the intense dispute that followed the discovery of the FLE, which has been hotly debated over the last thirteen years, this chromatic variety of the effect, manifesting itself as perceptual color decomposition, has not been accounted for as yet. Here I present a simple computational model that is not only able to reproduce the spatial misalignment between moving and stationary objects that is inherent to the FLE, but also reproduce the color decomposition of these chromatic stimuli. The present model is an improved extension of a neural network already successful in capturing several empirical phenomena related to the FLE (Baldo and Caticha, 2005). Composed of five processing stages (one input, three hidden and one output layer), the network is endowed with leaky integrate-and-fire neurons coupled with each other by means of excitatory and inhibitory connections, whose architecture is structured into convergent and divergent pathways. In this improved version, the network has been provided with two chromatic channels separately tuned to the spectral features of the

moving and stationary stimuli. Simulations have shown that the stimulus composed of a "red stationary flash" superimposed on a "green moving stimulus" (resulting in a yellow blend) is spatially decomposed along its neural processing through the five layers of the network. This decomposition leads to the activation of spatially segregated pools of neurons in the output layer. These pools of neurons have different spectral sensitivities. The ability of the present model to capture this chromatic decomposition could possibly increase the applicability of simple network models when attempting to explain the basic mechanisms that lead to flash-lag effect and other perceptual phenomena as well.

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Colour vision: phylogeny and ontogeny

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Very early in vertebrate evolution, four spectral classes of cone visual pigments evolved through a series of gene duplications from an ancestral single opsin gene. Although two of these spectral classes have been lost in mammals, many lower vertebrates are tetrachromatic, retaining all four cone classes. In teleost fish, however, the situation is more complex, because a duplication of the whole genome is thought to have occurred early in the evolution of ray-finned fish. As a consequence of this and further subsequent opsin gene duplications, many fish possess multiple functional cone opsin genes, which are differentially expressed through ontogenetic transformations. These changes are reflected during development in significant variations in the spectral sensitivity of cones and presumably in the colour vision of the fish. This is exemplified in the cichlid species flocks of the African Great Lakes where species express at least seven cone opsin genes: one LWS, three RH2, two SWS2 and one SWS1. In addition, many teleosts also express mixtures of visual pigment "pairs" based on Vitamin A1 and Vitamin A2, with the ratio of the pair varying during development or even seasonally. In the anguilliform eels both gene expression and the ratio of visual pigment pairs in cones change during metamorphosis, having significant effects on colour vision.

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Oil droplet distribution in three species of anoline lizard: Implications for colour vision

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The cones of diurnal lizards contain oil droplets within their inner segments that can act as filters affecting the spectral sensitivity of the cells. The Caribbean anoles represent a broad radiation inhabiting a number of photic environments. A microspectrophotometric (MSP) study has measured the visual pigments and associated oil droplets for a number of ecotypes in the hopes of correlating these with the photic environment and the coloured dewlap of displaying males. However, MSP cannot provide reliable information on the relative number of the different chromatic classes of cone (visual pigment λmax + oil droplet) or their distribution over the retina. For this study whole mounts were made from the eyes of individual lizards and the different spectral classes of oil droplet (yellow, green and colourless) counted in six retinal regions using the optic disc and foveae as landmarks. Intra- and inter-specific comparisons were made between the counts. Anolis cristatellus showed 80% green and 10% each yellow and colourless droplets with no intraspecific differences between sampled areas, eyes or sexes. A. sagrei showed 90% yellow with 5% each green and colourless droplets! A. carolinensis showed 50% yellow, 45% green and 5% colourless droplets. An attempt will be made to rationalize these findings in the context of image sampling and colour processing.

New knockout and overexpression data challenge our understanding of the "front-end" reactions in vertebrate rod phototransduction

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Advances in molecular biological methodologies now permit a molecule-by-molecule "dissection" of the biochemical cascade by selective deletion, insertion, over (OX)- or underexpression of specific cascade proteins and by site-directed mutagenesis. These manipulations have provided important insights into the role each protein plays in the photoresponse. We investigate here the mechanisms that turn off activated rhodopsin (R*). R* shutoff is thought to proceed via several steps in which rhodopsin kinase (RK) phosphorylates R*, followed by a final quench when arrestin (Arr) binds to multiply-phosphorylated R*. RK and G-protein are thought to compete for mutually exclusive binding with R*. The kinetics of the inactivation process are thought to be Ca^{2+}-sensitive. A prevailing view is that light elicits a drop in free internal Ca^{2+}, causing the Ca^{2+}-binding protein, recoverin (Rec), to unbind from RK, releasing it from inhibition; the resulting increase in free RK (RK*) speeds photocurrent recovery by speeding the phosphorylation steps in the inactivation of R* (Burns and Arshavsky, 2005). The above scheme predicts

that any manipulation that increases the steady-state amount of RK* should (i) attenuate the dim-flash response, speed recovery kinetics from the instant a flash is applied, and (ii) reduce the gain in both dim-flash and bright-flash regimes, with the magnitude of these effects depending on the magnitude of the increase in RK*. In striking contrast with prediction (i), Rec-/- and WT single-photon responses (SPRs) have identical amplitudes and kinetics up to (Makino *et al*., 2004) and beyond the peak of the response (Krispel *et al*., 2006). In addition, OX of RK by either 2x or 4x has no effect on either the amplitude or kinetics of the entire SPR waveform (Hamer *et al*., 2005). Consistent with prediction (ii), Rec-/- *does* reduce the gain in the bright-flash regime. However, surprisingly, OX of RK by 2x has no impact on the saturation period in response to bright flashes (Hamer *et al*., 2005). Using a recent model that was able to reproduce many rod response features in both SPR and bright-flash regimes (Sampath *et al*., 2005), we will examine the new data and the complexities they raise, and will show quantitatively how they are incompatible with the "front-end" chemistry summarized above. We will discuss at least one alternative scheme that may help unify our understanding of the data.

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The primordial, blue-cone color system of the mouse retina

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It is well known, that visual signals in the brain are processed in parallel, with movement, color, stereopsis. Even specific features, such as faces, are being analyzed in different parts of the cortex. Parallel processing starts as early as the first synapse of the retina, the cone pedicle, where the light signal is transferred onto at least nine different types of bipolar cells. The presentation will focus on the color selective pathway through the mammalian retina. Amongst mammals, only old world primates and humans have trichromatic color vision based on the comparison of signals from S-, L- and M-cones. It has evolved approximately 35 million years ago and represents a recent phylogenetic development. The L-, M- discrimination of the primates is based on the "private line" of an individual cone to a midget bipolar and a midget ganglion cell. Through this private line the brain has immediate access to the spectral differences of L- and M-cones. All other mammals are dichromats and their color vision depends on the comparison of L- and S-cone signals. Their cone-selective retinal circuitry is still unknown. We have recently identified S-cone selective bipolar cells of the mouse retina. They were labeled in a transgenic mouse expressing clomeleon, a chloride sensitive fluorescent protein, under the control of the *thy1* promotor. Blue-cone bipolar cells comprise only 1-2% of the bipolar cell population, and their dendrites selectively contact S-opsin-expressing cones. The blue-cone bipolar cells of the mouse retina and their cone selectivity are closely similar to primate blue cone bipolars. We suggest that they both represent the phylogenetically ancient color system of the mammalian retina, which has evolved approximately 400 million years ago.

Spectral responses of horizontal cells in the retina of chracinid fishes

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Characinid fishes live in the freshwaters of South America, Central America and Africa. Characinid fishes are considered to be a sister group of cyprinid fishes. Cyprinid fishes have a tetra-cone system and a corresponding tetra-horizontal-cell system. In this study, spectral properties of retinal horizontal cells of characinid fishes (13 species) were examined electrophysiologically. All experiments were performed under light-adapted conditions. Chromatic adaptations were also used to segregate particular cone inputs. Three types of spectral responses, one for luminosity and two for chromaticity, were recorded from horizontal cells of characinid fishes. Therefore, characinid fishes have a tri-horizotal-cell system. No sign of ultra-violet sensitive cone input was recognized in the horizontal cell responses of characinid fishes. The luminosity response was driven exclusively by long-wavelength sensitive (LWS) cones. Chromaticity responses were a colour-opponent R-G type and a Y-B type. The R-G type receives depolarizing input from LWS cones and hyperpolarizing input from medium-wavelength sensitive (MWS) cones. The Y-B type receives hyperpolarizing input from short-wavelength sensitive (SWS) cones and depolarizing input from MWS cones. A subtype of the Y-B type receives additional hyperpolarizing input from LWS cones. The action spectra of horizontal cells of the characinid were long-wavelength shifted compared to those of the cyprinid. The chromophore of photopigments was vitamin A2 dominant. These results suggest characinid fishes are evolutionally adapted to long-wavelength rich photo-environments. Peaks of absorbance

spectra of LWS and MWS cones of characinid fishes are proximal. Also some characinid fish have photo-stable yellow pigments in the cornea and retina. The eyes of characinid fishes may offer a hint about similar organization in the eyes of humans and Old-World primates.

Cone signal processing in the asymmetrical on- and off-electroretinograms

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The electroretinographical responses to rapid-on and rapid-off sawtooth stimuli are added to extract nonlinear inner retinal contributions to the ERG. Linear and simple nonlinear responses that most probably originate early in the processing pathway are cancelled out by this procedure. ERGs were measured to rapid-on and rapid-off sawteeth. The L- or the M-cones were selectively stimulated. In addition, a condition was used in which the two were simultaneously stimulated in phase with each other (L+M-cone condition). At each condition, four different contrasts were employed. S-cones were not stimulated in any of the stimuli. In all conditions, the response to the rapid change in the rapid-on sawtooth stimulus was triphasic with an initial trough (N1) with a latency of about 15 msec followed by a peak with maximum at about 35 msec and a second trough at about 60-90 msec after the rapid change. The response to the rapid-off sawtooth stimulus was biphasic with a positive peak, the maximum of which occurred after about 20 msec followed by a trough with a 60-90 msec latency. The addition of the two responses nearly completely abolished the N1 in the response to the rapid-on by a part of the positive response to the rapid-off, indicating that these signals have probably identical origins that occur early in the signal processing. In the M-cone isolating condition and in the L+M-cone modulation, the addition displays a positive peak and a subsequent trough. In the L-cone isolating condition there is only a trough. The trough in the cone isolating conditions has a larger delay time than in the L+M-cone condition, suggesting separated signal pathways in these conditions. This is possibly related to the fact that the cone isolating, but

not the L+M-cone stimuli, activate the red-green opponent (parvocellularly based) channel. The amplitudes of the trough are similar in the L- and M-cone isolating conditions. A response in the cone isolating conditions, that is parvovellular driven, might explain such a result, despite the fact that most subjects have more L- than M-cones and accordingly have larger amplitudes in the L-isolating conditions when modulated at 30 Hz flicker. The sum of the On- and Off-responses is reminiscent of the pattern ERG but is less sensitive to optical blur. Therefore, the technique may be used in subjects (e.g. cataract patients) and animals (e.g. mice) that have suboptimal optical quality.

High luminance L- & M-cone isolating ERGs: LED vs CRT stimulation

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Using double silent substitution, it is possible to generate L-cone and M-cone isolating electroretinograms (ERGs) on a CRT display (Kremers *et al.*, 1999). Although this means that spatially varying stimuli can easily be generated, depth of modulation of cone classes is limited by phosphor overlap. We have ported the technique onto a 4-colour LED Ganzfeld stimulus (Diagnosys ColourDome). This gives the advantage that much higher retinal illuminances, higher contrasts and even triple silent substitutions can be obtained. With careful control over retinal area stimulated, we show that the same data can be recorded from both stimuli when luminance, size and cone contrast are kept constant. Importantly, the different temporal profiles of the CRT and Ganzfeld do not influence the ERG amplitude and phase plots. We present data over a much wider range of luminances (up to ~6000Td) and contrasts with the LED stimulator than previously reported with CRT screens. With 30Hz stimulation, ERG amplitude increases linearly with increasing contrast. The slopes of the amplitude versus contrast plots are used to derive L/M ratio. In accordance with previous data, there is a large inter-individual

variability in L/M ratio. It does, however, change systematically with retinal illuminance. Response phases are fairly constant when contrast changes. But systematic effects are evident in the phase plots when retinal illuminance is varied. Generally, the M-cone driven responses are slightly phase advanced when compared to the L-cone driven responses. We conclude that the close resemblance between data obtained with an LED stimulator and with a CRT screen indicate that the effects have a purely physiological origin. L/M ratios in ERGs depend on retinal illuminance, indicating that the physiologically measured L/M ratios are proportional to the ratios of L- to M-cone numbers but that they are not necessarily identical.

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New World monkeys and color

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Seventy years ago, Walter F. Grether reported measurements of color discrimination in four species of primate. In doing so, he noted that "such data are of value for understanding the evolution of human color vision" (Psychological Bulletin, 1937, 34, 792). Because his results showed that discrimination among the long wavelengths was much poorer for a representative New World monkey than for other species, he further suggested that "their color vision may represent an intermediate developmental stage between that of lemur and man." Grethers´ views have turned out to be astonishingly prescient, with his work eventually leading to a large body of research on color vision in nonhuman primates. This talk summarizes what has been learned in recent years about color vision in New World monkeys and describes how studies of the biology of this capacity have both illuminated the understanding of an important group of primates and contributed significantly to our current appreciation of mammalian color vision.

Developmental programs coordinating size and niche variations in the primate eye and retina

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The size and niche variations of New World monkeys offer the opportunity to compare mature visual system variations with the developmental alterations of retinogenesis that produce the observed species differences. We have collected a number of measures of retinal cell number and conformation for six species of New World monkeys, including *Saguinus midas niger* (brain weight 9.7g), *Callicebus moloch* (16.6g), *Aotus azarae* (17.1g), *Saimiri sciureus* (22.1g), *Alouatta caraya* (42g) and *Cebus apella* (71g). In diurnal monkeys, eye size, rod, cone and retinal ganglion cell numbers scale with brain size, but rod number increases with a much greater slope. A conserved order of retinal neurogenesis (cones first, rods last) may automatically produce relatively greater proliferation of rods in larger eyes, serving the separate adaptive requirements of cones and rods to maintain acuity and sensitivity respectively. Compared to diurnal monkeys, owl monkeys have fewer cones and ganglion cells but many more

rods, and consequently greater photoreceptor convergence. The same order of neurogenesis that automatically adapts rod and cone numbers to eye size may also permit a coordinated alteration of proliferation for nocturnality and diurnality produced by shifting the onset and termination of cell proliferation with respect to the schedule of cell specification.

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Physiological properties of photoreceptors and retinal ganglion cells from a thrichromatic platyrrhine: the howler monkey, *Alouatta sp*.

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Three different cone photopigments have been found by electroretinographic recordings in male howler monkeys, indicating two opsin genes are present on the X chromosome. Molecular data have suggested that each M and L opsin gene has an independent locus control region, which raises the possibility that the retina co-expresses both M and L opsins in one cone. To test this hypothesis and to evaluate the temporal and chromatic properties of *Alouatta* retinal ganglion cells, we studied receptoral and post-receptoral physiological properties. Three adult male *Alouatta caraja* were used. *In vivo*

extracellular recordings were obtained from parafoveal retinal ganglion cells. Several kinds of stimuli were used: luminance or chromatic flashes to classify the cells as phasic or tonic; luminance or chromatic sinusoidal modulation at a range of temporal frequencies and contrasts to determine contrast gain and dynamics; heterochromatic stimuli modulated with different relative phases at six different temporal frequencies to study cell spectral sensitivity. Post-mortem microspectrophotometry (MSP) was performed to obtain rod and cone spectral sensitivities. Temporal properties of *Alouatta* ganglion cells were similar to those found in macaques and another New-World primate, the diurnal *Cebus apella*. M cells showed transient, non-opponent responses, and a contrast gain mechanism control, whilst P cells showed sustained responses with strong colour opponency, resembling those of macaques and trichromatic female *Cebus*, and absence of a contrast gain control mechanism. The MSP data are consistent with only a single opsin being expressed in each cone. It appears that this primate has a very similar retinal organization found in Old-World monkeys. Recent behavioural data from *Alouatta* strongly support these findings.

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Perceived Vernier phase shift due to contrast gain control

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In previous studies it has been shown that signals from the magnocellular (MC) pathway play an important role in Vernier tasks (Sun *et al*., 2003, 2004). MC ganglion cells show a phase advance for sinusoidal stimuli with increasing contrast due to a contrast gain control mechanism, while the parvocellular (PC) ganglion cells do not (Benardete *et al*., 1992; Yeh *et al*., 1995). If information in the response phase of ganglion cells was utilized by central mechanisms in Vernier tasks, one might expect systematic error due to the MC cells phase advance. Here we measured Vernier psychometric functions for a pair of gratings (0.4 cpd) of variable relative phase offsets to see if such errors might exist. The grating pair was modulated either in luminance or chrominance, and one grating had twice the contrast as that of the other (60% vs. 30% or 30% vs. 15%). The gratings were horizontal sinusoidal or square-wave gratings and were vertically drifted at 2 or 8 Hz. Two psychometric functions, upward drifting and downward drifting, were measured simultaneously in one experimental session. In associated electrophysiological experiments, MC and PC ganglion cell responses were measured with similar stimuli, and the amount of phase advance as stimulus contrast doubled were calculated. There were systematic shifts in Vernier psychometric functions for pairs of

luminance gratings drifting at 8 Hz, consistent with the high contrast grating being perceived phase-advanced in the drift direction compared to the low contrast grating. The size of the phase advance was comparable to that seen in MC cells under similar stimulus conditions. The amount of phase advance was slightly larger for sinusoidal than for square-wave gratings. At 2 Hz, the shift disappeared. These results are consistent with the MC cell phase advance hypothesis due to contrast gain control mechanisms. The shifts in Vernier psychometric functions were negligible for pairs of chromatic gratings at conditions tested here, consistent with the lack of phase advance in responses of PC ganglion cells.

Benardete, E.A., Kaplan, E., Knight, B.W. (1992). Contrast gain control in the primate retina: P cells are not X-like, some M cells are. *Visual Neuroscience*, 8, 483-486.

Yeh, T., Lee, B.B., Kremers, J. (1995). Temporal response of ganglion cells of the macaque retina to cone-specific modulation. *Journal of the Optical Society of America. A, Optics, image science, and vision*, 12, 456-464.

Sun, H., Lee, B.B., Rüttiger, L. (2003). Coding of position of achromatic and chromatic edges by retinal ganglion cells. In: Mollon, J.D., Pokorny, J., Knoblauch, K. (Eds.), *Normal and Defective Colour Vision*. pp. 79-87. Oxford: Oxford University Press.

Sun, H., Rüttiger, L., Lee, B.B. (2004). The spatiotemporal precision of ganglion cell signals: a comparison of physiological and psychophysical performance with moving gratings. *Vision Research*, 44, 19-33.

Colour vision perception in howler monkeys (*Alouatta caraya*)

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Electrophysiological and molecular genetic studies have shown that howler monkeys (*Alouatta*) display a type of colour vision that is unique amongst all studied platyrrhines: males and females are trichromats. This study examined the colour discrimination abilities of four howler monkeys (*Alouatta caraya*) through a series of tasks involving a behavioural paradigm of discrimination learning in semi-natural conditions. The animals were maintained and housed as a group in the Zoological Gardens of Brasília and were tested in their own home cages. The stimuli consisted of pairs of Munsell colour chips, used in earlier experiments with other monkeys, presented in random brightness values in order to assure that discriminations were based on colour rather than brightness cues. Results indicate that the animals (three males and one female) presented an above-chance performance for all presented pairs, including stimuli that would be difficult to discriminate by a dichromatic monkey. Furthermore, these stimuli resembled hue conditions under which howler monkeys forage.

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Model of adaptive processing for reconstructing chromatic information from the random mosaic of cones

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The separation of spatial and chromatic information from a randomly arranged cone mosaic in the visual system is not yet fully understood. It appears that it involves complex processing (Ingling *et al*., 1983, Kingdom *et al*., 1995). Although the parvocellular pathway carries the opponent L/M chromatic information, we show here that the spatial information contained in the magnocellular pathway can be used to facilitate the separation between details of luminance and hue. We present a model for adaptive processing of chromatic (or colour opponent) information coming from a simulated cone mosaic. We estimate a coarse version of luminance, which we subtract from signal of the cone mosaic, leaving an empty location in low spatial frequencies. This spectral hole is the location where the color oppositions will be located after colour demultiplexing. From the coarse version of luminance we compute a gradient used to adaptively interpolate the chrominance information. Once the colour oppositions are computed, we use them to retrieve a fine version of the luminance with all frequencies resolved. The simulation shows that we can reconstruct spatial and chromatic information with good accuracy from a randomly sampled cone mosaic. Moreover, the model is compatible with the architecture of the visual system. First, the estimate of a coarse version of luminance is compatible with processing of the outer-plexiform layer of the

retina and could serve as the signal for the magnocellular pathway. Second, the low-pass version of the luminance that we subtract from the signal of the cone mosaic could explain the band-pass behaviour of the parvocellular pathway. Finally, the fact that the model uses both magnocellular and parvocellular pathways, corroborates the approach, arguing that the separation of colour and spatial information should occur in the visual cortex rather than in the retina itself.

