



A Symposium on Colour Vision  
In Memory of Yves Le Grand  
18-19 April 2013 – Paris, France





# A Symposium on Colour vision in memory of Yves Le Grand

18-19 April, 2013

Muséum national d'Histoire naturelle, Paris, France

Auditorium de la Grande Galerie de l'Evolution, 36 rue Geoffroy Saint-Hilaire, 75005

Besides numerous contributions in Physiological Optics, Photometry and Colorimetry, Yves Le Grand has been known from the three-volume treatise he wrote on Physiological Optics, two of which have been translated in English:

Vol. 1. La dioptrique de l'œil et sa correction, Ed. de la Rev. d'Optique, Paris, 1952.

Vol. 2. Light, Colour and Vision (English translation, 2nd edition, Chapman and Hall, London, 1972),

Vol. 3. Form and Space Vision (English translation, Indiana University Press, Bloomington, Ind. And London, 1968).

He was awarded the Tillyer Medal in 1974 by the Optical Society of America. He has been the Professor of the Laboratory of Physics Applied to Biology, Director of the Muséum national d'Histoire naturelle (1971-1976), and Vice-President of the CIE (1967-1971).

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**Thursday, April 18**

10:00	Opening for registered attendees	
10:30	Welcome	
	Pierre Pénicaud <i>Conservateur en Chef</i> <i>Directeur par intérim du Département des Galeries</i>	
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10:30	Marc Théry <sup>1</sup> , Doris Gomez <sup>1</sup> , Christina Richardson <sup>2</sup> , Thierry Lengagne <sup>2</sup> <i><sup>1</sup> Muséum national d'Histoire naturelle, Brunoy, France</i> <i><sup>2</sup> Université Lyon 1, Villeurbanne, France</i> Animal colour vision at night: the case of a tree frog	19
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### *Organizing committee*

Françoise Viénot, CRCC, Muséum national d'Histoire naturelle, Paris  
Kenneth Knoblauch, Inserm U846, Stem-cell and Brain Research Institute, Bron  
Pascal Mamassian, Vision Group, Laboratoire Psychologie de la Perception, Paris  
Philippe Lanthony, Ophthalmologist, Centre Hospitalier des Quinze-Vingts, Paris

### *Local Organising Committee*

Françoise Viénot, CRCC, MNHN, Paris  
Alban Fournier, CRCC, Paris  
Clotilde Boust, C2RMF, Université de Versailles  
CIE 100 Years Logo : Benoît Mosset  
Group photograph : Jean Le Rohellec - : <http://jr.clic.free.fr/>

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### *Acknowledgements*

Gilles Boeuf, Thomas Grenon, Pierre Pénicaud, Bertrand Lavédrine  
Cyril Chain, Marie-Pierre Alexandre, Gaël Obein, Eric Dumont, Jean-Jacques Ezrati,  
Annie Monot, Alain Azaïs, Peter Zwick, Martina Paul, Ronnier Luo, Ann Web  
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Vernhes, Aurélie Truchelut, Julie Castiglione, Stéphane Trinh, Jean-Brice Rolland,  
Frédéric Vernhes, Régis Cardoville

## Color and the Cone Mosaic

David R. Williams

*Center