Ingling, C., Martinez-Uriegas, E. (1983). The spatiochromatic signal of the r-g channel. In: Mollon, J.D., Sharpe, L.T. (eds.) *Colour Vision: Physiology & Psychophysics*, p. 433-444. London, England: Academic Press.

Kingdom, F. A., Mullen, K. T. (1995). Separating colour and luminance information in the visual system. *Spatial Vision*, 9, 191-219.

Estimation of relative L-cone and M-cone sensitivities from a performance measure and from a phenomenological measure

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In two psychophysical tasks, the relative sensitivities of L and M cones were estimated in the parafovea. In the first task, Landolt Cs were presented for 100 ms either to L- or to M-cones in isolation and observers indicated the test orientation for target sizes from 0.7 to 4 degrees. In the second task, the Webster-Mollon (1993) method of minimum flicker detection was adapted for peripheral targets: counterphasing rectangular gratings were created using the red and green monitor guns and observers indicated which of two simultaneous gratings gave the stronger flicker. Three spatial frequencies were tested (0.5, 1 and 2 c/deg) at a duration of 400 ms. In both tasks, the stimulus centers were located on an imaginary circle of 5 deg radius and were presented on a monitor screen. The Stockman-Sharpe (2000) 10-deg fundamentals were used to generate colours. In the recognition task, the L/M threshold ratio increased with decreasing target diameter on average from 1.2 to 4; i.e., L-cones are more sensitive at higher spatial frequencies than M-cones. The minimal-flicker method gave relative sensitivities to red and green phosphors 1.15-1.25. The relative excitations of L- and M-cones, reconstructed from these data, were in the range of 4, which corresponds to the relative sensitivities measured with the smallest Landolt Cs.

Webster, M.A., Mollon, J.D. (1993). Contrast adaptation dissociates different measures of luminous efficiency. *Journal of the Optical Society of America. A, Optics, image science, and vision*, 10, 1332-1340.

Stockman, A., Sharpe, L.T. (2000). The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. *Vision Research*, 40, 1711-1737.

Sensitivity to luminance and chromaticity of the parvocellular pathway: an ideal observer model

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In trichromatic primates, the centre of foveal parvocellular (PC) cells receives input from either L or M cones, while the surround may receive input from both types of cells. The difference between the centre and surround gives the L-M colour opponent signal. This signal reaches its maximum when the surround receives input from one cone type different from that of the centre. A random input of L and M cones to the surround decreases the chromatic signal. To reveal the cost of random wiring in the (PC) pathway for chromatic coding, I estimated the sensitivity to luminance and chromaticity of an ideal observer. Because PC cells have centre surround organisation they convey mixed message about spatial distributions of luminance and chromaticity. The distributions of luminance and chromaticity can be extracted from the signals of an array of cells having different inputs of cones to their receptive fields. To estimate the error of reconstruction of chromatic and luminance signals, I assumed that the signals are reconstructed so that the mean square error is minimal, i.e. assumed an ideal observer performance. The model is based on the following assumptions: i) PC cells respond linearly to the light stimulation, ii) the receptive fields of PC cells are described by the difference of Gaussian functions and iii) the accuracy of reconstruction is limited by noise. The noise may originate either in cones or in PC cells. The model predicts that random inputs of cones to the receptive field decrease the sensitivity to isoluminant gratings. However, both random and non-random versions of the model reasonably agree with psychophysically derived sensitivity to sinusoidal gratings modulated in chromaticity or luminance.

Psychophysical models, physiological reality and the specificity of retinal signals

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The goal of physiological measurement of the visual system is to relate cell responses to behavior, especially in the primate. Early physiological measurements were undertaken using a stimulus context that often bore little relation to the psychophysical paradigms that had provided evidence for discrete visual mechanisms with potential physiological substrates. More recent physiology made a more direct attempt to use psychophysically relevant stimulus paradigms, with considerable success. On the other hand, psychophysical models of perceptual processes have often been oblivious of the messy physiological reality that may underlie a simple psychophysical result; an example is Weber's law, which rests on a complex set of physiological mechanisms. I shall discuss specificity of cone connectivity in the retina and specificity of the segregation of chromatic and luminance signals in the retinal output as examples of how the physiological substrates of performance may be more complex than often assumed by ideal psychophysical models. For example, retinal connectivity may be more specific than assumed by random wiring models, but only as specific as it has to be.

The perception of reflectance properties of natural surfaces using image statistics

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We are able to judge reflectance properties (e.g., lightness, color and gloss) of natural surfaces and identify materials (e.g., plastic, paper, metal) quite accurately, just by looking at them. This ability is striking. How does the human visual system estimate reflectance parameters of surfaces? The visual system could do "inverse optics" i.e. to invert physical optics by using estimates of the 3D surface layout and incident illumination and thereby recover the reflectance properties. However, doing inverse optics is difficult, computationally. Such an approach would prove impossibly difficult for natural surfaces with mesostructure and complex BRDFs. Our studies suggest that the visual system might instead use simple 2-D image statistics that are diagnostic of surface reflectance properties. The importance of image statistics was hinted at by a finding that the perceived reflectance similarity between two surfaces with different shapes could be predicted well by the similarity in the luminance histograms of the images of the two surfaces (Nishida and Shinya, 1998). In line with this idea, we recently showed that the skewness of the luminance histogram and the skewness of sub-band filter outputs are

correlated with surface gloss and inversely correlated with surface albedo. We also found evidence that human observers use skewness, or a similar measure of histogram asymmetry, in making judgments about surfaces (Motoyoshi *et al*., 2007; Sharan *et al*., in preparation). When the image of a surface has positively skewed statistics, it tends to appear darker and glossier than a similar surface with lower skewness, and this is true whether the skewness is inherent to the original image or is introduced by digital manipulation. We also found a visual aftereffect based on skewness, which suggests that there are neural mechanisms sensitive to skewed statistics, and that such mechanisms might be employed in estimating surface properties.

Nishida, S., Shinya, M. (1998). Use of image-based information in judgments of surface-reflectance properties. *Journal of the Optical Society of America. A, Optics, image science, and vision*, 15, p. 2951-2965.

Motoyoshi, I., Nishida, S., Sharan, L., Adelson, E.H. (2007). Image statistics and the perception of surface qualities. *Nature*, 447, p. 206-209.

Color, gloss, and 3D objects

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The light reflected from different locations on a single object can vary enormously, even when the object is made of a uniform material. One source of variation is inhomogeneity in illumination; another is that the relative contributions of diffuse and specular reflectance change across the object. Yet humans have no trouble assigning color names to most things. We have begun to study how this works. Subjects viewed a graphics simulation of a three-dimensional scene containing two objects, test and match. The subject's task was to adjust the match sphere until its color appearance was the same as the test object. The match sphere was always matte, and subjects varied its color by changing the simulated diffuse spectral reflectance function. Different test objects and materials were simulated by varying the object's shape and the strength and roughness of its specular reflectance component. Materials were specified within Ward's parametric BRDF model. The test object's diffuse reflectance component ('body color') was also varied. Scenes were rendered as stereo pairs using RADIANCE, combined with custom software that ensured spectral accuracy. Subjects viewed the stereo pairs on a calibrated computer-controlled haploscope. For fixed test body color, observers' matches depended on the simulated test sphere material. This effect is small relative to the change in spatial average of the reflected light produced by the change in material. In addition, there are effects with changing the location on a 3D object whose color is being judged.

The effects of colored lenses on the number of discernible colors perceived by dichromats in natural scenes

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The number of discernible colors perceived by normal trichromatic observers when viewing natural scenes can be estimated computationally from hyperspectral data and color appearance models (Linhares *et al*., 2004). The purpose of the present work was to use a similar methodology to quantify the impairment in chromatic diversity experienced by dichromatic observers when observing the scenes with and without colored lenses. Images of a set of natural scenes acquired over 400-720 nm at 10-nm intervals and calibrated to obtain the spectral radiance for each pixel of the scene were used for the computations (Foster *et al*., 2004). The number of discernible colors perceived by normal observers was estimated by representing the scenes in CIELAB space and counting the number of non-empty unit cubes (Pointer and Attridge, 1998). For dichromats, an algorithm simulating for normal observers the appearance of the scenes for dichromats was used (Brettel *et al*., 1997). The number of discernible colors was then computed as for normal trichromats. The effects of colored lenses were estimated by filtering the spectral radiance from the scenes with the spectral transmittance function of the lenses. It was found that in dichromatic vision the number of discernible colors was about 10% of that perceived in normal trichromatic vision. For some of the colored lenses tested, large improvements in chromatic diversity were obtained for tritanopes and moderate improvements were obtained for deuteranopes and

protanopes, which is a result suggesting that colored lenses may enrich the chromatic content of natural scenes for color deficient observers.

Brettel, H., Vienot, F., Mollon, J.D. (1997). Computerized simulation of color appearance for dichromats. *Journal of the Optical Society of America. A, Optics, image science, and vision*, 14, 2647-2655.

Pointer, M.R., Attridge, G.G. (1998). The number of discernible colours. *Color Research and Application*, 23, 52-54, 1998.

Foster, D.H., Nascimento, S.M.C., Amano, K. (2004). Information limits on neural identification of colored surfaces in natural scenes. *Visual Neuroscience* 21, 331-336.

Linhares, J.M.M., Nascimento, S.M.C., Foster, D.H., Amano, K. (2004). Chromatic diversity of natural scenes. *Perception*, 33, 65-65, Suppl.

Color constancy of real 3-D objects and the roles of spatial and temporal mechanisms

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Color constancy describes the extent to which an object appears of unchanged color despite changes in illumination conditions. The effect of a change in the spectrum of the illuminant on the light reflected from different objects in a scene to the eye depends on each material's spectral reflectance. Within each cone class, however, the effect is decently approximated by multiplication by the same constant for all materials. This suggests that if the cone-coordinates of the illuminant can be estimated, then a neural process could invert the effect. We examined color constancy of 344 natural and man-made 3-D objects (Foster *et al*., 2004) in variegated scenes under a change from sunlight to skylight (Taylor and Kerr, 1941). The virtual image of an illuminated three-dimensional test cube was projected by a large 50/50 beamsplitter onto a three-dimensional carbon mask in a three-dimensional scene (de Almeida *et al*., 2002). The scene and the test object were illuminated independently by a computer-driven color projector using a periscope technique. We measured changes in the color appearance of test-reflectances by determining the

locations of boundaries between color categories (Smithson and Zaidi, 2004). Under prolonged adaptation to each illuminant, observers demonstrated a high degree of appearance-based color constancy. Classification of test materials on chromatically balanced or biased backgrounds were similar to classifications without a background, indicating that this stability does not depend on spatially extended estimates of the illuminant's cone-coordinates. To critically compare the roles of local and extended spatial and temporal processes, we then (unknown to the observer) simulated different illuminants on the test and on the background. Observers continued to demonstrate reasonable color constancy. The results suggest that observers can invert the effect of illuminant spectrum changes by collating spatially local information over time.

Taylor, A.H., Kerr, G.P. (1941). The distribution of energy in the visible spectrum of daylight. *Journal of the Optical Society of America*, 31, 3-8.

de Almeida, V.M.N., Fiadeiro, P.T., Nascimento, S.M.C., Foster, D.H. (2002). Colour constancy under illuminant changes with 3-D and 2-D views of real scenes. *Perception*, 31, 135-135, Suppl.

Foster, D.H., Nascimento, S.M., Amano, K. (2004). Information limits on neural identification of colored surfaces in natural scenes. *Visual Neuroscience*, 21, 331-336.

Smithson, H., Zaidi, Q. (2004). Colour constancy in context: roles for local adaptation and levels of reference. *Journal of Vision*, 4, 693-710.

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Keeping track of colour contexts

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By determining the locations of boundaries between colour categories (red-green, yellow-blue), we measured changes in the appearance of coloured patches that simulated surfaces viewed under particular illuminants. A sequence of test surfaces was presented on a variegated background comprised of many surfaces, and colour context was manipulated by changing either the illumination or the sets of reflectances. Under these conditions, colour classifications can be influenced by both spatial and temporal contexts (Smithson and Zaidi, 2004). Here we characterized the time-course of the mechanism that maintains a perceptual record of the temporal context, by (a) using a regression analysis to relate the observers' decisions to the recent history of test surfaces, and (b) manipulating the time-course of changes in context. With a presentation rate of one sample per second, observers' judgments were influenced by the previous 10 to 15 samples. In a second experiment, we tested whether observers were able to collate information over time separately for different spatial regions. Two streams of test surfaces, with different illuminants, were presented on a variegated background. Observers' judgments were consistent with separable tracking mechanisms for the two streams. The ability to keep track of multiple chromatic contexts is important in a world with multiple illuminants and distinct sub-populations of reflectances.

Smithson, H., Zaidi, Q. (2004). Colour constancy in context: roles for local adaptation and levels of reference. *Journal of Vision*, 4, 693-710.

Color-based identification of real 3-D objects

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Color provides one of the more salient qualities used to identify objects, particularly when objects do not differ in shape or texture, e.g. fruits differing in ripeness. Since the daylight spectrum changes with time, season, and weather, so does the spectrum of light reflected from an object. Whether people are good at color-based object identification is thus an empirical question. If they are, then it is important to identify what strategies, automatic or volitional, can account for this performance. A change in illumination spectrum causes complex changes in reflected spectra, but because cone photo-pigments have broad absorption bands, cone responses to objects are multiplied by roughly the same constants. This multiplicative transform can be used in a number of identification strategies. When objects can be seen under two simultaneously present illuminants, identical objects have demonstrably different colors under the two lights. For such cases, the multiplicative transform can be used as a heuristic in pattern matching identification algorithms. We test such algorithms with pairs of real objects presented under two lights. Three of the objects are made from the same material and observers have to pick the odd object. This procedure provides simultaneous measures of object identification thresholds across illuminants and discrimination thresholds within illuminants. The results show that object identification is generally accurate, but with systematic inaccuracies that rule out identification algorithms incorporating the generic transform. Instead, observers infer relative colors of the illuminants from weighted spatial means, and those objects are picked as identical that are seen

as most similar along the vector parallel to the illuminant color change. These experiments suggest the feasibility of geometric operations in perceptual color space that are compatible with an affine structure.

The Caerulean Line and the Unique Hues

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Historically, the basis for the four unique hues has been sought within the visual system, but physiology has not so far revealed structures or processes that correspond to the red-green and yellow-blue axes of phenomenological space. H.C. Lee and R. Shepard have raised the possibility that the yellow-blue axis of colour space coincides with a line passing through the two natural illuminants of our world, skylight and sunlight. Traditional measurements of daylight, such as those of Judd, MacAdam and Wyszecki (1964) fall on a curved line in the CIE chromaticity diagram, a line that follows the Planckian locus. At any one time and place, however, we find that the spectroradiometrically measured chromaticity of a white plaque (barium sulphate) moves along a straight line as the plaque is held in different orientations relative to the sun and sky. This line passes tightly through wavelengths that match the average values of unique blue and unique yellow, typically 476 nm and 576 nm. We suggest that the phenomenological yellow-blue axis adheres to this Caerulean Line, and is continuously re-calibrated as the spectral transmission of the ocular lens changes with age.

Judd, D.B., MacAdam, D.L., Wyszecki, G. (1964). Spectral distribution of typical daylight as a function of correlated color temperature. *Journal of the Optical Society of America*, 54, 1031.

Surface color perception of color defective observers under dim illuminations

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At ICVS 2005 we reported on the color appearances of 24 paper color samples viewed by color normal observers under various illuminations including dim illuminations where rods alone mediated vision. Here we extended the study to include observations of observers with defective color vision, including 2 protanopes, 3 deuteranopes and 2 deuteranomalous trichromats. The appearances of color samples from the OSA Uniform Color Scales were gauged under successively dimmer illuminations from 10 to 0.0003 Lux. Eight triads of samples were chosen, each triad representing one of eight basic color categories; red, pink, orange, yellow, green, blue, purple and gray. Samples within triads varied in lightness. A sample was 8-10° of visual angle when viewed directly from 0.30-0.35m. Observers sorted samples into groups that they could categorize with specific color names. There were no dramatic differences in the use of color names among the protanopes, deuteranopes and deuteranomalous trichromats. At the higher light levels (≥ 0.32 Lux), the color defective observers sorted red, orange, yellow, green, purple and blue samples into the original representative color groups with some exceptions. Differences from normal sorting were found for the gray samples, which were

identified, as either gray or green, and the pink samples which were identified as pink or gray. At the intermediate light levels (0.01-01 Lux), the assigned color names were similar to those of the color normal observers, that is, the red and orange samples were usually identified as either red or orange, and the remaining samples tended to be grouped into two categories, associated with the scotopic sample reflectance. The only difference was that color defective observers frequently used the terms purple and pink interchangeably for purple and pink samples, and used the terms green and gray interchangeably for green and gray samples. At the lowest light levels (≤ 0.0032 Lux), where rods alone mediated vision and where the color normal observers assigned color categories reliably on the basis of the scotopic reflectances of the samples, color defective observers also used a variety of color terms. However the color defective observers' color category assignments were not systematic. For color normal observers, we speculated that developmental and long-term experience with viewing familiar objects in the natural environment under dim illumination allowed an observer to infer that bright appearing objects are richer in shorter wavelength light compared to dim appearing objects. Our results show that at photopic luminance levels, color defective observers used most basic color terms in the same way as color normal observers. Unlike color normal observers, at scotopic luminance levels the assigned color categories of the color defective observers do not reveal an association of scotopic brightness and spectral composition.

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Modeling rod influence on hue perception

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We have previously shown that rod signals influence the balance of both red-green and blue-yellow opponent hue dimensions, but in a pattern that is inconsistent with simple additive combinations of rod and cone signals in opponent-color models (e.g., rods can produce both a red bias and a green bias). The shifts are instead consistent with non-linear models in which rod influence requires non-zero cone signals. Cone-signal strength may modulate or gate rod influence, or rod signals may change the gain of cone pathways. Here, we explore ways that rod influence may be incorporated into opponent-color models that relate photoreceptor stimulation (rods and L, M, and S cones) to hue perception. We extend prior work by considering the changes in rod influence with changes of light level and stimulus duration. Candidate models are evaluated in relation to prior empirical data on rod-induced shifts of unique hue wavelengths and hue-scaling functions. Models have a quasi-anatomical basis in that they assume that rod signals combine with cone signals in midget and small-bistratified ganglion cell pathways in the retina.

Chromatic discrimination with rod contrast

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To investigate how signals from rods alter chromatic discrimination, we measured discrimination ellipses in a normalized cone-space using a 4-primary photostimulator to provide independent control of rod and cone excitation. The stimulus was a 2° circular field set within a 13° surround positioned at 7.5° temporal eccentricity. The chromaticity of the center and surround fields had a chromaticity metameric to the equal-energy-spectrum. The retinal illuminance was 2 Td. Chromatic discrimination was measured using a 3-alternative, 2-Yes-1-No double random staircase procedure for 3 conditions: 1) no rod contrast (the center and surround had identical rod stimulation), 2) rod increment (the rod stimulation in the center was pulsed as a 20% Weber contrast increment), and 3) rod decrement (the rod stimulation in the center was pulsed as a 20% Weber contrast decrement). An equiluminant change in cone stimulation along different axes in the cone space was pulsed simultaneously with the rod pulse in one of the three intervals (400 ms, 500 ms between intervals). The observer identified the interval and direction of color change. Initially, chromatic discrimination along the cardinal axes (0°, 90°, 180°, 270°) was determined; a normalized cone space was defined with the measured cardinal axes thresholds representing unit distances from the

origin. In the normalized cone space, discrimination was measured along diagonal axes (45°, 135°, 225°, 315°). In the absence of rod contrast, the major axis of the discrimination ellipse had a 45° angle in the normalized cone space. Rod contrast changed the shape of the discrimination ellipse, but in an asymmetric way. Discrimination along the 0°, 270°, and 315° direction was degraded in the rod increment condition and was improved in the rod decrement condition. Discrimination along other directions (45°-225°) did not change appreciably for rod increments or decrements. Consequently, rod increments enlarged the discrimination ellipse but rod decrements shrank the ellipse. A model with simple linear combinations of rod and cone signals in the PC- and KC-pathways does not account for the asymmetrical alteration in chromatic discrimination accompanying positive and negative to rod contrast. An additional source of variation in discrimination may involve the addition of rod stimuli to cone defined stimuli. The equiluminant plane is defined in terms of cone excitations. Thus the rod contribution is independent of cone defined stimulus variation. Rod increments and decrements could alter brightness and this could have played a role in discrimination.

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Colour induction and rod-cone interactions

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Colour contrast describes the influence of one colour on the perception of colours in neighbouring areas. This study addresses two issues: (i) the accurate representation of the colour changes; and (ii) the underlying visual mechanisms. Observers viewed a haploscopic display in which a standard display was presented to one eye and a matching display to the other. The two displays formed a single fused binocular image, with the standard (neutral, Illuminant C) and the matching squares inset within their own surrounds, and vertically aligned with each other. In separate blocks of trials, the standard square was either a slight luminance increment, or decrement, relative to the inducing surround, but it nonetheless appeared the complementary colour to the surround in which it was inset. Matches were made with four standard inducing surround colours: red (+L(-M) relative to neutral), green (-L(+M)), blue (+S) and yellow (-S). Matches were made either with the surround luminance in each eye's display equal, at 18 cd m^{-2}, or with the match surround luminance reduced to 2.3 cd m^{-2}. The matches when the luminance of the surrounds was equal could be represented accurately as vector shifts using a diagram that is a logarithmic transformation of the MacLeod–Boynton (r, b) chromaticity diagram, as described previously (Shepherd, 1997; 1999). Matches made in the low luminance surrounds were, however, generally displaced further from the neutral chromaticity, as if larger chromatic differences were needed at low luminances. The precise direction of the displacements differed, however, for luminance increments and decrements. For the decremental stimuli only, the matches were displaced vertically downwards in the MacLeod-Boynton

diagram, with a small further horizontal offset away from the chromaticity coordinates of the neutral. For the incremental stimuli, the matches were principally displaced horizontally. Since haploscopic presentation has been described as isolating retinal processes, the results are discussed in terms of receptor sensitivity changes and the ratio of receptor contrasts. Rod intrusion in S-cone pathways may have boosted the S-cone signal for the lowest luminance decrement matches and account for the vertical shift in MacLeod-Boynton co-ordinates. The distinct pattern of displacements for low luminance increment and decrements may be explained if the match is set at a cone-opponent, rather than a cone contrast, site.

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Shepherd, A.J. (1999). Remodelling colour contrast: implications for visual processing and colour representation. *Vision Research*, 39, 1329-1345.

Time-course of rod influences on hue perception

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Stimulation of dark-adapted rods can shift the hues associated with specific wavelengths throughout the spectrum, under mesopic conditions. Thus, rods exert a green bias (strengthen green relative to red) at longer wavelengths and a blue bias (strengthen blue relative to yellow) at low-middle wavelengths. A third rod influence at shorter wavelengths is more complicated because it reverses direction with change of stimulus duration. Thus, for 30-ms stimuli, rods exert a green bias like that observed at longer wavelengths. However for 1-s stimuli, rods exert a red bias that is observed nowhere else in the spectrum. We examined the latency (time course) of rod hue biases by measuring the shifts of the 3 spectral unique hues under dark-adapted vs. bleached (cone plateau) conditions by means of a forced-choice, double-random-staircase procedure. Three female observers viewed 1.0-log-scotopic-troland, 7°-diameter test stimuli centered 7° from fixation in temporal visual field and presented for 1000, 500, 100, 50, 30, or 20 ms with minimum 5.5 s inter-stimulus interval. The rod green bias at unique yellow (typically 5-15 nm) and the rod blue bias at unique green (typically 10-30 nm) were not systematically affected by test stimulus duration. For two observers, near unique blue, rods exerted a green bias (range 2-8 nm) for test stimuli less than 50 ms, and a red bias (range 3-13 nm) for longer test stimulus durations. A third observer always showed a rod red bias. A quick rod green bias is shown at unique blue for some observers

but is dominated by a slower rod red bias after 30-50 ms of rod stimulation. These opposing rod influences may reflect competing effects of rod signals on ML-cone and S-cone pathways. However, questions remain about their relationship to the rod blue bias at unique green and the rod green bias at unique yellow, which are also plausibly mediated by S-cone and ML-cone pathways, respectively.

The role of spatial and temporal chromatic contrast for S-cone chromatic discrimination

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S-cone discrimination depends on the difference in S-cone excitation between the test field and surrounding area. However, it is not clear whether chromatic contrast in space, or in time, has equivalent effects on S-cone discrimination. To address this, we designed S-cone stimuli with spatial-and-temporal contrast, spatial contrast alone, temporal contrast alone, or no chromatic contrast. The stimulus paradigm included a 4.0° square pedestal that centered within an 18.5° x 13.8° rectangular adapting surround. The pedestal was continuously present within the surround (steady-pedestal) or pulsed as a 1.5 sec raised cosine envelope during the trial period (pulsed-pedestal). Thresholds were measured for a 1° test square presented as a 1.5 sec raised cosine in an inner quadrant (a corner of the test square located at the center of the pedestal or an outer quadrant (a corner and two borders abutting the surround) of the pedestal. The steady-pedestal paradigm produced either spatial chromatic contrast signals for the outer quadrant presentation, or no spatial or temporal chromatic contrast for the inner quadrant presentation. The pulsed-pedestal paradigm produced both spatial and temporal contrast for the outer quadrant presentation, but only temporal contrast for the inner quadrant presentation. The stimuli had a constant L/M cone excitation (l= 0.665) and a constant retinal

illuminance of 108 Td. The surround was either metameric to the equal energy spectrum (*EES*, *s*= 0.997, "white"), or of higher (*s*= 5.0, "purple") or lower (*s*= 0.4, "yellow") S-cone chromaticity. The pedestal had higher or lower S-cone chromaticity relative to the surround. S-cone discrimination was assessed in a 4-alternative choice, double random staircase procedure. During the trial, the test square was randomly positioned in one quadrant of the pedestal and the observer was required to identify the quadrant of the test and direction of color change of test relative to the pedestal. The results indicated that in the absence of spatial and temporal contrast, S-cone discrimination was determined by the S-cone chromaticity of the pedestal. S-cone discrimination in the presence of spatial or temporal contrast was best near the adaptation chromaticity and degraded for increasing chromatic differences away from the "white" or the "yellow" surround. For the "purple" surround, however, discrimination did not vary, indicating a saturating response. A comparable L-M discrimination experiment (Zele *et al*., 2006) did not reveal a saturating response for high L- or M-cone excitation surrounds. A chromatic discrimination model based on bistratified ganglion cells in the KC pathway could describe the data. In conclusion, spatial and temporal chromatic contrast between the test and surround have equivalent deleterious effects on S-cone discrimination.

Zele, A.J., Smith, V.C., Pokorny, J. (2006). Spatial and temporal chromatic contrast: Effects on chromatic discrimination for stimuli varying in L- and M-cone excitation. *Visual Neuroscience*, 23, 495-501.

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Performance of the Lanthony New Color Test by young children

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The Lanthony NCT has not previously been used to study children's colour vision. It is known to be successful in assessing colour vision in the elderly, who also have cognitive difficulties compared with a younger adult population. The NCT has been shown to be sensitive in identifying blue-yellow changes to colour vision. The Chroma 4 series has the same colour differences between caps as the D15, which has been used with children, but has more uniform spacing around the hue circle. Given that they undertake the D-15 successfully, it can be expected that children possess the appropriate cognitive skills to complete the hue arrangement phase of the NCT. To accommodate the shorter attention span of children, a modified procedure was used where, rather than performing all four boxes of the NCT from Chroma 8 to 2, they began with Chroma 4 and proceeded to Chroma 2, with the option of completing Chroma 6 and 8 if errors were made with Chroma 2. The results confirm that colour vision test performance is improving between the ages of 5 and 12. The errors made by younger children were both more frequent and more specific than the errors of older children. The fact that the types of errors were not due to random cap ordering errors about the hue circle indicates that children are competent in their colour seriation skills. The errors of the younger children are blue-yellow in direction. The few errors made in the separation phase of the NCT are also strongly blue-yellow.

Mass screening for color-vision deficiencies in Norwegian children

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2966 children, aged 6-13 years, from four municipalities in Norway were screened in their school classrooms with the Neitz Test of Color Vision. Children who made errors on the test were then retested. 187 boys and 157 girls made one or more errors on the retest, and each was tested individually on the Hardy-Rand-Rittler Pseudoisochromatic Plates 4th Edition (HRR 2002). The HRR 2002 was administered under the True Daylight Illuminator with Easel (color temperature 6200 K) in an otherwise darkened room. Applying a double criterion for failing the screening, that is, one or more errors on the Neitz test and two or more errors on the HRR 2002, gives a frequency of color-vision deficiency of about 8 % of boys and 3 % of girls. The high frequency of color-vision deficiency in girls is considered in relation to previous reports of increased frequencies of errors with Ishihara Pseudoisochromatic Plates by female carriers of deutan color-vision deficiency.

Color deficiency correction – methodology and experiment report

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Research and development on color deficiency correction with optical filters has been ongoing for about 20 years in the Department of Mechatronics, Optics and Instrumentation Technology of Budapest University of Technology and Economics. Currently the evolution of corrective glasses has reached a level where most types of protanomals and deuteranomals can be corrected at a high percentage. First, the primary diagnosis of the color deficiency type is carried out with the classical Nagel anomaloscope. Further categorization is made with an instrument developed in our lab that can be used to identify the color deficiency subtype (i.e., slight, medium, severe or "anope"). According to the diagnosis, adequate correction glasses are selected. After sufficient color adaptation is achieved, verification of the correction is carried out by means of classical color vision tests, such as the Ishihara plates and the Munsell-Farnsworth hue test, as well as a lab developed test for color identification purposes. In our report, we show the evolution of the correctional method as well as the status of the latest version of the correction paradigm. We present the results and statistical evaluation of the correction for the color vision tests. We present the results of several dozen case studies that provide evidence for the correction method functioning, not only for color discrimination but also for color identification ability.

Influence of color on Müller-Lyer illusion in dichromats and trichromats

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One of the best-known geometrical illusions is the Müller-Lyer configuration, in which two identical straight lines appear perceptually different in length. In this case, one of them is flanked by inward-pointing arrowheads, which always appears longer, while the other is flanked by outward-pointing arrowheads, which always appears shorter. This study investigated the influence of color on the Müller-Lyer illusion in dichromats (n=13) and trichromats (n=13). Stimuli were presented on a computer-controlled color television monitor in two groups of test in random order: 1) arrangement with opponent colors - green straight lines and orange/red arrowheads vs. blue straight lines and yellow arrowheads, and 2) arrangement with non opponent colors - blue straight lines and orange/red arrowheads vs. green straight lines and yellow arrowheads. Results indicated the following: a) in condition 1, the effect of the illusion was stronger in dichromats in the red/green stimuli, when compared to the blue/yellow stimuli in the same group or to the trichromats; b) in condition 2, the dichromats were also more susceptible to the illusion when compared to the trichromats. The findings are consistent with the idea that the geometrical optical illusions of length and size are mediated by the parvocellular system, which is weaker in dichromats.

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Colour and luminance increment thresholds in poor readers

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The hypotheses of a visual basis to reading disabilities in some children have centred around deficits in the transient system, although hyperactivity in the sustained system has also been proposed as a mechanism. In addition, there is clear evidence that coloured lenses and/or coloured overlays and/or coloured backgrounds can modify performance in reading and may assist in providing comfortable vision for reading and the ability to maintain reading for longer times. It is surprising that colour vision is relatively little studied. We assessed luminance increment thresholds and equi-luminous red-green and blue-yellow increment thresholds using a computer-based test in central vision and at 10° nasally employing the paradigm pioneered by King-Smith. We examined 35 poor readers (based on the Neale Analysis of Reading) and compared their performance with 35 normal readers matched for age and IQ. Poor readers produced similar luminance contrast thresholds for both foveal and peripheral presentation compared with normals. Similarly, chromaticity contrast discrimination for the red/green stimuli was the same in normal and poor readers. However, poor readers had significantly lower thresholds for the blue/yellow system, for both foveal and peripheral presentation compared with normal controls. This hypersensitivity in blue-yellow discrimination

may point to why blue lenses and blue overlays are often found to be effective in assisting many poor readers.

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Does color misbind to form in afterimages?

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Misbinding of color to form occurs during dichoptic viewing of rivalrous, orthogonal equiluminant gratings. For example, a red/white vertical grating in one eye and a green/white horizontal grating in the other eye often gives the percept of a red/green grating oriented either horizontally or vertically. The present study focused on afterimages that follow viewing of rivalrous gratings chosen to give percepts with color misbound to form. Afterimages can depend on retinal adaptation but also on the percept during rivalry (Gilroy and Blake, 2005). If a neural representation of the percept (as opposed to the stimulus) contributed to the afterimages, we predicted that (i) the misbound percept should occur in the afterimage and (ii) the duration of the misbound percept in the afterimage should be directly related to the duration of the misbound percept during rivalrous viewing. Both predictions were confirmed. The afterimage alternated between a percept of one of the monocular stimuli and a red/green grating (the misbound percept). The duration of the misbound afterimage increased with the duration of the misbound percept during rivalrous viewing ($F_{1,46} = 10.3$, $p < 0.005$). On the other hand, the duration of the afterimage of monocular stimuli had no significant relation with their duration in the percept during rivalrous viewing ($F_{1,94} = 1.33$, $p = 0.25$). The results are consistent with a contribution to the afterimage from two separate

neural processes, one retinal and the other following resolution of rivalry and thus dependent on the image perceived during dichoptic viewing.

Gilroy, L.A., Blake, R. (2005). The interaction between binocular rivalry and negative afterimages. *Current Biology*, 15, 1740-1744.

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Object segmentation influences perceived temporal variation of brightness

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Perception of a temporally varying light is strongly affected by temporal variation of surrounding light. In particular, perceived modulation depth of a central light is suppressed by surrounding light varying at the same temporal frequency and phase as the central field. A possible neural mechanism is center-surround antagonism of receptive fields in the retino-geniculate pathway (cf. Kremers *et al*., 2004). Here, we show instead that object segmentation, such as stereoscopic depth or real and illusory contours, alters suppression by the surround. Observers matched the perceived brightness modulation at the center of a 6 deg disc modulated in luminance at 2 Hz. In Experiment 1, the central part of the disc was separated from the surround by (1) a triangle formed by 3 thin dark lines, (2) an illusory triangle formed by 3 "pac-men", (3) as (2) but with "pac-men" rotated 180 degrees so as not to form any illusory contours ("pac-men" control), or (4) nothing (no-separation control). In Experiment 2, the circular disc was viewed haploscopically with separation between center and surround by (1) a concentric thin dark circular ring (a "gap ring", 2.5 deg diameter), (2) as (1) but with the gap ring perceived nearer than the circular field by stereo disparity (gap-only-in-depth), (3) as (1) but with the gap ring and its interior both raised to the nearer depth plane (gap-and-interior-in-depth), or (4) no gap ring (control). In Experiment 1, the perceived modulation of brightness was similar in the control and "pac-men"

control conditions but clearly suppressed (almost identically) by the presence of either a real or illusory triangular edge segmenting the central part of the 6 deg disc. In Experiment 2, perceived brightness modulation was suppressed most strongly in the two conditions that had the gap ring and its interior in the same depth plane. Suppression was reduced or abolished when the gap ring alone was perceived in depth. These results demonstrate that suppression of perceived brightness modulation by a temporally varying surround cannot be explained by a simple receptive field model. Cues to object segmentation alter suppression, suggesting instead that perception of temporal brightness modulation in context depends on the neural representation at an object level of visual processing.

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Binocular rivalry between identical retinal stimuli with an induced color difference

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An open question in color rivalry is whether alternation between the two colors is caused by a difference in receptoral stimulation or a difference in the neural representation of color appearance. This question was examined with binocular rivalry between physically identical lights that differed in appearance due to chromatic induction. Perceptual alternation was measured between gratings of the same chromaticity; each one was presented within a different patterned inducing surround (Monnier and Shevell, 2003). The patterned inducing surrounds caused the gratings, one to each eye, to appear different in hue because of chromatic induction. The gratings were presented dichoptically with binocular disparity so the grating appeared in front of the surround. Perceptual alternation was found for the two physically identical chromaticities that appeared different due to chromatic induction. Stereoscopic depth also was perceived, corroborating binocular neural combination despite color rivalry (Treisman, 1962). In a separate control condition, perceptual alternation was measured during dichoptic presentation of two physically different chromaticities within a uniform equal-energy-spectrum surround. The chromaticities were chosen to match the appearance of the physically identical gratings on their patterned inducing surrounds. This condition, therefore, had rivalrous stimuli with the same color-appearance difference as

in the main condition. In sum, the results show that color rivalry is resolved after color-appearance shifts caused by chromatic context. Color rivalry does not require competing unequal cone excitations but instead can result from rivalrous neural representations of color appearance.

Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. *Quarterly Journal of Experimental Psychology*, 14, 23-37.

Monnier, P., Shevell, S.K. (2003). Large shifts in color appearance from patterned chromatic backgrounds. *Nature Neuroscience*, 8, 801-802.

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The role of luminance edges in misbinding of color to form

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Perceptual misbinding of color during binocular rivalry reveals separate neural representations of color and form followed by a neural binding process. During misbinding of color, the neural representation of color from a suppressed form is expressed within a region of the dominant form. Perceptual misbinding during rivalry is influenced by luminance edges: increasing the luminance-contrast at edges decreases perceptual misbinding (Hong and Shevell, 2006). Previous work, however, did not address the question of whether misbinding depended on equiluminance in the eye (i) contributing the misbound color or (ii) incorporating the misbound color. This study answered that question. For 90 seconds, a 2 cycle/deg square-wave vertical grating was presented to one eye and a tooth-shaped vertically oriented grating (top half of grating phase-shifted by one-half cycle relative to bottom half) to the other eye. A grating with luminance-contrast (e.g. a red/black grating) in one eye and an equiluminant grating (e.g. a green/white grating) in the other eye were presented dichoptically. The exclusive visibility time was measured for the percept of each eye's stimulus alone (monocular dominance) and for a two-color vertical or tooth-shaped grating (e.g. a perceived red/green grating--misbinding). The two different forms (vertical vs. tooth-shaped) distinguished whether misbinding was perceived in the form with luminance contrast or the form at equiluminance. Misbinding of color was perceived more frequently

within the equiluminant form than the luminance-contrast form. Misbinding of the chromatic response from the suppressed luminance-contrast form shows that location information provided by luminance-contrast edges does not inhibit binding of color to a non-retinotopic location in the equiluminant form. If filling-in of color occurs within regions defined by edges, these edges are defined perceptually, not retinotopically.

Hong, S.W., Shevell, S.K. (2006). Resolution of binocular rivalry: Perceptual misbinding of color. *Visual Neuroscience*, 23, 561-566.

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Local and global integration of color and orientation in form perception

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How are invariant object properties extracted from locally ambiguous information encoded from the retinal image? One hypothesis is that an important step in this process involves the integration at higher visual stages of coherent, local (low-level encoded) features across the visual field. We used Glass patterns, images of globally-coherent, locally-oriented dipoles, to investigate the role of color in how orientation is integrated locally and globally in form perception. Glass patterns are constructed in two steps: 1) a field of random points is generated, 2) a second point is added near each point, the pair forming a dipole, with the orientation of each dipole following a specific rule. For example, when the dipoles are constrained to fall on concentric arcs, a global concentric pattern appears. Previous studies have indicated that perception of the global form requires extraction of the local orientation of the dipole followed by integration of the global flow in the orientations across dipoles. We used functional Magnetic Resonance Imaging (fMRI) to examine whether the sites implicated in the global integration of local orientations depended on the chromatic properties of the stimulus. Observers were presented with a 10 deg field of 640 random dots (7′ diameter) for 500 ms, followed by replacement of half of the dots by a new set for 250 ms. The new dots were positioned either randomly (RP), to form randomly oriented

dipoles (RD) or to form a concentric Glass pattern (GP) (separation of 12' for the conditions RD and GP). The dots were either achromatic (A), (1646 cd/m^2), or chromatic equiluminant (C), composed of a single chromaticity, CIE (x, y) = (0.323, 0.605) and presented on a grey background, (x, y, Y) = (0.353, 0.448, 823 cd/m^2). Fourteen observers classified each stimulus as being either RP, RD or a GP, while fMRI scans were obtained (3 Tesla, Bruker scanner, event-related paradigm). For the achromatic and chromatic conditions, reaction times (RT) to the GP patterns were significantly shorter than for RD or RP patterns (RT difference: A: 268 ms, $p < 0.001$; C: 287 ms, $p < 0.001$). Observers classified nearly all GP correctly but performed less well, though above chance, for the RD and RP patterns. The comparison RD/RP revealed diffuse activity in many cortical areas, including activity in early visual areas (V1/V2). The comparison GP/RD revealed activity along the fusiform gyrus, with substantial overlap in the regions activated by chromatic and achromatic stimuli. The functional cerebral imagery supports the hypothesis that the local coding differentially activates early visual areas while the global processing requires higher visual areas. The similarity in activations for A and C along the fusiform gyrus raises a question as to the chromatic selectivity of the site of global integration.

Amodal completion of chromatic and achromatic colors

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Amodal completion is the most common form of visual completion occurring when portions of an object are hidden, due to their occlusion behind another object (Michotte and Burke, 1951). This phenomenon can also be perceived in 2-D conditions where the object perceived as occluded is perceived clearly as a unitary object with boundary contours that amodally complete them behind the perceived overlapped modal object. The term "amodal" refers to the fact that, despite observers not actually seeing a contour (a contrast border), they have a vivid perception of completeness and object unity. Just as a shape is completed amodally behind another occluding shape, so is a color behind another occluding color or behind a shine or a lighting: a bright light reflected by a three dimensional object. To study the amodal completion of chromatic and achromatic colors, two extreme references with opposite coloration effects were used: the watercolor and the discoloration illusion. The watercolor illusion (Pinna, 1987) is a coloration effect sending out from a thin colored line running parallel and contiguous to a darker chromatic contour and imparting a strong figural effect. By increasing the number of contiguous contours of the watercolor illusion: (i) the coloration effect decreases or is annulled, (ii) the object-hole and volumetric effects increase, and (iii) the lighting effect also increases. The discoloration illusion (Pinna, 2006) originates from the juxtaposition of eight chromatic parallel contours on a white background, creating a luminance gradient and enclosing a light red region. Under these conditions, the light red discolors and appears white. Under these conditions there are two kind of possible amodal completion results: (i) the completion

of each chromatic line behind the following ones going from the periphery to the inner region of the figure, and (ii) the completion of the bunch of lines behind the inner bright area where the lighting effect occurs. The questions are: Does the amodal completion of colors occur, and which one of the two kinds previously described? Which line defines the color of the object? Do chromatic and achromatic lines elicit the same amodal result? We asked the subjects: "after discounting the illumination effect, what is the color of the figure?". The results showed the effectiveness of the amodal completion of colors and that it depends on a combination of the two kinds of completion previously described. Finally, chromatic and achromatic conditions reveal different results.

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The object-hole effect in the watercolor illusion

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The watercolor illusion is a long-range color assimilation (coloration effect) imparting a figure-ground segregation (figural effect) across large enclosed areas (Pinna, 1987; Pinna *et al*., 2001; Pinna *et al*., 2003). The watercolored figure has a very poorly reversible or univocal figure-ground segregation and strongly enhances the unilateral belongingness of the boundaries (e.g. Rubin vase), which is a principle stating that the boundaries belong only to the figure and not to the background. The figural effect determines grouping and figure-ground segregation more strongly than the well-known Gestalt principles. Under watercolor conditions, both the figure and background assume new properties, becoming respectively a bulging object and hole, both with a 3-D volumetric appearance (object-hole effect). Our purposes were: (i) to demonstrate that the hole induced by the watercolor illusion has unique figural properties comparables to those of the object and not present in the background induced by the known figure-ground principles; (ii) to demonstrate a dissociation of the object-hole effect from the coloration one; and (iii) to demonstrate that the object-hole effect depends on a new principle. This was psychophysically tested by weakening (ungrouping) the whole figural organization due to the watercolor illusion through imparting motion to only some components of a stimulus, while other components remain stationary. The results showed that: (i) Subjects perceived more strongly moving holes and not figures or objects enlarging and shrinking. (ii) Paradoxically moving holes appear more as figures than the bulging surfaces. (iii) When motion was imparted to components that, when stationary, were perceived as objects,

their figurality is further enhanced (summation effect). (iv) When object-hole and coloration effects were dissociated, no significant difference compared to illusory colored conditions was reported. Coloration can be considered independent from the object-hole effect of the watercolor illusion. The object-hole effect may depend on the "asymmetric luminance contrast principle" (Pinna, 2005).

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Stimulus correlates of object colour

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The fundamental achievement in colour science is the tristimulus (vector) representation of the classes of visually indistinguishable (metameric) lights, which is guaranteed by Grassmann's laws. Although the empirical status of these laws is not clear yet, the tristimulus values, by and large, allows one to predict light metamerism. Unfortunately, an analogous representation cannot be established for objects because of so-called metamer mismatching. This means that objects reflecting metameric lights under one illumination can reflect not metameric lights under the other. As a palliative, a finite number (usually, three) of object descriptors have been suggested so as to predict object colour under different illumination. However, many of these models are assumed to be applied only to finite-dimensional subspaces of objects and lights. This assumption is far too restrictive. For three-dimensional subspaces metamer mismatching simply does not exist. I propose a new set of object descriptors based on a different approach. Given a fixed illuminant, for any spectral reflectance, $r(\lambda)$, there exists a unique metameric spectral reflectance of a particular form (referred to *canonical metamer* of $r(\lambda)$) which takes only two values $r_{\min}$ and $r_{\max}$ with only two transitions (between $r_{\min}$ and $r_{\max}$) across the visible spectrum, such that $r_{\min} + r_{\max} = 1$. I call $r_{\min} - r_{\max}$ *chromatic contrast* of the canonical metamer. The canonical metamer is fully specified by its chromatic contrast and the two wavelengths, λ_1 and λ_2, where the transitions (between $r_{\min}$ and $r_{\max}$) occur. The distance between the transition wavelengths, $|\lambda_1 - \lambda_2|$, λ is called *spectral bandwidth*. The centre of the interval between the transition wavelengths, $(\lambda_1 + \lambda_2)/2$, is called *central wavelength*. These three numbers (chromatic contrast, spectral bandwidth, and central wavelength) formally

characterize the class of metameric surfaces to which the canonical metamer belongs. Therefore, they specify any surface from this metameric class. I propose to use these as surface descriptors. Central wavelength and chromatic contrast can be considered as an analog (for reflectance) of dominant wavelength and chromatic purity for light. The canonical metamers for the reflectance spectra of 1600 Munsell chips were evaluated for the CIE illuminant D_{65} using Smith & Pokorny's cone fundamentals. It was found that central wavelength correlates with chromatic hue, and spectral bandwidth with achromatic hue (whiteness/blackness). The chips which have the same central wavelength and spectral bandwidth, that is, differ only in chromatic contrast, have a similar colour appearance. Specifically they differ in a perceptual dimension, which is close to what is usually called saturation. Intuitively, this perceptual dimension indicates the strength of the chromatic quality (specified by the central wavelength and spectral bandwidth). Admittedly, the descriptors can change when the illumination changes. Yet, these variations are lesser than that of the tristimulus values of the reflected light.

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Perceived dissimilarity of yellow-blue surfaces under neutral light sources differing in intensity: Separate contributions of light intensity and chroma

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As illumination decreases, the lightness continuum shrinks and black and white become less dissimilar (Logvinenko and Maloney, 2006). We report an analogous phenomenon for the yellow-blue chromatic dimension. Observers viewed two arrays, each containing seven Munsell papers that fell along a yellow-blue continuum (10B5/12, 10B5/8, 10B6/4, N6.5, 2.5Y7/6, 2.5Y8/10 and 2.5Y8/16). Each array was illuminated independently with light intensity 440, 40, or 8 cd/m^2. Six combinations of light intensities were set as illumination conditions. Over the course of the experiment, the observer was asked to rate the dissimilarity between each chip in one array and each chip in the other by using a 30-point scale. Five judgments were made for each illumination condition. We analyzed this data using non-metric multi-dimensional scaling to determine how light intensity and surface chroma contributed to dissimilarity and how they interacted. Dissimilarities were captured by a two-dimensional fan-like pattern with three concentric seven-point arcs. Distance along each arc corresponded to the contribution of yellow-blue surface chroma differences to dissimilarity, while spacing between arcs represented the contribution of light intensity differences. Arc length decreased with increasing illumination.

Logvinenko, A.D., Maloney, L.T. (2006). The proximity structure of achromatic surface colors and the impossibility of asymmetric lightness matching. *Perception & Psychophysics*, 68, 76-83.

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Colour vision assessment in patients with acquired loss of chromatic sensitivity

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A range of ophthalmic and neurological conditions can cause diminished visual performance, even when the subject is often unaware of any problems and the loss of vision remains undetected in conventional perimetry and visual acuity tests. We investigated a number of subjects with diseases of the retina and/or the optic nerve, as well as patients with selective damage to central visual pathways. The visual assessment included tests for red-green (rg) and yellow-blue (yb) chromatic sensitivity. We examined patients with various stages of glaucoma, photoreceptor dystrophies, diabetes, optic neuritis, age-related macular degeneration as well as tobacco and alcohol toxicity. The loss of chromatic sensitivity tends to affect both the rg and the yb channels. Significant differential effects have, however, been observed in relation to stimulus size, retinal location and state of light adaptation. The problems associated with testing and quantifying acquired colour vision loss in patients with congenital colour deficiencies have also been investigated and will be reported. The findings from these studies show that, in the majority of these conditions, the loss of chromatic sensitivity is the most sensitive measure of early changes in diseases of the eye.

Colour in disorders of the visual cortex

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Colour plays a prominent role in the symptomatology of occipital lobe disease. The following topic will be discussed with illustrative clinical examples: Coloured phosphenes are reported by patients in both migrainous and epileptiform paroxysmal disorders. Patients with severe visual impairments report visual hallucinations which are frequently gorgeously coloured (Charles Bonnet syndrome). These may be formed objects or unformed sheets of colour. In hemianopia hallucinations, vividly coloured geometric shapes are occasionally reported in the blind hemifield. "Filling in" processes, in cases of homonymous scotoma, are more readily triggered by areas of colour (or texture) than by shapes or patterns. In cases of cortical blindness, there may be remarkable preservation of chromatic discrimination. Loss of colour vision following damage to occipito-temporal cortex (cerebral achromatopsia) is a well established phenomenon. In cases with some preservation of chromatic processing, there is a double dissociation between impairment of hue discrimination and the detection of structure from colour. The question of whether or not colour constancy is also impaired is problematic when hue discrimination is poor and shifts in colour appearance cannot be measured. Therefore dyschromatopsia caused by damage to the optic nerve or radiation demonstrates losses in opponent colour pathways, recent studies have shown that damage to the visual cortex reveals mechanisms which are specific to the processing of hue and are released from colour opponency.

Color vision loss in Duchenne Muscular Dystrophy

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Duchenne Muscular Dystrophy (DMD) is the most common form of progressive muscular dystrophy disease. It is caused by a deficiency in the protein dystrophin with deletions in the dystrophin gene in 60-65% of the patients, duplications in 5-10% and point–mutations or small rearrangements in the remaining 20-30%. The main pathological effects are in the skeletal and cardiac muscles. However, dystrophin is present in the nervous system, including the retina, and abnormalities in visual function had been detected in the ERG of DMD patients. The DMD gene is responsible for the transcription of dystrophin, a large protein, and four other smaller isoforms, two of which (Dp260 and Dp71) are found in the retina. Dp260 has been implicated in scotopic and photopic electroretinogram responses. We evaluated color vision of 44 Duchenne Muscular Dystrophy (DMD) patients (mean age= 14.8 ± 4.9) who were submitted to a battery of four different color tests: Cambridge Colour Test - CCT, Neitz Anomaloscope, Ishihara and AO H-R-R) and a control group composed of 70 age-matched healthy male subjects with no

ophthalmological complaints. Genetic analysis in the DMD patients showed deletions in the dystrophin gene upstream exon 30 (n= 12) and downstream exon 30 (n= 32). Color vision was impaired in 66% of the DMD patients with deletion downstream exon 30, whereas patients with deletion upstream exon 30 presented no color defect. All patients with color vision losses had a red-green color vision defect in the CCT, confirmed by the Neitz Anomaloscope ($p< 0.001$). A much lower percentage of losses were seen with the Ishihara and the AO-H-R-R, 5% and 7%, respectively. Results of these two tests were not correlated with CCT or Anomaloscope results. Color discrimination improved with age both in controls and DMD patients suggesting a non- progressive color defect. In conclusion, most DMD patients (66%) with deletions downstream exon 30 present a red-green defect, while deletion upstream exon 30 was associated with normal color vision. Our results agree with ERG studies showing losses in photopic and scotopic functions of patients with the same type of deletion. This color defect might be partially explained by a retinal impairment related to the dystrophin isoform Dp260.

Costa, M. F., Oliveira, A. F., Feitosa-Santana, C., Zatz, M., Ventura, D. F. (2007). Red-green color vision impairment in Duchenne Muscular Distrophy. *The American Journal of Human Genetics*, 80, 1064-1075.

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The Nagel anomaloscope 1907-2007

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Among the instruments commonly used in the study of colour vision, the anomaloscope has been pre-eminent for a century. It was introduced in 1907 by W. A. Nagel under the description "kleines Spektralphotometer oder Apparat zur Mischung von Spektralfarben für diagnostische Zwecke (Anomaloskop)." Nagel retained the primary wavelengths (536, 589, 670 nm) that had had already been standardised by Donders in 1884 for testing the Rayleigh equation; and of these, the red and yellow primaries have survived to the present day (e.g. in the German standard DIN 6160). The anomaloscope allows precise measurement in a clinical setting, but it does have imperfections: for example, the exact wavelengths of the primaries vary as the subject adjusts the slits (Moreland, 1974) and as room temperature changes (Jordan and Mollon, 1993).

Nagel, W.A. (1907). Zwei Apparate für augenärzliche Funktionsprüfung. *Zeitschrift für Augenheilkunde*, 17, 201-222.

Moreland, J.D. (1974). Calibration problems with the Nagel anomaloscope. In *Colour Vision Deficiencies II* (pp. 14-18). Basel: Karger.

Jordan, G., Mollon, J.D. (1993). The Nagel anomaloscope and seasonal variation in colour vision. *Nature*, 363, 546-549.

Failure of the Farnsworth D15 test and the Nagel anomaloscope matching range in anomalous trichromatism

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The Farnsworth D15 test (D15) was developed for use in occupational guidance. Hue discrimination ability is assessed for a series of Munsell hues with fixed colour difference steps. People with slight colour deficiency are intended to pass the D15 and people with significant colour deficiency are expected to fail, including all dichromats. The Nagel anomaloscope is a gold standard reference test for identifying and classifying red-green colour deficiency. The matching range on the red/green mixture scale is an indication of the severity of the discrimination deficit in anomalous trichromatism. We compare failure of the D15 with the anomaloscope matching range for 107 protanomalous and 410 deuteranomalous trichromats, using 2 different pass criteria. Thirty - six percent of subjects failed the D15 using the criterion of a single isochromatic error. In this case, 84% of deutans with a matching range > 30 scale units failed but only 12% failed with a matching range < 19 scale units. In comparison 50% of protans with a matching range > 15 scale units failed and 30% failed with a matching range < 9 scale units. Twenty-three percent of subjects failed when one red-green isochromatic error was allowed as a pass. This criterion favoured severe protans and "moderate" deutans. Only 24% of protans with matching ranges > than 15 units failed and the failure rate for deutans, with a matching range of 20 - 29 scale units dropped from 50% to 31%. The D15 result was related to the Nagel matching range in deuteranomalous but not in protanomalous trichromatism. Motivated subjects apply careful observation to obtain good results on the D15 and an exact relationship with

the anomaloscope matching range should not be expected. Protans make fewer errors than deutans because perceived lightness difference clues are available. A circular results diagram with no isochromatic errors is therefore the preferred pass criterion for occupational selection.

A study of the variables that can affect the parameters of the yellow match

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Anomaloscope matches provide useful information that reflects differences in the properties of the mechanisms involved in the processing of chromatic signals. The midpoint and range of red-green mixtures that subjects accept as a match to a spectrally-narrow, yellow field vary significantly, both within "normal" trichromats and within colour deficient observers. The latter require either more red or more green light to match the colour appearance of the yellow field. This observation and the pattern of variation in the intensity of the yellow field needed to match the extremes of the mixture of red and green lights are used to detect and classify the type of colour deficiency involved. A narrow red-green range, i.e., a high red-green discrimination index (RGI), is often taken to indicate high chromatic sensitivity, which is often associated with normal trichromatic vision. Some unusual matches that remain difficult to explain may provide useful information on the properties of colour mechanisms. Some subjects accept most, but not all, of the red-green mixture range, and others require significantly more red or green light in the match but only accept a very narrow range of red-green mixtures that yield RGI values equivalent to or better than a normal trichromat. As a result, the subject's

ability to discriminate colour differences under more normal conditions of illumination is often difficult to predict from the parameters of the yellow match. In order to explain such findings we produced a model of the yellow match that predicts how shifts in λmax, selective changes in optical density of photoreceptors and post-receptoral amplification of L and M cone signals can affect both the subject's midpoint and the range on the Nagel anomaloscope. The predictions of the model show that unusual yellow match parameters measured in some deuteranomalous and protanomalous observers could be predicted well with only small δλmax separations by appropriate changes in optical density and post-receptoral amplification of cone signals. Predictions of δλmax based on genetic analysis of cone pigment genes in 24 subjects with varied degrees of colour vision loss were used to constrain the parameters of the model. The red-green sensitivity of these subjects was also assessed using the CAD test and results were compared against model predictions of chromatic sensitivity based on the reciprocal of the Nagel range. The results suggest that subjects with minimum red-green colour vision loss, who often pass conventional colour vision tests, rely on a δλmax value as small as 10 nm. L to M wavelength separations greater than 20 nm yield chromatic sensitivities that fall within the normal range.

Anomaloscope design with tunable primaries

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We present a prototype design for an LED-based, variable-wavelength, computer-controlled anomaloscope. The optical design permits dual and extended Rayleigh matching via three tunable sources (535-560 nm, 575-600 nm, 600 – 620 nm). A microprocessor-based actuation and control system enables automatic operation. The system permits the use of an adapting field and control of the duration of the bipartite field presentation. User interface software permits method-of-adjustment measurements as well as adaptive algorithms for fitting of the subject's matching boundary. Results from normal, deutan and protan cases will be presented, with comparison data from a conventional anomaloscope.

The contribution to Rayleigh matches of the third red-green photopigment of color-defect carriers

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The mother or daughter of a male with X-chromosome-linked color-vision deficiency is a carrier of the defective gene. A female carrier's defective gene is posited to be expressed, so carriers may have more than one type of M or L cone. An open question is how the carrier's extra cone pigment affects the post-receptoral neural signals encoding color. Here, a model considered how the signal from an extra red-green pigment combines with signals originating from the normal L and M cones. The model examined three different possible assumptions about the signal from the extra cone pigment: it combines with the signal from (1) normal L cones, (2) normal M cones, or (3) both types of cone. Spectral-sensitivity peaks, optical density, and the relative number of cones were factors in the model. The model predicted individual differences in color matching among carriers, based on individual differences in the relative number of cones, the spectral location of the pigment's sensitivity peak and the pigment's optical density. To test the model, carriers' Rayleigh matches were measured using a standard Nagel-type anomaloscope; in addition, high-retinal-illuminance Rayleigh matches were measured using a Maxwellian-view optical system in order to vary optical density. The matches, which were normal or slightly shifted from normal, were not consistent with the signal from the extra red-green pigment combining only with the signal from normal

M cones. The matches could be accounted for by the extra-pigment response combining with L-cone signals, either exclusively or not. The assumption that the signal from cones containing the third red-green pigment combines with signals from both normal L and M cones is consistent with a random mosaic of cones within the retina (Solomon and Lennie, 2007).

Solomon, S.G., Lennie, P. (2007). The machinery of colour vision. *Nature Reviews Neuroscience*, 8, 276-86.

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Abstracts
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Software development for psychophysical measurements of color vision in infants and children based on the commercial version of Cambridge Colour Test

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The aim of this project was to develop a color vision test for children and non-human primates. The stimulus consists of a background of circles of various sizes and luminances, presented in a constant chromaticity, with the target defined by a subset shown at a different chromaticity, to prevent the use of luminance or contour differences to make discriminations. Stimulus chromaticities are calculated in the 1976 CIE diagram along the protan, deutan and tritan color confusion lines. The logic structure of the software is based on the Cambridge Colour Test (Cambridge Research Systems, CRS) whose code was generously made available to us. An independent code was developed in Object Pascal language (Borland's Delphi 7.0) and Microsoft Windows platform with VSG8 hardware/software interface, compatible with a Philips 202P4 high-performance monitor and with VSG 2/5 cards (CRS). Reaction time measures of the subject's response are also automatically provided.

Changes were made in the stimulus shape and its positions on the monitor. The new stimulus is an approximately square patch of circles subtending about 7 deg of visual angle at 50cm from the monitor. With this target, the test instructions are simpler and the response more intuitive for the child who chooses from four possible target positions (up, down, left and right). Reinforcement can be programmed in this situation as well as in the testing of non-human primates, for which nine target positions were programmed. Children sit facing the monitor and are instructed to point at or touch the color patch while an observer enters the responses using the response box, the keyboard or the mouse. A touch screen situation will also be implemented. A preferential look task applicable to infants was also designed at the left and right extremes of the monitor screen along the horizontal midline. The infant's response is recorded by an observer standing behind the monitor who reports the direction of the infant's gaze. Subjects are always given unlimited time to respond. The software has been tested in ten children, one to five years old. Thresholds in *u'v'* units were comparable to those obtained in older children (>5 yrs of age) tested with the Landolt C target, where tritan thresholds were more elevated than protan and deutan, repeating the same pattern of results obtained in adults (Ventura *et al.*, 2003). Infants were also tested in the preferential look situation, which yielded comparable results. We conclude that the new testing situations provided a successful means of measuring color discrimination thresholds in infants and children. Norms are currently being determined in a large sample of subjects.

Ventura, D.F., Silveira L.C.L, Rodrigues, A.R., Gualtieri, M., Souza, J.M., Bonci, D, Costa, M.F. (2003). Preliminary norms for the Cambridge Colour Test. In: J. D. Mollon, J. Pokorny & K. Knoblauch. (Org.). *Normal and Defective Colour Vision* (pp. 327-334). Oxford, UK: Oxford University Press.

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Visual dysfunctions in workers exposed to mercury vapor below the safe levels

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Mercury (Hg) vapor intoxication can lead to neuropsychological damage and impairment of different visual functions that have been demonstrated by psychophysical and electrophysiological methods with persistent effects for years after the exposure was ceased. In the present study, color vision, spatial luminance contrast sensitivity, and visual field sensitivity were evaluated with psychophysical methods in 10 workers (mean= 32.5 ± 8.5 yrs; 8 males (m)) exposed to Hg vapor in their work place (Hg recycling). We also evaluated their neuropsychological functions with a battery of tests. The exposure period: 4.3

± 2.8 yrs, and the urinary Hg concentration: 22.3 ± 9.3 µg/g creatinine, within the safe levels (35 µg/g creatinine) as defined by the Americam Conference of Governmental Industrial Hygienists (ACGIH). Inclusion criteria: Snellen VA 20/30 or better, and absence of ophthalmologic disease or disease that could affect visual system. Color vision was assessed with the Farnsworth D-15 test and the Lanthony D-15d test (20 controls: 34.5 ± 9.1 yrs; 13 m), and the Cambridge Colour Test (CCT) (20 cont.: 39.3 ± 5.6 yrs; 12 m). The spatial luminance contrast sensitivity was measured with the computerized program PSYCHO (10 cont.: 35.5 ± 8.5 yrs; 7 m). Visual fields (VF) were analyzed with the Humphrey Field Analyzer II: the standard automated perimetry white-on-white (SAP) and the short wavelength automated perimetry blue-on-yellow (SWAP) (20 cont.: 39.7 ± 6.9 yrs; 12 m). The neuropsychological battery included measures of inhibitory control (Stroop), verbal memory (Buschke Selective Reminding), visual memory (WMS Visual Reproduction), manual dexterity (Grooved Pegboard), verbal fluency (FAS), visuo-spatial function (WAIS Block Design), depression (BDI), and anxiety symptoms (STAI) (9 cont.: 37.1 ± 5.7 yrs; 8 m). The statistical analyses: Mann-Whitney ($p< 0.05$) and Spearman. We have found a significant reduction of VF for both tests compared to controls for mean deviation ($p< 0.01$) and pattern standard deviation ($p< 0.05$). Compared to controls, we have not found a significant difference for all color vision tests (D-15, $p> 0.66$; D-15d, $p> 0.35$; CCT, $p> 0.27$), for contrast sensitivity ($p> 0.36$), for neuropsychological tests ($p> 0.05$). We have found no correlation of any result with age, exposure time or urinary Hg concentration. The finding of losses of VF sensitivity, suggests that occupational exposure to Hg vapor within accepted safety levels may not be safe. This result reinforces earlier suggestions (Meyer-Baron *et al*., 2002) of reduction of accepted safety levels of the urinary Hg concentration during occupational exposure to Hg vapor.

Meyer-Baron, M., Schaeper, M., Seeber, A. (2002). A meta-analysis for neurobehavioural results due to occupational mercury exposure. *Archives of Toxicology*, 76, 127-136.

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Comparison of two methods to study very-long-term chromatic adaptation

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Two methods for establishing very-long-term chromatic adaptation were assessed. Shifts in equilibrium yellow were measured following very-long-term chromatic adaptation (over days or weeks) to either longer-wavelength room illumination for several hours per day (classical paradigm) or a long-wavelength CRT pattern for one hour per day. The aim was to test whether the briefer CRT pattern produced very-long-term chromatic adaptation comparable to that invoked by the longer room illumination. In the classical condition, the subject spent four hours/day for fourteen days in a windowless room in which overhead light passed through a filter that allowed only 5% transmittance of wavelengths below 540nm (Judd x = 0.408, y = 0.420, 140 lux). In the new method, the subject viewed a grating that changed orientation every five seconds for one hour per day. The chromaticity of the grating on the CRT monitor was Judd x = 0.598, y = 0.345 (22.4 cd/m^2), which was close to the chromaticity of the R phosphor. [We thank Dr. J. Neitz of the Medical College of Wisconsin, who suggested this approach.] Measurements to assess color perception were performed either twenty-three hours (CRT) or twenty hours (room illumination) after the previous adapting period. The subject set an admixture of 540-plus-660nm light to appear equilibrium yellow at four luminance levels between three and one hundred trolands. Both methods of chromatic adaptation produced similar shifts in equilibrium yellow as well

as similar shifts back toward baseline during the two-week post-adaptation recovery period. Thus, the CRT stimulus is more efficient than room illumination in establishing very-long-term chromatic adaptation. In addition, CRT stimulation is more flexible than room illumination for studying very-long-term chromatic adaptation because it can be (1) retinotopically localized, (2) dichoptic (unequal in the two eyes) and (3) precisely controlled with respect to chromaticity and cone stimulation.

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Methylmercury within safe WHO limits causes losses of fish ON-bipolar cells

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The purpose of this study was to quantify ON bipolar cells in the retina of fish intoxicated with sublethal doses of methylmercury. Anaesthetized thrairas (*Hoplias malabaricus*) received an intraperitoneal injection of either 0.01 (N = 2) or 0.05 (N = 2) µg MeHgCl/g followed by 15 depuration days. After dark-adaptation (2h), the posterior eyecups containing the retina were dissected from the sclera and pigment epithelium, and fixed in 4% paraformaldehyde in 0.1 M sodium phosphate buffer, pH 7.4, for 3 h. The retinae were incubated with mouse monoclonal antibody against rabbit anti αPKC (1:1.000, Sigma) for 72h, and revealed with goat antisera against rabbit IgG tagged with rhodamin (1:200, Jackson) for 2 h. Retinal cells were photographed in different

retinal sample fields with a fluorescence microscope camera (Leica) and images sampled at 1mm intervals were digitized . The total population and the cell density throughout the retina were estimated. Bipolar cells stratified in sublamina b from the inner plexiform layer were immunoreactive to the antibody against αPKC (αPKC-IR). The effect of both mercury doses used - 0.01µg/g (110 ± 14,000) and 0.05µg/g (131 ± 15,000) (p= 0.01 and p= 0.0004, *student T*- test) was to reduce total ON bipolar cell population relative to the control group (180 ± 14,000). For the 0.01µg/g dose PKC-IR cell loss was 35% in the peripheral retina (p= 0.007) and 54% in the central region (p< 0.000) At the highest dose: a similar loss was found in the periphery of the retina (39% cell loss; p= 0.005) but the central region showed a much smaller reduction (12%) (p= 0.09). Within retinal quadrants, the temporal region was the most affected - reduction of 43% and 50% for the 0.01 (p= 0.007) and 0.05 (p= 0.002) µg/g doses, respectively. At the other retinal quadrants there was a non-significant cell loss in the MeHg exposed groups relative to the control group. No difference in ON-bipolar cell loss was found between doses used here and higher doses (2 and 6 µg/g MeHg) used previously (Bonci *et al*., 2006). We conclude that acute sublethal methylmercury intoxication (0.01 e 0.05 µg/g) reduced the total population of ON-bipolar cells αPKC-IR as extensively as observed in higher doses. The largest losses of on ON-bipolar cells were observed in intoxication levels below the lower limit established by the World Health Organization (0.5 mg/kg MeHg).

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Visual field asymmetries due to different contribution from magno- and parvo-cellular pathways

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There is a strong body of evidence that the magno-cellular pathway (MC) dominates the lower visual field (LVF); nevertheless there is no clear evidence, so far, if the upper visual field (UVF) is dominated by the parvo-cellular pathway (PC). This study was aimed to investigate, using simple reaction times (RTs), the contribution of MC and PC pathways on LVF and UVF. Ten participants from the Max Planck Institute for Biological Cybernetics Subject's Database, all of them with normal color vision, took part in this study. Two experiments were performed in a colored calibrated monitor and color coordinates were measured with a PR-650 SpectraScan Colorimeter (Photo Research, Inc.). In the two experiments, subjects pressed a response key to the onset of the target (RTs), a dot subtending 1° of visual angle, briefly presented (150ms) on a grid of 82 different positions (covering an area of 24° by 16°) on the computer screen. Participants were asked to always fixate their gaze to a fixation cross located to the center of the screen and eye movements were monitored with an eye tracker (EyeLink II - SR Research Ltd). In experiment I, a white dot (CIE x, y = 0.313, 0.329) with a luminance of 80 cd/m^2 was presented against a black background. In the first phase of experiment II, heterochromatic flicker photometry was used for every participant to reach isoluminance of the target and background, using a green dot (CIE x,y = 0.212, 0.260) presented against a red background (CIE x, y = 0.360, 0.260). Results from experiment I confirm previous findings of a MC advantage on the LVF (319±15ms) against UVF (332±9ms) ($T = 4.52$, $p < 0.0001$). Experiment II showed,

instead, a PC facilitation on the UVF (350±17ms) when compared to the LVF (362±20ms) (T= 2.96, *p*= 0.004). In conclusion, with this simple and classical approach (RTs) it was possible to demonstrate the different contribution from each pathway to LVF and UVF.

Normality of color vision in compound heterozygous females carrying a protan and a deutan defect

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Inherited red-green color vision defects are quite common in males, affecting nearly 1 in 10, but uncommon in women, affecting only about 1 in 250. However because red-green defects are X-linked, nearly 15% of females are heterozygous carriers of red-green color deficiency. In addition, about 1 in 150 females are ''double carriers'', where both of their X chromosomes have L/M gene arrays encoding a red-green defect. If a woman carries the same type of color vision defect on each X-chromosome, she will be red-green color blind, while if she carries opposing defects (protan vs. deutan) on each X chromosome she will be trichromatic, owing to the process of X-inactivation. These trichromatic ''double carriers'' are referred to as compound heterozygotes, though very few have been reported. Moreover, questions remain as to whether the color vision capacity of these women is comparable to that of ''normal'' trichromats. Here we examined two unrelated compound heterozygotes who were carriers of both protanopia and deuteranomaly. We also examined male members of their families representing both forms of red-green defect carried by the female probands. Genetic analyses provided direct confirmation that both females were indeed compound heterozygotes. Flicker-photometric ERG estimates of L:M cone ratio were obtained, as were C100 settings. One of the compound heterozygotes clearly showed Schmidt's sign, consistent with an extreme skew in her L:M cone ratio. Complete color vision testing was done, including Rayleigh matches, pseudoichromatic plates, unique hue measurements, and

100-Hue tests. We found the color vision of the compound heterozygotes to be indistinguishable from that of other trichromats. This suggests that LCR/promoter interactions and X-inactivation are equivalent mechanisms for determining cell identity.

Contrast sensitivity and colour discrimination of subjects with a history of chronic alcoholism

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We have studied the performance of the visual system of patients with clinical histories of chronic alcoholism. We have utilized the results of psychophysical tests of chromatic and achromatic spatial vision with the purpose of evaluating two fundamental features of the human vision: spatial contrast sensitivity and color discrimination. In the study, we tested 15 patients with a history of diagnosed chronic alcoholism (age= 38±11, both sex) and without a clinical history of ophthalmologic and/or neurological injury. The patients performed the tests after they had been submitted to clinical inquiry, an ophthalmologic exam and Humphrey visual field analysis. We have applied the following psychophysical tests: assessment of the Contrast Sensitivity Function; the Mollon-Reffin Test for color thresholds determination; and the Trivector Test for color thresholds determination in the protan, deutan and tritan axis. The results were compared with three similar control groups (group a n= 53, age= 25±7; group b n= 25, age= 38±7; group c n= 15, age= 45±7) with the respective age and similar populations parameters. For ends of study and analysis, the subjects have been divided into three groups, according to the age. The data has shown that 13 out of 15 subjects with chronic alcoholism present varied and accentuated dysfunction in chromatic vision and a small dysfunction

in achromatic vision, which includes: a little diminution in spatial contrast sensitivity; significant increase of the color thresholds; and an increase in errors for the trivectors. The results suggest that the visual alterations related with chronic alcoholism are important aspects to be considered in the clinical evolution of this disease.

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Contrast sensitivity mediated by ON- and OFF-subsystems of the magno- and parvocellular pathways in mercury vapor intoxication.

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Our aim is to measure contrast sensitivity thresholds of the ON- and OFF-subsystems of the parvocellular (PC) and magnocellular (MC) pathways using a computerized psychophysical task, in former workers occupationally intoxicated by mercury vapor. Contrast sensitivity was measured in 36 patients intoxicated by mercury vapor (mean age= 41.3 yrs; SD= 6.7; 23 males) and 21 controls (mean age= 39.7 yrs; SD= 4.9; 14 males). The measurements were performed with white on grey (ON) and black on grey (OFF) checkerboards at two spatial frequencies (MC, 0.5 cpd; PC, 4.0 cpd), presented at either 33 ms or 1500 ms duration on a uniform gray background, with an interstimulus interval of 300ms. The sensitivity was expressed as the mean of 3 ascending and 3 descending thresholds obtained for each condition (Parvo ON, Parvo OFF, Magno ON, Magno OFF). Mercury intoxicated patients differed statistically from controls at all conditions: Magno ON (p= 0.0009); Magno OFF (p= 0.0003); Parvo ON (p< 0.0001); Parvo OFF (p< 0.0001). No correlation was found between time of exposure and urinary mercury levels with contrast results (p< 0.05). There were also no differences between male vs. female for controls and for mercury patients (p< 0.05). We conclude that losses in contrast sensitivity were non selective for either the magnocellular or the parvocellular functions

in patients occupationally intoxicated with mercury vapor. This result is in agreement with our previous data showing a reduction in luminance contrast sensitivity obtained in the same population (Ventura *et al*., 2005).

Ventura, D.F., Simões, A.L., Tomaz, S., Costa, M.F., Lago, M., Costa, M.T.V., Canto-Pereira, L.H.M., Souza, J.M., Faria, M.A.M., Silveira L.C.L. (2005). Colour vision and contrast sensitivity losses of mercury intoxicated industry workers in Brazil. *Environmental Toxicology and Pharmacology*, 19, 523-529.

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Rho GTPases in the mice retina and ciliary body

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Ciliary body (CB), a structure adjacent to the retina, is a nonneural tissue derived from the optic cup, which normally does not contain neurons and functions to produce components of the aqueous humor. Neural stem cells/progenitors that give rise to neurons and glia have been identified in a mitotically quiescent state in the CB of the adult mammalian eye (Ahmad *et al*., 2000; Tropepe *et al*., 2000; Coles *et al*., 2004). Considering the potential applications of such stem cells in treating retinal degenerative diseases, the aim of the present study was to characterize the presence of small Rho GTPases, important proteins in signaling pathways that regulate gene transcription, cell cycle entry and cell survival, in the CB of mice, and the effects of their activation and inhibition on cell proliferation and differentiation. Adult Balb/c mice were anesthetized and lysophosphatidic acid (LPA, Rho GTPases activator, 1μM), toxin A (Rho GTPases inhibitor, 10 ng/ eye) or PBS (control) with BrdU (1μg) were injected into the eyes. After 6, 12 and 24 hours they were sacrificed and the retinas were processed for immunohistochemical. In some animals, growth factors (FGF+ insulin) were also injected to their eyes (100 ng and 2μg/eye, respectively) for 4 days. Immunohistochemical analysis was performed with the antibodies against RhoA, RhoB and Rac1, and markers for microglia (Ox42), proliferation (BrdU and Ki67) and progenitor cells (Pax6, Chx10 and Nestin). In control retinas, RhoA was observed in cell bodies and segments of photoreceptors,

in the inner nuclear layer and it was weakly expressed in the CB. RhoB was predominantly expressed by Müller cells and pars plana of the CB, whereas Rac1 was mostly observed in photoreceptor segments and plexiform layers, but it was diffusely distributed in the CB. After LPA injections, RhoA and RhoB expression was increased in the central retina and CB, and Rac1 was detected in photoreceptor cell bodies. In addition, Ki67 and BrdU-positive cells were observed in the plexiform and ganglion cell layers, and CB. Cell counts did not show statistical differences between the PBS and LPA injections; the Ox42 marker suggested that they were microglial cells. However, nestin-positive cells were seen in the CB 6h after LPA injection, disappearing after 12 and 24h, when Pax6 and Chx10 co-expression was observed. ToxA appeared to increase cell proliferation. Although all investigated GTPases changed their expression after LPA activation, LPA did not induce proliferation of progenitor retinal cells. On the other hand, an increased number of progenitors in the CB, as shown by nestin expression, as well as Pax6 and Chx10 co-expression, indicated that LPA might induce undifferentiated patterns. Rho GTPases inhibition by Toxin A may potentiate the mitogenic effects of growth factors.

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Irreversible color vision losses in patients with chronic mercury vapor intoxication

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In this follow-up study, we assessed the reversibility of color vision losses in patients with diagnosed occupational mercury vapor intoxication in fluorescent lamp industries. Color vision was evaluated in 20 patients (mean age = 42.4 ± 6.5 years; 6 female) with chronic exposure to mercury vapor for 10.5 ± 5.3 years and away from the work place for 6.8 ± 4.2 years. The mean mercury urinary concentration was 47 ± 35.4 μg/g creatinine during exposure or up to one year after exposure. There was no information about mercury urinary concentration at the time of testing in 2002. Three years later, at the time of the follow-up testing, this value was 1.4 ± 1.4 μg Hg/g creatinine. Inclusion criteria: best corrected Snellen VA >20/30, absence of known ophthalmological pathologies or diseases known to affect the visual

system. A control group comprised 21 patients (mean age= 40.0 ± 6.4 years; 8 female). Both eyes of all subjects were tested monocularly. Color vision was assessed using the Cambridge Colour Test (CCT), version 2.0 (Mollon and Reffin, 1989). Within the CCT protocol, two tests were performed (with the reference background chromaticity u'= 0.197, v'= 0.469): the Trivector test and one Ellipses test. The Trivector test estimates thresholds along protan, deutan, and tritan confusion lines, and the Ellipses test estimates the MacAdam ellipses with eight vectors. This protocol had been applied in 2002 (Ventura *et al*., 2005). In patients' worst eyes, color discrimination, as indicated by all parameters, was significantly worse than in the control group. The difference between the patients' results of 2002 and 2005 (the follow-up testing) was not significant for any parameter: best eye: protan, p= 0.65; deutan, p= 0.36; tritan, p= 0.07; area, p= 0.21; axis ratio, p= 0.80; worst eye: protan, p= 0.82; deutan, p= 0.82; tritan, p= 0.82; area, p= 0.24; axis ratio, p= 0.10. Further analysis, using Spearman correlation, showed no significant relationship between the 2002 and 2005 outcome of color vision testing with the exposure duration, time away from the exposure, mean urinary concentration, and age (with an exception for age and axis ratio for both best and worst eye, a moderate correlation). Previously, for workers exposed to mercury vapor for one year in a non-controlled exposure, reversibility of color vision impairment was demonstrated (Cavalleri & Gobba, 1998). Our findings indicate that, following a long-term exposure to mercury vapor and several years away from the source of intoxication, the impairment of color vision remains irreversible.

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Color vision in *Cebus apella*

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Catharrine primates, humans included, have trichromatic color vision, based upon the presence of three classes of cones, each preferentially sensitive to wavelengths in the short (S), medium (M), or long (L) parts of the visible spectrum. Platirrine primates show polymorphic color vision: some of the females are full trichromats, while all the males and the remnant of the females show one of the two forms of dichromacy determined by the absence of either M or L cones – protanopy and deuteranopy. The present study assessed the color discrimination of two male and two female capuchin monkeys. Two experiments were performed, each comprising a few successive series of simple discrimination tasks with 8-9 different pairs of hues and one test session presenting two novel pairs among the trained ones. In every session, each trial displayed 16 choices, only one of which (S+) was programmed with a different color. The two experiments differed only in the control of luminance, which had the same nominal value for all stimuli in Experiment 1, but varied among stimuli in Experiment 2. In both experiments, subjects had difficulties with the yellow-red, yellow-green, and red-green discriminations, all likely to be poor and even impossible in both forms of dichromacy. Preliminary data suggest that one of the females succeeded in performing the yellow-red discrimination. The accuracy of these results will be further assessed in future studies using equipment specifically designed for research on color-vision related phenomena.

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Distribution and total number of the photoreceptors in calltrichini primates: *Callithrix jacchus jacchus* and *Saguinus midas niger*

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The diversity of species among New World primates has raised great interest about a number of aspects of their visual system. We have investigated the photoreceptor density and total number in six species of New World primates: *Alouatta caraya*, *Cebus apella*, *Saimiri ustius*, *Callithrix jacchus*, *Saguinus midas niger*, and *Aotus azarae*. Cones and rods were counted along the horizontal, vertical and two oblique meridians at 0.25 mm and 1 mm intervals in the central and peripheral retina regions, respectively, in retina whole mounts prepared by the method of Curcio *et al.* (1987). We analyzed four retinae from *Alouatta*, seven from *Cebus*, four from *Saimiri*, four from *Saguinus*, two from *Callithrix* and three from *Aotus*. Isodensity contours were constructed and the number of cones and rods along the retina estimated from density values integration. The peak of cones (in cones/mm^2 ± s.d.) was 394,532 ± 49,719 for *Alouatta*; 164,062 ± 13,811 for *Cebus*; 138,021 ± 8,132 for *Saimiri*; 132,813 ± 27,622 for *Callithrix*; 160,391 ± 2,762 for *Saguinus*; and 17,090 ± 6,215 for *Aotus*. The cone density reached a minimum in the temporal and dorsal periphery. The peak of rods (in rods/mm^2 ± s.d.) was 209,228 ± 51,576 for *Alouatta*; 174,967 ± 42,132 for *Cebus*; 137,939 ± 23,046 for *Saimiri*; 87,646 ± 44,569 for *Saguinus*; 79,102 ± 13,811 for *Callithrix*; and 399,413 ± 11,881 for *Aotus*. The total number of photoreceptors was 3.6 ± 0.52 millions of cones and 58.7 ±

5.58 millions of rods for *Alouatta*; 4.5 ± 0.62 millions of cones and 51.9 ± 5.97 millions of rods for *Cebus*; 3.4 ± 0.30 millions of cones and 33.6 ± 4.36 millions of rods for *Saimiri*; 3.7 ± 0.31 millions of cones and 11.2 ± 0.24 millions of rods for *Saguinus*; 3.7 ± 0.21 millions of cones and 10.7 ± 1.25 millions of rods for *Callithrix*; and 2.3 ± 0.13 millions of cones and 140.6 ± 25.6 millions of rods for *Aotus*. Photoreceptor topography thus revealed some interesting species differences The peak cone density was similar in all of the diurnal species studied but in *Alouatta*, which was more than twice as high as the rest. Since its total number of cones was not atypical, the high foveal receptor density was produced by reduced peripheral density. In contrast, the *Callithrix* retina had high cone density even in the periphery, possible because of its smaller overall retinal size. *Aotus* had the lowest number of cones and the highest number of rods among all species. For these diurnal retinae, therefore, retinal differences can best be described as topological rearrangements of a roughly fixed number of photoreceptors, but for nocturnal *Aotus*, the photoreceptor complement is changed.

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Differential expression of GABA receptors in the primate retinae

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$GABA_C$ receptors have a higher sensitivity for GABA, compared with $GABA_A$ receptors. These receptors also differ in their pharmacological profile compared with $GABA_A$ and $GABA_B$ receptors. $GABA_C$ receptors are ligand-gated chloride channels that mediate bicuculine and baclofen insensitive GABA responses. These receptors are composed of ρ-subunits, which can readily form homomeric receptors with many properties similar to those of the $GABA_C$ receptors present on neurons. In order to determine whether $GABA_C$ receptor ρ-subunit co-assembled with another receptor subunit, double-labelling experiments were performed with subunit specific antisera in sections of the *Cebus apella* retinae. In vertical sections of retinae, strong punctuate immunoreactivity was present in the inner plexiform layer (IPL), and weaker immunoreactivity was also present in the outer plexiforme layer. Punctuate, putative synaptic clustering was observed with all antisera applied, however, in the retinae $GABA_C$ receptor expressing puncta did not coincide with $GABA_A$ receptor subunit containing puncta. Our results suggest, as in rodent retinae, that there are no synaptic GABA receptors in the primate retinae, in which $GABA_A$ and $GABA_C$ receptor subunits are co-assembled.

Effect of temporal configuration in colour discrimination ellipses of trichromats measured with Visual Evoked Potential (VEP)

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Differences in colour discrimination can be assessed by psychophysical measurement of MacAdam ellipses. Recently, Gomes *et al*. (2006) obtained colour discrimination ellipses by using transient Visual Evoked Potential (tVEP). The purpose of this work is to further pursue this approach by measuring colour discrimination thresholds with VEP under three presentation modes and to compare these data with psychophysics using the same stimulation of the VEP and the Mollon-Reffin stimuli. Four normal trichromats (23.8 ± 3.1 years old) were monocularly tested. Stimuli consisted of sinusoidal isoluminant chromatic gratings made from chromaticity pairs located along four different colour directions centered on one reference point (CIE 1976: u′ = 0.225; v′ = 0.415). Heterochromatic Flicker Photometry (HFP) protocol was used to obtain the isoluminance condition for every subject and for all chromaticity pairs. Spatial frequency was 2 cycles/deg. Presentation modes: transient, onset (300 ms) / offset (700 ms) periods; steady-state, onset

(50 ms) / offset (50 ms) periods; and steady-state, 5 Hz phase reversion. For transient presentation, the biphasic negative-positive (N-P) amplitude of the VEP was related to the chromatic difference. For steady-state onset / offset and reversal presentations, a Fast Fourier Transform (FFT) procedure was used to obtain the amplitude of the VEP 10 Hz harmonic, which was then related to the chromatic difference. These parameters were plotted against distance in the colour space between the chromaticities of each grating component and fitted with a regression line; colour thresholds were found by extrapolating the fitting to the null amplitude value. Thresholds were plotted as MacAdam ellipses. For all subjects and all stimulation methods, the ellipses showed small sizes, low ellipticities, and were vertically oriented. Despite the fact that VEP ellipses were consistently smaller than those obtained with the Mollon-Reffin test, there was no statistical difference between ellipses obtained with VEP and both psychophysics methods, either gratings or Mollon-Reffin stimuli (One-way ANOVA; $p > 0.05$). The VEP ellipses obtained with the transient presentation were more related in size with those obtained with steady-state reversal than steady-state onset / offset presentation. We concluded transient onset/offset and steady-state reversal VEPs can be reliably used in objective studies of colour discrimination in normal trichromats.

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Psycophysical evaluation of congenital colour blindness: Mollon-Reffin´s ellipse 3 as a good way to discriminate between protan and deutan subjects

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Sensitive and specific psycophysical methods were used to measure colour vision performance among protan and deutan subjects living in Belém (State of Pará, Brazil). Such methods included computer versions of the Farnsworth-Munsell 100-hue test (FM 100) and the Mollon-Reffin (MR) test. The study evaluated the colour vision of 93 subjects (30.4 ± 9.7 years-old) who were referred by the State of Pará Traffic Department (DETRAN-PA) or selected among employees and students of the Federal University of Pará (UFPA). Criteria of selection were absence of systemic neurophtalmological pathologies. All individuals were evaluated with versions of both tests built in the University´s Laboratory of Neurophysiology. These tests were developed for usage in IBM Power StationRISC 6000 workstations. For the MR test, measurements were taken along 20 directions in the CIE 1976 colour space in order to determine five colour discrimination MacAdam's ellipses. Three variables were used to compare results obtained among the various subjects: the orientation angle of the ellipse long axis; the diameter of the circle with the same area; and the ratio between the ellipses long and short axes. For the FM 100 test, measurements were: the logarithm of mean error; the left and

right error central points; the upper and lower error central points. Results were also analysed in two and three dimensions as well as through cluster analysis for both tests. Results show that it is possible to extend validation of our software for the FM 100 and MR tests. Preliminary statistical norms were established in order to classify the subjects in the protan and deutan groups. Usage of a larger sample will be necessary in order to formulate definite rules. For the MR test, ellipse 3 ($u' = 0.225$, $v' = 0.415$) when compared to the other four ellipses, most easily separates protans and deutans due to its distinct large angle orientation in the colour space for these two red-green colour blind subjects. Finally, the MR test is more sensitive than the FM 100. It separates individuals by dysfunction groups more precisely and its use is appropriate for more refined evaluation of colour blind phenotypes.

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A computer-controlled color vision test for children based on the Cambridge Colour Test

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The present study aimed at providing conditions for the assessment of color discrimination in children, for which the task of indicating the gap of the Landolt-C in the commercial version of the Cambridge Colour Test (Cambridge Research Systems, CRS) proved counterintuitive and/or difficult to understand. We thus adapted the stimulus generation routine of the CCT, whose source code was generously provided by CRS, to obtain a new target: a patch of color approximately the size of the Landolt C gap (subtending about 7 deg of visual angle at 50cm from the monitor). We also adopted operant training techniques for establishing and maintaining the subjects' responding. In a pilot study, we tested two 3-year old and two 5-year old children. They sat facing the monitor and were verbally instructed to touch the colored patch in the screen. Correct responses were followed with positive reinforcement. Thresholds were plotted in the CIE 1976 color space and fell within the range of thresholds obtained in the original CCT, for children aged 7-11 years (means in 10-4 u' v' units= 81±24, 77±25, and 109±34 for the protan, deutan, and tritan respectively). Protan and deutan thresholds were

consistently lower than tritan thresholds, replicating a pattern obtained for adults in the original test. Encouraged by these results, we developed an independent software, based upon the CCT rationale and incorporating our alternative stimulus arrangement. The software was developed in Object Pascal language (Borland's Delphi 7.0) and Microsoft Windows platform with VSG8 hardware/software interface, the whole system being compatible with a Philips 202P4 high-performance monitor and with VSG 2/5 cards (CRS). We are currently testing children aging 2-6 years in order to further assess the applicability of our software. The mean thresholds obtained for 5 year-olds (n=7) – 56±10, 49±7, and 63±10 – are within the tolerance limits established for adults (means 43±11, 47±15, and 68±20) (Ventura *et al.*, 2003). Our test was capable of producing color discrimination thresholds compatible with those obtained with the original CCT test, with children taking the test in approximately the same number of trials (60±7) as adults (59±5), an aspect of great relevance in testing children since session length is an important concern.

Ventura, D.F., Silveira L.C.L, Rodrigues, A.R., Gualtieri, M., Souza, J.M., Bonci, D, Costa, M.F. (2003). Preliminary norms for the Cambridge Colour Test. In: J. D. Mollon, J. Pokorny & K. Knoblauch. (Org.). *Normal and Defective Colour Vision* (pp. 327-334). Oxford, UK: Oxford University Press.

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Density and topography of the photoreceptors of the retina of the turtle *Trachemys scripta elegans* determined with immunocytochemistry of opsins

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The importance of the identification of the types of photoreceptors of a species that has been intensively studied and is a model for color vision work, such as *Trachemys scripta elegans*, is related to the understanding of how chromatic

information is used in its vision. The recent confirmation that there are four types of opsins in cones of this species, and therefore the potential for tetrachromatic vision, reopens the question of how the different types of photoreceptors are arranged in its retina. The knowledge of their density and of their regional and general topographic distribution, with possible retinal specializations such as the visual streak and the *area centralis*, is necessary for the understanding of the vision of this species and is relevant for the comparative study of color vision. However, the only two descriptions available are very incomplete, with results that do not allow a detailed vision of the density and topographic distribution of its photoreceptors. Thus, the main objective of this work was the investigation of the density and topography of the photoreceptors throughout all regions of the retina. The finding of a probable *area centralis* was a result of the topographic study of the visual streak. To identify and count the six different types of cones and the rod of *Trachemys scripta elegans* we labeled them with antibodies anti-opsin (JH492, Zebrafish Red e Green Opsin e RcVP-MS). The specificity of each antibody was tested in radial sections and the counts for the determination of the topographic distribution of density were made in flattened wholemount retinas. The results showed that the cones are organized horizontally in a visual streak, a region with higher density of photoreceptors that ends temporally in the far periphery and more centrally in the nasal side. Therefore, this band of high density of photoreceptors is not symmetrical about the center of the retina, but it is displaced towards the temporal side. It is found for each photoreceptor type. Within the streaks of each photoreceptor type there was a region of very high density which is suggestive of an *area centralis*. This region was located in the temporal area. Its existence suggests the possibility of binocular vision. We also observed a dorso-ventral asymmetry in photoreceptor density, with greater density in the ventral region. The asymmetry was discrete in the cones, but it was very pronounced in the rods.

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Psychophysical assessment of magnocellular and parvocelular responses in unaffected carriers of 11778 LHON using a luminance contrast sensitivity procedure

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Leber's Hereditary Optic Neuropathy (LHON) leads to ganglion cell loss in the affected individuals mainly at the papillomacular bundle. Unaffected carriers, however, have sub-clinical visual abnormalities that include contrast sensitivity deficits (Ventura *et al.*, 2005). We looked for evidence of impairment of parvocellular (PC) or magnocellular (MC) function. We used a version of the Pokorny and Smith (1997) pulsed/steady pedestal paradigms (PPP/SPP) that elicit PC and MC responses. A luminance pedestal (four 1^ox1^o squares) was presented at 7, 12, or 19 cd/m^2 on a 12 cd/m^2 surround. One of the pedestal squares (trial square, TS) was modulated for either 17ms or 133ms. In the SPP, the pedestal was fixed, and the TS modulated. For the PPP, the pedestal pulsed for 17 or 133ms, while the TS pulsed up or down relative to its 3 neighbors. For each duration and pedestal level, the observer's task was to detect the TS. Luminance contrast discrimination was measured in 18 carriers (35±13 yrs, 16 male) and 18 controls (40±10 yrs, 7 male). Carriers contrast thresholds were significantly higher than controls' in both paradigms. As a measure of 'net temporal integration (TI)', we used the difference between the log contrast thresholds for the two stimulus durations. Although TI data from carriers and controls did not differ statistically, there was a clear trend for the carriers' thresholds to be more affected by stimulus duration than the controls, consistent with the carriers having slower temporal processing. Our data imply that unaffected carriers have impaired contrast gain control in both systems (MC and PC). Since the test can identify deficits in unaffected carriers, the test may be helpful for early detection/characterization of the disease.

Pokorny, J., Smith, V.C. (1997). Psychophysical signatures associated with magnocellular and parvocellular pathway contrast gain. *Journal of the Optical Society of America. A, Optics, image science, and vision,* 14, 2477-2486.

Ventura, D.F., Quiros, P., Carelli, V., Salomão, S.R., Gualtieri, M., Oliveira, A.G.F., Costa, M.F., Berezovsky, A., Sadun, F., Sadun, A.A. (2005). Chromatic and luminance contrast sensitivity functions of asymptomatic carriers of 11778 Lebers Hereditary Optic Neuropathy from a large pedigree in Brazil. *Investigative Ophtalmology & Visual Science,* 46, 4809-4814.

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Cortical processing of chromatic gratings, as assessed by transient VEPs, is impaired in type II diabetics

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We evaluated chromatic contrast responses from type 2 diabetic patients by recording transient Visual Evoked Potentials (tVEP). We examined 11 patients (9 females and 2 males, mean age = 63 ± 9 years) with no or minimal background retinopathy (mean time of disease = 11 ± 10 years). Stimuli were horizontal, 2 c/d sinusoidal gratings subtending a 14-deg square field, presented repetitively for 300 ms at 1 Hz. Between each stimulus presentation, the screen was blank at the mean luminance of the gratings (17.15 cd/m^2). Two chromatic modulation conditions were used: *red/green* (R/G) axis, and *blue/yellow* (B/Y) axis. Chromatic stimuli were adjusted to equiluminance for each subject by using Heterochromatic Flicker Photometry. Chromatic tVEPs were recorded at 5 contrast levels (5, 10, 20, 40 and 80%). For each condition, contrast

thresholds were estimated by measuring tVEP N1, and by extrapolating to zero amplitude. Using the same stimuli we also obtained psychophysical measures for all conditions. Patients' ON responses to the chromatic gratings were characterized by negative tVEP waveforms at stimulus onset (as observed in normals; Porciatti and Sartucci, 1999), but only above 20% color contrast. As expected, the tVEP amplitude increased as a function of contrast in all conditions. Chromatic contrast thresholds from diabetic patients were 5.2 ± 4% (R/G) and 12.3 ± 26% (B/Y), higher than normal for these parameters (2.0 and 2.8 % for R/G and B/Y stimuli; Porciatti and Sartucci, 1999). Chromatic tVEP latencies were also longer than normal. At 80% contrast, mean tVEP latencies were 172 ± 32 ms (R/G) and 180 ± 30 ms (B/Y), compared with normal values of 120 ms for both axes (Porciatti and Sartucci, 1999). Psychophysical contrast thresholds confirmed the tVEP findings for chromatic stimuli. Our findings of abnormal chromatic tVEP and psychophysical responses in type 2 diabetics are consistent with damage somewhere in the neural pathways between the retina and the cortical tVEP generators. The extent to which retinal lesions contribute to these losses requires further research.

Porciatti, V., Sartucci, F. (1999). Normative data for onset VEPs to red-green and blue-yellow chromatic contrast. *Clinical Neurophysiology*, 110, 772-781.

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A comparative study of retinal photoreceptor density and topography of *Phiolodryas olfersii* and *P. patagoniensis* (Serpentes, Colubridae), with opsins immunohistochemistry

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During evolution, the visual system suffered many modifications according to the needs of different species. In addition to different eye morphologies and different photoreceptor types, a third adaptation of the visual system is related to the organization, density and distribution of the cells in the retina. The snakes are a diversified group, found in many habitats and occupying different niches, with great differences in the demands upon the visual systems of different species. Studies on photoreceptor density and distribution in snakes are limited and incomplete. The aim of this study is to investigate and compare the presence of different photoreceptors and analyze their topographic distribution in the retina of two diurnal Colubridae snakes, *Philodryas olfersii*, a green arboreal snake and *P. patagoniensis*, a brown terrestrial snake, using immunohistochemistry methods. Adult snakes from each species were obtained in the Laboratorio de Herpetologia, Instituto Butantan, São Paulo, Brazil. After sacrificing with a lethal dose of anesthetic, the eyes were removed, hemisected, fixed in paraformaldeid 4% and then

washed in 0.1M PB. One retina of each species was processed to cut serial semithin sections, to test different antibodies against opsins. The antibodies tested were: rabbit antibody against human blue and red/green opsins (Chemicon), rabbit antibody against zebrafish UV opsins and mouse antibody against frog rhodopsin (RcVP). The reactions were revealed with rodamin fluorescent molecule (Jackson). The other retinas were wholemounted and incubated with streptavidin conjugated with the fluorescent molecule Cy3, to label the outer limiting membrane, in which we counted total population of photoreceptors. The retinas were observed in a fluorescence microscope. Digital images of the entire retina were taken to count the photoreceptors and trace the isodensity contours maps. In the serial sections a great number of large simple and double cones were labeled with antibody against red/green opsins and a small number of cells were labeled with antibody against blue opsins. No cells were labeled with antibodies against UV and rhodopsins. The total populations and average density of photoreceptors were, respectively, 1,225,494 cells and 32,212 ± 8,146 cells/mm^2 in *P. olfersii,* and 1,212,908 cells and 35,413 ± 10,964 cells/mm^2 in *P. patagoniensis*. In both species the photoreceptor average density was higher in the central region (38,477 ± 6,099 in *P. olfersii* and 42,172 ± 9,047 in *P. patagoniensis*) than in the peripheral region (31,804 ± 8,487 in *P. olfersii,* and 30,157 ± 9,475 in *P. patagoniensis*). The distribution of total photoreceptors in both species was very similar, suggesting that central vision is relevant for both life styles. Despite differences in light intensity and spectral quality in the habitats occupied by these species, suggesting different visual needs, these two snakes are very close phylogenetically, meaning that they have great similarity in their natural history. It is not surprising, therefore that their retinal morphology is similar, but it remains to be seen if these similarities also hold for the distributions of different photoreceptor types.

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Chromophore-opsin interactions in salamander red cone photopigment: the 9-methyl group of retinal is required for rapid Meta II decay

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Cones of the retina are responsible for our vision in bright light conditions due to their ability to rapidly adapt to gross illumination changes. A faster process of dark adaptation in these cells, compared to rods, is partly achieved by the substantially more rapid rate at which cones terminate their response to light. Recent studies have demonstrated that the rapid recovery of cone responsiveness after bright stimuli is determined by the fast decay of the photoactivated state of their visual pigment (Meta II). Both electrophysiological data on intact salamander red cones and biochemical *in vitro* experiments have suggested that the latter process critically depends on steric interactions between the 9-methyl group of retinal and the red cone opsin that cause an efficient hydrolysis

of the Schiff base linkage between the chromophore and opsin. However, no direct measurements of the Meta II decay have been performed on intact cones reconstituted with the chromophore lacking the 9-methyl group. This study measured the kinetics of the visual pigment photolysis and subsequent retinol production in intact isolated salamander red cones regenerated with 11-*cis*-9-demethyl retinal. Whole retinae from *Ambystoma mexicanum* were completely bleached with red light and regenerated with either 11-*cis*-9-demethyl-retinal or 11-*cis*-retinal, for comparison (final concentration of both retinoids was 35 μM in the Ringer solution containing 1% BSA). The decay of photolysis products (metapigments I/II) and reduction of released retinal to retinol were traced using a high-speed dichroic microspectrophotometer. In addition, retinol production was measured by microfluorimetry. Our results show that the absorbance spectrum of red cones regenerated with 11-*cis*-9-demethyl-retinal was significantly blue-shifted (λ_{max} = 524 nm) as compared to intact cones containing their native 11-*cis*-retinal/dehydroretinal (A_1/A_2) mixture (λ_{max} = 580–606 nm) or cones regenerated with 11-*cis*-retinal (λ_{max} = 566 nm). The time course of Meta II decay in red cones containing 11-*cis*-9-demethyl-retinal is approximately six-fold slower (τ = 22.3 s) than in cones having 11-*cis*-retinal (τ = 3.5 s), and 4.5 times slower than in native A_1/A_2 cones (τ = 4.8 s). Virtually no Meta III is present in salamander red cones. The retarded release of the chromophore from Meta II and lowered activity of retinol dehydrogenase toward all-*trans*-9-demethyl-retinal are two factors that most likely limit the rate of retinol production in red cones with pigment lacking the 9-methyl group of retinal. Thus, the 9-methyl group of retinal is required for steric chromophore-opsin interactions favouring the fast decay of Meta II in salamander red cones, which, in turn, contributes to the ability of these photoreceptors to carry out rapid dark adaptation.

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Topography of long- and middle-wavelength sensitive cone ratio assessed with the wide-field multifocal color electroretinogram

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Previous experiments to examine the topography of messenger RNA (mRNA) from long- (L) versus middle-wavelength (M) sensitive cone opsin genes showed that the ratio of L:M gene expression increases dramatically with increasing eccentricity. Although one explanation for the mRNA results has been that it represents a change in cone ratio with eccentricity, it has not been possible to rule out several alternate possibilities, including a relative increase in the amount of mRNA in individual L versus M cones in the periphery. The flicker photometric ERG that has long served as our standard method to estimate cone ratio gives an average value for the central ~70 degrees of retina but provides no information about topographical changes in cone distribution. Adaptive optics imaging together with retinal densitometry have allowed direct counting of the relative numbers of cones in images taken near the fovea giving accurate ratios, but the method is limited to small areas just a few degrees eccentric from the fovea. In order to obtain accurate maps of cone ratio across the entire retina we have developed a wide-field, color multifocal ERG apparatus. Results using this new apparatus show that humans can have a dramatic increase in the relative contribution to the ERG of L compared to M cones with retinal eccentricity. The new ERG results provide strong support for the hypothesis that the proportion of L cones increases precipitously in the far peripheral retina. This finding powerfully constrains theories about the genetic mechanism that determines the ratio of L:M cones in the human eye.

Identification and distribution of rod bipolar cells in the retina of *Cebus apella*

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New World monkeys differ from Old World monkeys in the variety of colour vision phenotypes they present. It is an interesting question to compare the organization of the rod system in these two primate groups. The rod bipolar cells of the capuchin monkey, *Cebus apella*, were stained by immunocytochemistry using an antibody against the alpha isoform of protein kinase C (αPKC) with the intention to evaluate the distribution of this class of retinal cells. Six retinae of adult capuchin monkeys were used. With a vertical thickness of 20 μm and horizontal thickness of 50 μm, retinal sections were obtained and processed using a standard immunocytochemistry protocol (Greferath *et al*., 1990; Grünert and Martin, 1991). Rod bipolar cells were identified by their characteristic morphology of dendrites and axons. Immunoreactivity was present in the cell body cytoplasm, primary dendrite, dendritic branches, axon, and axon terminals of rod bipolar cells. Another bipolar cell class was also stained, the DB4 cone bipolars, and distinguished from rod bipolar cells by the level of axon terminal branching in the inner plexiform layer (Grünert

et al., 1994). Cell counts of labeled cell bodies were performed throughout the retinae along the vertical and horizontal quadrants in order to estimate spatial density. The density of rod bipolar cells increases from 741/mm^2 in the central region to 14,818/mm^2 at 4 mm of eccentricity and then decrease more gradually to the retinal periphery. The mean total number of 6,360,000 rod bipolar cells/retina has been found in our study. The anti-PKCα antibody has shown to be a good marker of rod bipolar cells in the capuchin monkey retina as in other previously studied New World and Old World monkeys (Grünert and Martin, 1991). The rod bipolar cell density and distribution in the capuchin monkey is similar to that of macaque, paralleling the similar density and distribution of rods in these two monkeys (Grünert and Martin, 1991). Thus, the rod system seems to be similar in Old World and New World monkeys with retinas of similar sizes.

Greferath, U., Grünert, U., Wässle, H. (1990) Rod bipolar cells in the mammalian retina show protein kinase c-like immunoreactivity. *Journal of Comparative Neurology*, 301, 433-442.

Grünert, U., Martin, P.R. (1991). Rod bipolar cells in the macaque monkey retina: immunoreactivity and connectivity. *Journal of Neuroscience*, 11, 2742-2758.

Grünert, U., Martin, P.R., Wässle, H. (1994). Immunocytochemical analysis of bipolar cells in the macaque monkey retina. *Journal of Comparative Neurology*, 348, 607-627, 1994.

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The special status of the cardinal axes

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If a disc is divided radially into coloured segments arranged in spectral order as a hue circle, the predominant colour seen is different when the disc is spun clockwise (CW) and counterclockwise (CCW). This can be explained by a temporal delay between the opponent chromatic processing channels of the early visual system (Stromeyer *et al*., 1991). These channels are thought to feed into multiple cortical channels. Firstly, following Stromeyer *et al*., we constructed a hue circle stimulus by combining sinusoidal temporal modulations along the cardinal axes of colour space corresponding to the chromaticities encoded by the opponent channels. By varying the phase difference between these modulations, we produced loci of chromatic modulation of varying eccentricities. At a modulation frequency of 10 Hz, the temporal order of different hues cannot be distinguished. However, discrimination of CW and CCW modulations was most difficult not when the phase difference between the physical modulations resulted in a circular locus, but when the locus was elliptical. This is consistent with a constant neural delay between the opponent mechanisms, which results in a circular

stimulus locus reaching the central channels. The required phase difference suggests a neural delay of ~50ms. Secondly, we constructed a hue circle stimulus by combining modulations on intermediate axes (at 45° to the cardinal axes). With this stimulus, there is no phase difference that produces very high discrimination thresholds, and the maximum occurred with zero phase difference. This result suggests that modulations along intermediate axes stimulate both opponent mechanisms, so the neural delay does not affect them differently. Our results therefore provide further evidence that the cardinal axes of colour space represent exclusive stimulations of the opponent chromatic channels.

Stromeyer 3rd, C.F., Eskew Jr, R.T., Kronauer, R.E., Spillmann, L. (1991). Temporal phase response of the short-wave cone signal for color and luminance. *Vision Research*, 31, 787-803.

The chromatic contrast sensitivity function: a comparison spanning different age-control groups

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This work intended to define control norms for spatial chromatic contrast sensitivity in different age groups along two chromatic axes that were chosen to coincide with common CRT monitor phosphors at CIE 1931 [red: x= 0.576, y= 0.382; green: x= 0.243, y= 0.626; blue: x= 0.141, y= 0.067]: red–green (RG) and blue–green (BG). For the RG chromatic axis, 106 normal subjects were evaluated: early aged group, 16 to 30 years old, n= 49 (21.6 ± 2.8 years); middle aged group, 31 to 45 years old, n= 30 (36.6 ± 5.0 years); elderly aged group, 46 to 60 years old, n= 27 (50.3 ± 3.9 years). For the BG chromatic axis, 85 normal subjects were evaluated: early aged group, n= 43 (21.0 ± 2.5 years); middle aged group, n= 20 (37.8 ± 4.8 years); elderly aged group, n= 22 (50.6 ± 4.2). Stimuli consisted of stationary sinewave gratings, defined by chromatic contrast, presented in a rectangular field of 6.5º per 5º of visual angle, average luminance of 15 $cd.m^{-2}$. Subjects were evaluated monocularly at spatial frequencies of 0.1, 0.2, 0.5, and 1 cpd where chromatic proportions in the color gratings were modulated according to the Mullen (1985) paradigm. The method of adjustment was used to obtain four measurements of color

contrast sensitivity at each spatial frequency. The average of those scores was considered as representative of the chromatic contrast sensitivity function at each spatial frequency. For both RG and BG conditions, the chromatic contrast sensitivity function had a low-pass profile for all age groups. Despite this, all groups showed a slightly lower value for contrast sensitivity at 0.1 cpd for both chromatic conditions when compared to the all three tested spatial frequency (one way ANOVA, $p < 0.05$). The RG contrast sensitivity mean value of the three control groups were statistically similar at 0.1, 0.2, and 0.5 cpd, just differing at 1.0 cpd where the elderly group differed from the two younger groups ($p < 0.05$). For the BG contrast sensitivity, the mean values for the elderly group were lower than the values for the two younger groups at all tested spatial frequencies ($p < 0.05$), whilst the two younger groups showed similar contrast sensitivities. Comparing groups and chromatic conditions, all groups showed higher RG than BG contrast sensitivity. The results are in agreement with previous studies that found low-pass chromatic contrast sensitivity function and higher chromatic contrast sensitivity along RG chromatic directions in the colour space. The lower values of sensibility at 0.1 cpd probably resulted from the few spatial cycles present in the grating stimulus at the viewing distance that was used. The decrease of contrast sensitivity observed in the elderly subjects may be due to attenuation in the spatial frequency transfer by aged dioptric means especially at the level of the lens.

Mullen, K.T. (1985). The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings. *Journal of Physiology*, 359, 381-409.

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Normal and anomalous discrimination of colour assessed by means of a new psychophysical method

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We present a new test to measure acquired anomalies in chromatic vision based on the estimation of saturation. We should remember that Mattiello and Gonella (1976) already proved how an increase in saturation and/or in the size of the Munsell Panel D-15 facilitated colour detection. Eight young normal trichromats (24 ± 5 years old) and 12 elderly persons (70 ± 5 years old), who presented no evident alterations in an ophthalmic examination were tested. The corrected VA was 20/25, or above. These observers had previously been assessed with the Ishihara, Panel D-15 test and the Farnsworth chart for tritanopes. The test consists of eleven scales of variable colorimetric purity (CP) in barely perceptible stages, with Caps similar to Panel D-15, which keep the tone and luminosity constant, covering a chromatic space between 440 and 700 nm. They were grouped by levels of reflectance between 7, 13, 22, and 50% R. The test was presented monocularly with one cap at a time starting with a grey pawn. In response, the CP value of the first sample perceived by the observer as coloured was recorded. These thresholds were adjusted to the traditional measures of saturation. The older observers, mostly tritanopes, presented higher thresholds. Two cases of protanopia were observed in patients with cardiac medication. No significant differences were found between observers with and without IOL. We verified the Helmhotz-Kohlrausch effect and an inflection point/turning point (20% R) that separated the highest or

lowest saturation requirement to perceive a colour threshold. It should be noted that the Munsell-Farnsworth test adopts value 5 on the Munsell scale, which corresponds to a similar reflectance. We concluded that this new test, thanks to its easy and economical reproduction, is useful in analysing the loss of chromatic vision and its depth.

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Assessment of visual funtions in patients with multiple sclerosis

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The purpose of this study was to assess color discrimination, foveal sensitivity and spatial contrast sensitivity function (sCSF) in patients with multiple sclerosis (ME), with or without history of optic neuritis. We evaluated eighteen patients (mean age = 34.8 ± 10.34 years; 4 male) with diagnosis of multiple sclerosis, with and without optic neuritis. All patients had visual acuity between 0 and 0.1 logMAR and presented no alterations in a complete ophthalmologic exam. Foveal sensitivity was measured with a Humphrey Perimeter, SITA algorithm, central 30-2 strategy, in Standard Automated Perimetry (SAP). sCSF was evaluated with the PSYCHO software (Cambridge Research Systems). The sCSF thresholds were measured in 15 patients, at 0.2, 0.5, 1.0, 1.9, 5.3, 9.7 and 19.4 cpd. Color discrimination was performed with Cambridge Colour Test (CCT) along the protan, deutan and tritan cone isolation axes. All patients were evaluated monocularly in both eyes. Color discrimination measured in eyes with history of optic neuritis differed significantly from the control group in all Trivector axes (p< 0.001). Results

from eyes without history of optic neuritis differed significantly from the control group only in the protan axis ($p< 0.001$). All patients showed decrease in sCSF, when compared to the control group, at all spatial frequencies ($p< 0.001$). Comparison of results from eyes with and without history of optic neuritis showed statistical difference only for 0.2 cpd ($p< 0.001$). Foveal sensitivity measured in SAP was reduced in ME patients, but with statistical difference only for eyes with history of neuritis ($p= 0.014$). Most of the central visual functions were impaired in patients with ME, who had no impairment in visual acuity. Episodes of optic neuritis are a factor that increases the chance of reduction in color discrimination, spatial contrast sensitivity and foveal sensitivity. These results show that patients with diagnosis of ME may present damage in several visual functions and that the measurement of visual acuity alone is not sufficient for their evaluation.

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Evaluation of sweep VEP acuity and contrast sensitivity in healthy premature and term infants

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Prematurity at birth is a risk factor for vision, since it may lead to retinopathy of prematurity (ROP) – a condition in which there is retinal detachment. ROP occurs in a relatively small percentage of premature infants. It is not known if the remainder follow the same developmental course as that of term babies born after a complete gestational period, or if they also suffer some loss from having been born before complete development. Alternatively, because these infants are exposed to visual stimuli earlier than term babies, they could have an accelerated visual development compared to term infants due to their longer exposure to the visual world. To examine if prematurity accelerates, slows down, or does not affect visual development, the present study compared the development of visual acuity and contrast sensitivity (CS) in premature and term babies. Possible correlations between visual thresholds obtained during the first year of life and gestational age, Apgar index and birth weight, were examined. Participants were 57 infants of both genders, recruited by the University Hospital of São Paulo University, of which 31 were healthy premature infants (no evidence of ROP) and 26 were term infants. Infants'

CS and visual acuity was measured at 4, 6 and 12 months of age. The age of preterm infants was corrected for gestational age in order to allow comparison with the term infants. Adults were also tested with the same visual stimuli, 14 in the CS task and 9 in the visual acuity task. Visual acuity and CS measures were obtained using the sweep visual evoked potential method (Norcia and Tyler, 1985; Norcia *et al.*, 1990). In the acuity sweeps, the stimuli were square wave gratings at 80% contrast. Contrast thresholds were obtained using sine wave gratings at 0.2, 0.8, 2.0 and 4.0 cycles per degree (cpd). For both types of sweeps, the gratings had a mean luminance of 160 cd/m^2, and were phase-reversing at 6 Hz. Preterm and term infants did not show statistical differences in either CS or visual acuity at any of the 3 age groups. A peak in CS occurred between 0.8 and 2.0 cpd at 4 months of age, and it progressed to higher spatial frequencies with age to 2 cpd at 6 months, and to 4 cpd (the peak of the adult CS function) at 12 months of age. Our data suggest that development of spatial vision in healthy pre-term infants is not speed up or facilitated relative to term infants, implying no advantage to early visual experience. But, in contrast to the results in a prior pattern-reversal VEP study (Rudduck and Harding, 1994), we find no evidence that healthy pre-term infant's visual development is impaired by their shorter gestational age.

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Fruit detection in the Brazilian savannah's marmoset (*Callithrix penicillata*): differential advantages of colour vision phenotypes

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Callitrichids (marmosets and tamarins) display a sex-linked polymorphism characteristic of New World primates. This visual polymorphism allows the existence of trichromatic and dichromatic females and only dichromatic males, in a total of six different phenotypes. Polymorphic trichromacy seems to represent a balance between dichromatic advantages for detecting cryptic keystone resources and trichromatic advantages for detecting conspicuous fruits. Our aim was to analyze the advantages and disadvantages of each callitrichid colour vision phenotype in detecting fruits against a mature foliage background. The reflectance spectra of consumed fruits and their respective leaves, from 10 different Brazilian savannah's native species, were measured with an Oceanoptics USB2000 spectrometer. The detection performances (JND) of all six colour phenotypes were modeled for 10 different foraging conditions. In almost 50% of the analyzed situations, phenotype 543/563 nm

demonstrated the highest JNDs values, outperforming other trichromatic phenotypes. Our results are in accordance with other studies in literature, and shows that differential advantages of colour vision phenotypes, related to fruit consumption, can correctly predict the phenotypic and allelic frequencies already described in callitrichid's populations.

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Distinguishing L from M pigment coding sequences by hybridization to novel chemically modified oligonucleotide probes

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Many attempts have been made over the years to distinguish L from M cone photoreceptors using either immunohistochemistry or in situ hybridization using nucleic acid probes. These attempts have been unsuccessful due to the very high degree of identity between the sequences of the L and M proteins and encoding mRNAs. The recent development of chemically modified oligonucleotide probes, referred to as locked nucleic acid (LNA) probes, which hybridize with greater affinity to the target nucleic acid, has greatly increased the potential for differential hybridization to L and M coding sequences. We have designed LNA oligonucleotide probes that are complementary to either the L or M coding sequences located in exon 5 of the Macaca nemestrina L and M pigment genes. We have shown that the LNA-M and LNA-L probes hybridize specifically to their respective target nucleic acid sequences in vitro. This result strongly suggests that these probes would be instrumental in distinguishing the L from M cones in the retina, and define the cone mosaic during development and in adults.

Partial dissociation between coloration and figural-depth effects in the watercolor illusion

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The watercolor illusion is a long-range assimilative spread of color emanating from a thin colored line running contiguous to a darker chromatic contour and imparting a figure-ground effect across a large area (Pinna, 1987; Pinna *et al*., 2001; Pinna *et al*., 2003; Pinna and Reeves, 2006). The watercolored figure appears evenly colored by an opaque light veil of chromatic tint (coloration effect), with a clear surface color property spreading from the lighter edges. At the same time, the watercolored figure manifests a strong figure-ground organization and a solid figural appearance comparable to a bas-relief illuminated from the top (figural effect). It appears similar to a rounded surface segregated in depth, which extends out from the flat surface. The complementary region appears as a hole or empty space. The phenomenal properties of coloration and figure-ground effects raise some questions. Can the two effects be considered relatively independent? Under which conditions does a possible dissociation occur? How does the dissociation of one effect, say the coloration, influence the figure-ground effect and vice versa? When dissociated, which are the phenomenal properties of each effect taken individually? Do new properties emerge when the integration of the two effects occur? To answer these questions two new effects due to the watercolor illusion were psychophysically studied: (i) the ''watercolor surface capture'', where oblique lines within the a watercolor figure appear bulging, curved in depth and segregated from those that are perceived as placed in the background or perceived through holes, and (ii) the ''in patches fade

watercolor'', based on a modified 'watercolor' figure without volumetric and 3D properties but with a strong coloration effect that appear faded in patches. The results suggest that the figural effect can be only partially dissociated from the coloration effect and that, by separating the two effects, new properties emerge. We infer that the two underlying processes interact and converge at a subsequent processing stage where the coded color and figure-ground properties are integrated and processed in a new way.

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Amino acid substitutions in opsins tune the temporal characteristics of the L and M cones

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A complete understanding of the mechanisms underlying color vision requires detailed information about the characteristics of the different types of cones. There is a long history of interest in the possibility that the L and M cones may have distinguishing characteristics in addition to their different spectral sensitivities. Classically, dichromats have been studied to characterize the properties of the L vs. M cones with protanopes serving as the model for normal M cone responses and deuteranopes serving as the model for normal L cone responses. More recently it has become apparent that even among pigments with similar spectral sensitivity curves, there can be large variability in amino acid sequence that has little to no effect on spectral peak, but may nonetheless affect other molecular characteristics, such as the temporal properties of the photopigments. We have examined critical flicker fusion frequency (CFF) as a function of light intensity using L and M cone isolating stimuli in males whose L and M opsin sequences have been deduced through gene sequencing. We found wide variability in CFF but the differences were not consistent between L and M pigments; however, the differences seem to correlate with non-spectral tuning amino acid differences. These results suggest that amino acid differences in the opsins tune the temporal properties of the cones. Because the cumulative life-time amount of all-trans retinal produced by a photoreceptor is directly proportional to the number of times the photopigment goes through the visual cycle, and hence to the amount of

toxic A2E that is produced, the temporal characteristics of the photopigments are likely to prove important in predicting risk factors for age related macular degeneration.

Colour coding with UV input in the inner retina of the turtle (*Pseudemys scripta elegans*)

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To investigate the influence of the ultraviolet (UV) input in the chromatic responses of inner retina neurons of the turtle and to describe the types of color-coding mechanisms involved. Intracellular recordings were made in everted eyecup preparations of the turtle *Pseudemys scripta elegans*. The retina was superfused with oxygenated Ringer's solution (pH 7.5) and stimulated with spots of light centered in the receptive field, and/or with annuli. Stimuli of equal numbers of quanta of UV (370nm), blue (450nm), green (540nm), and red (620nm) light, were presented at three intensities (see Ventura *et al*., 1999). In the same experiment, neurobiotin was injected iontoforetically after recording. Afterwards, the retina was disected, fixed for 1 hour in 4% paraformaldehyde in 0.1M phosphate buffer and incubated in Cy3-streptavidin. The retina was then mounted on a glass slide and visualized using confocal microscopy. We

recorded from a total of 181 neurons of the turtle inner retina, 36 of which were spectrally opponent. Among these there were ten amacrine (≈ 5 %) and 26 ganglion cells (≈ 15 %). Morphological identification of the chromatically opponent neurons was obtained in 2 amacrine (A23b and A19) and 4 ganglion cells (G20, G21, G17 e G24). Many cells showed a very intricate picture, with a variety of response types and a potential for complex processing of chromatic stimuli, with intensity- and wavelength-dependent response components. Eleven types of chromatic opponency were found in ganglion cells, and adding previous results from the laboratory, a total of 12 types of opponent responses have been found. The majority of the ganglion cell recordings showed R+UVBG- and RG+UVB- chromatic opponency. Other types of chromatic opponency were less frequent. The results of the present study confirm the participation of a UV channel in the processing of color opponency in the inner retina of the turtle. This study shows that the turtle has the physiological mechanisms for reproducing almost all of the possible chromatic combinations.

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M-cone absence in ERG-measured spectral sensitivity of mice with a Trβ2 gene point mutation

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Morphological data has indicated that M-opsin differentiation depends on levels of thyroid hormones and the integrity of the thyroid hormone receptor beta 2 (TRβ2). This study analyzes the M-opsin retinal expression in transgenic mice with a TRβ gene point mutation (Δ337T) using the electroretinogram. This mutation reduces the affinity of the receptor for thyroid hormones. We used wild-type mice (wt), and transgenic mice with the 337T mutation homozygote (hm) $TR\beta^{\Delta 337T/\Delta 337T}$ and heterozygote (ht) $TR\beta^{\Delta 337T}/+$) from both genders. Mice were anesthetized with an intramuscular injection of a mixture of xylazine

hydrochloride (21 mg/kg) and ketamine hydrochloride (108 mg/kg) and the pupil was dilated by topical application of atropine sulfate (0.04%). ERGs were recorded with DTL fiber electrodes contacting the corneal surface through a layer of 1% methylcellulose. The signal was filtered with a bandpass set at 0.3 - 1000 Hz, monitored and continuously digitized at a rate of 1 kHz by a computer equipped with a data acquisition board. Peak-to-peak amplitudes of the a- and b-waves were measured for 14 different wavelengths (340, 360, 380, 400, 420, 440, 460, 480, 500, 520, 540, 560, 580, 600 nm) with same number of quanta (4.6×10^{14} q/s/cm^2). Electroretinograms of wt mice revealed high sensitivity in the UV and green regions of the wavelength spectrum. Wt mice gave clear responses to UV light (mean amplitude = 129 µV ± 31.56 at 360 nm), while in hm mice responses were substantially reduced (61 µV ± 18.75) and in ht mice responses intermediate amplitudes were found (91 µV ± 38.44). Responses to the middle wavelength region (500 nm) recorded in wt mice had mean amplitude of 91 µV (±12.5) and were of similar amplitude for ht mice (80 µV ± 33.44). On the other hand, hm mice produced only very small or inconsistent responses at 500 nm. ERGs recorded in mice without a functional thyroid hormone receptor β (hm) had normal amplitude of responses to short wavelengths but lacked responses to the middle (green) wavelength region of the spectrum. This result corroborates the morphological finding of direct participation of the gene TRβ in the expression of M opsin.

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The effect of adaptation to different backgrounds on the colour discrimination ellipses

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Colour discrimination ellipses can be measured by a reliable protocol designed by Mollon and Reffin (1989). A similar psychophysical computer-controlled system for colour vision evaluation was developed for IBM RISC/6000 workstations, yielding equivalent results, which has been applied for the determination of control norms (Ventura *et al.*, 2003). In this work, we assessed the effects of two different backgrounds on the colour discrimination thresholds as measured using our version of the Mollon-Reffin test. Stimuli consisted of a circular mosaic made up of circles arranged randomly and differing in luminance and diameter, which give rise to a spatial and luminance noise that forces the subject to respond to the psychophysical test only based in the stimulus chromaticity. A central portion of that mosaic forms a Landolt C target that changes in chromaticity along the test. The subject is instructed

to indicate the C's opening orientation. According to a staircase procedure, the chromatic contrast between target and background is modulated until the discrimination threshold is determined. Twenty colour discrimination thresholds were determined around two reference points in the colour space: C_2 (CIE 1976: u'= 0.219; v'= 0.480) and C_3 (CIE 1976: u'= 0.225; v'= 0.415). The thresholds were evaluated using two test protocols: (i) the mosaic embedded in a black background; (ii) the mosaic embedded in a background with chromaticity equal to that of the reference point and luminance equal to the mosaic mean luminance. We monocularly evaluated 31 subjects with normal colour vision (22.4 ± 2.1 years old). The resulting thresholds were plotted in the CIE 1976 coordinate system and fitted as MacAdams ellipses. On average, for both test conditions the circle of equal area from the C_3 ellipses had a larger diameter, larger angle of inclination in relation to the u' axis, and a larger ellipticity (semi-axis a / semi-axis b) than C_2 ellipses. Both the C_2 and C_3 ellipses were smaller, and C_2 ellipses had smaller ellipticity when the target was embedded in a (ii) background (One-way ANOVA; $p< 0.05$). The increase in subject performance occurred along directions in the colour space that were near the tritan axis for the C_2 ellipse or the red-green direction for the C_3 ellipse. The results indicate that certain aspects of the background have a strong influence on the chromatic discrimination thresholds. In this case, embedding the Landolt C target in a background with equal mean luminance and chromaticity equal to that of the reference point increases subject performance along some directions of the colour space (which depends of the colour space location).

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Cone and rod interactions at retinal and thalamic cells from the owl monkey, *Aotus sp.*

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Morphological data has shown that the retina and lateral geniculate nucleus (LGN) of the owl-monkey, Aotus sp., share similar characteristics with other New World and Old World Anthropoidea: M and P ganglion cell morphologies differ from diurnal species essentially by a scale factor (Yamada *et al*., 2001); the LGN exhibits a conspicuous pattern of magno and parvocellular layers that resembles that of diurnal monkeys. Despite several electrophysiological studies about the Aotus visual system, there is a lack of data concerning how receptoral signals interact in the retina and LGN. In this work, we assessed photoreceptor inputs to M and P retinal and LGN cells of

the owl monkey using in vivo extracellular recording. We estimated relative rod and cone strengths by measuring cell responses to stimuli previously used in studies of Macaca and Cebus retinal ganglion cells (Lee *et al*., 1997, 2000) as well as Callithrix LGN neurons (Weiss *et al*., 1998). Rod input usually dominated the visual response in all retinal cell types, even at 2000 Td.The one influence was highly variable from cell to cell at 2000 Td, but became undetectable at 200 Td. M and P LGN cells were also found to be dominated by rod responses up to unusually high retinal illuminances when compared with data from diurnal monkeys. It seems that during evolution, the owl monkey retina and LGN have undergone changes compatible with a more nocturnal lifestyle, including more prominent rod vision, without a change in the basic organization common to the visual system of all primates. The generally stronger rod input to ganglion cells in platyrhines when compared with catarrhines is in agreement with the high rod-to-cone ratio as was found in morphological studies and supports the hypothesis that the former went through a nocturnal stage during evolution.

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Variability of morphology and firing patterns in layer I neurons from mammalian visual cortex

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Mammalian chromatic and achromatic vision depends of distinct pathways connecting the retina to the lateral geniculate nucleus and the visual cortex. At the primary visual cortex these visual pathways are distributed in different compartments which give origin to anatomical and functionally distinct cortical pathways. The mammalian cortical layer I is a convergence site for axons of sub- and intracortical origin, and the apical dendritic tufts of pyramidal neurons. His main features is the low neuronal density when compared with the other layers and the presence of GABAergic neurons that, in last analysis, help to inhibit and to regulate the complex neural net composed by the apical tufts of all pyramidal neurons that arrive from deeper layers. During the development, play crucial role in the migration, positioning and origin of the neurons of the cortical plate and his impairment is associated to the emergence of several neurological and psychiatric pathologies. The role of this inhibitory projection in the activity of visual cortical networks has not yet to be determined. In this study, we tried to describe the passive and active membrane properties of neurons in this layer, as well, analyze the effect of the membrane potential and external Ca^{+2} concentration in his repetitive properties. We used whole-cell patch-clamp technique to record 244 cells stimulated by depolarizing and hyperpolaryzing current pulses in brain slices of Wistar Rats with ages between 14 and 21 days. Our results indicate, at

least, six interneurons firing patterns. Three of them, had not been described in the layer I until now. They are: classic no accommodating fast-spiking cells; regular-spiking non pyramidals cells; cells presenting quiescent periods (stuttering); late-spiking cells; low-threshold spiking cells and cells with characteristic spikes of immature cells. We concluded that the repolarization currents of layer I neurons are dependent as much of the tension as of the readiness of Ca^{+2}, however this last one seems to be not essential for generation of fAHP, characteristic of cortical interneurons.

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Interaction between impulse responses to S-cone increments and decrements

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Chromatic impulse response functions (IRF) of isolated S-cone pathways were measured by modulating stimuli along a tritan line. IRFs for S-cone increments in excitation were slower than for luminance modulation, but faster than IRFs for S-cone decrements. This is consistent with detection by separate ON- and OFF- S-cone pathways. Here, we describe interactions between these putative pathways. Thresholds for a series of double pulses, separated by varying interstimulus intervals (20-360 ms), were measured for chromatically modulated stimuli. Isoluminance and the location of tritan lines were determined individually. The stimuli were presented as a Gaussian patch (+ 1 SD = 2.3 deg) on an equiluminant white background in one of four quadrants around a central fixation cross so that detection could be measured with a four-alternative forced-choice method and interleaved staircases for each ISI. Different chromaticities for the first and second flashes were used to probe the interaction between responses to S-cone increments and decrements. Thus, there were four double-pulse conditions: (1) thresholds measured by varying the incremental (from white to blue) flash followed by a fixed decrement (from white to yellow); (2) fixed increment with thresholds measured for decrement; (3) thresholds measured for decrement followed by a fixed increment; and (4) fixed decrement with thresholds measured for the following increment.

IRFs were calculated by varying four parameters of an exponentially-damped sinewave. S-cone increment and decrement IRFs are both characterized by a single excitatory phase, but the time to peak amplitude of S-cone increment IRFs is about 50-70 ms whereas the decrement duration is about 100~120 ms. When increments and decrements were combined in a pulse pair, there was an interaction that resulted in a threshold reduction (improved detection) of the second flash. This is consistent with model assumptions that flash interactions between increments and decrements result from the same response to the first flash as obtained under isochromatic conditions, plus a (weaker) response component of the opposite polarity. The latter component has a time delay and causes interaction between the response to the second flash and the trailing activity from the first flash. The total response can be modeled as the summation of these components and the response to the second flash.

The amplitude of the transient Visual Evoked Potential (tVEP) as a function of achromatic and chromatic contrast: the contribution of different visual pathways

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We evaluate the amplitude of the transient Visual Evoked Potential (tVEP) as a function of chromatic and achromatic contrast. Twelve healthy young subjects (22.3 ± 2.3 years old) were studied. Visual stimuli were 2 cpd sinewave gratings monocularly presented in a circle of 5° diameter. Stimuli: achromatic horizontal gratings, 1 Hz pattern reversal (n= 10); achromatic 300ms onset/700ms offset (n= 6); and chromatic 300ms onset/700ms offset (n= 6). The stimuli had the same mean chromaticity (CIE 1976: u'= 0.215; v'= 0.480). Mean luminance 40 cd/m^2 for pattern reversal and 34.3 cd/m^2 for onset/offset. The background had the same mean luminance and mean chromaticity. Each chromatic grating was composed of two chromaticities, equally distant from the reference point and located along four different axes in the CIE 1976. We used 20 Hz HFP to minimize the individual variability including that due to the distribution of different cone classes. Eight to ten contrasts were used to obtain the tVEP amplitude versus contrast functions. Amplitude measurements:

P100 for achromatic pattern reversal, C2 for achromatic onset/offset, and N1 for chromatic onset/offset stimulation. Contrast thresholds were estimated by fitting straight lines to data points representing tVEP amplitude at different log contrasts and extrapolating these lines to the zero amplitude level. For the achromatic pattern reversal presentation, double slope functions described the amplitude x log contrast relations, which had a limb at high contrast and another limb at medium-to-low contrasts. Only the tVEP amplitudes at low contrasts were used to estimate contrast thresholds in this condition. We suggest that a double slope function is a signature of the contribution of several visual pathways to the visual evoked response and that the activity of the pathway with the highest contrast sensitivity, the M pathway, determines contrast thresholds. For the achromatic onset/offset presentation, the tVEP amplitude saturated at high contrasts and single straight lines described the tVEP amplitude x contrast functions in the medium-to-low contrast range. The similarity between contrast thresholds obtained with these stimuli and contrast thresholds obtained from the medium-to-low contrast limbs in the pattern reversal presentation, indicates that the M pathway activity is the major contribution to the visual response in the achromatic onset/offset stimulation. The tVEP amplitude as a function of log chromatic contrast was well described by single straight lines; contrast thresholds were estimated using all data points. We suggest that depending on the chromatic axis, the P or K pathway dominates the visual response in this case.

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Brief exposures to colored video stimuli produce long-term changes in a plastic neural mechanism mediating color perception

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Daily exposure to an altered chromatic environment using colored filters has been shown to produce progressive shifts in color perception. The changes in hue perception can last for more than a week after chromatic alteration is discontinued. Long-term studies of the plastic neural mechanism underlying this phenomenon have been difficult because of the inconvenience subjects must endure in lengthy daily exposures to chromatic alteration. We developed a more user-friendly and efficient method of producing long term shifts in color perception. In the new paradigm subjects view randomly generated monochromatic lines on a video display each day. To combat boredom, observers are allowed to play simple video games presented in the same color and superimposed on the monochromatic line stimulus. Subjects participated in daily chromatic alteration sessions ranging in duration from 15 minutes to 2 hours and viewed the adapting stimulus either binocularly or monocularly. Unique hues were tested each day. The monochromatic video method produced lasting changes in color vision after brief daily exposures. Even the shortest binocular duration (15 minutes) produced significant changes in unique yellow. Within a subject, longer daily exposures resulted in asymptotic unique yellows that were shifted farther from baseline values than short exposures. However, there was a limit to the exposure duration beyond which lengthening exposures further did not produce larger asymptotic

shifts in unique hue. Monocular stimulus exposures produced smaller yet still dramatic adaptation effects, and interocular transfer of these effects was investigated. The lessons learned through these studies have potential for uncovering basic principles about how visual information can instructively modify the nervous system throughout life.

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Assessment of an adapted version of the Cambridge Colour Test and preliminary study of color vision in infants and children

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The goal of this research was to verify the correlation between an adapted version and the original version of the Cambridge Colour Test (CCT) and to investigate the color vision in infants and children. In the adapted version a colored patch replaced the Landolt C target. To compare performance in the two versions, adults with normal (n= 29) and defective color vision (3 protanomalous; 3 deuteranomalous; males) with no ophthalmological complains were exposed three times to each version. The Pearson coefficient of correlation (r) was determined for the mean values of the Protan, Deutan, and Tritan thresholds obtained for each of the three exposures to each version. For normal subjects moderate correlation was found for both Protan (r= 0.61, $p< 0$) and Deutan (r= 0.69, $p= 0$) thresholds. Tritan thresholds showed a lower correlation (r= 0.46, $p= 0$). For the color defective subjects high correlation was

found for both Protan (r= 0.85, *p*= 0) and Deutan (r= 0.99, *p*= 0) thresholds. Tritan thresholds also showed a lower correlation (r= 0.86, *p*= 0).This result could be related to the smaller number of S-cones in the retina, compared to L and M cones and to their distribution with an S-cone free are in the central retina. Despite this discrepancy, the results ensure the compatibility between the adapted and the original versions of CCT. Infants and children (n= 5) aged 3-18 months were exposed to test sessions in which the colored patch was alternated between the left and right positions. The experimenter judged the direction of the subject's gaze and responded accordingly (preferential looking technique). Thresholds for children over 12 months (n= 2) were close to those obtained with adults. All children showed lower thresholds in the Deutan axis than in the other two, the difference being less conspicuous as age increased. These results suggest a faster development of the M-cone system in early infancy. Further studies are needed in order to confirm this hypothesis.

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Imaging Retinal Mosaics in the Living Eye

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By compensating for the significant monochromatic aberrations in the eye's cornea and lens, adaptive optics can provide microscopic views of the living primate retina with a transverse resolution high enough to resolve the mosaics of cone photoreceptors. More recent work has now revealed the mosaics of RPE cells and ganglion cells as well as that of the cones. In collaboration with Joe Carroll and Jay and Maureen Neitz of the Medical College of Wisconsin, we have also been using adaptive optics to reveal the cone mosaics of color-deficient eyes in which the genotype has been characterized. Though dichromats have only two pigments instead of the usual three, their cone mosaics usually appear normal otherwise, with normal numbers of cones and without gaps in the mosaic. However, individuals with mutations in a photopigment gene, rather than the loss of that gene, can have mosaics with blind gaps in their cone mosaics or unusually low numbers of cones. Aside from their color deficiency, these patients often appear completely normal using conventional clinical visual tests. For example, a patient who has lost 30% of his cones has normal (20/16) visual acuity. This result hints that adaptive optics may eventually play a useful role in the early detection of disease: presumably changes in the mosaics of single cells precede the more gross structural changes that are the hallmarks of advanced disease. Adaptive optics also has a role to play in psychophysical experiments as well as in retinal imaging. It has been known since Holmgren that the color appearance of a tiny flash of monochromatic light fluctuates from flash to flash, presumably depending on the specific photoreceptors that are excited by each flash. Adaptive optics can produce more compact light distributions on the retina, enhancing these color fluctuations and making them easier to study. We find that cones containing the same photopigment produce different chromatic sensations when stimulated. These experiments showed that the color sensation produced by stimulating a cone depends on the circuitry each cone feeds rather than simply on the photopigment the cone contains. Future experiments will allow us to target specific cones with such stimuli and to measure the contributions of individual cones to extracellular recordings of cortical cell receptive fields.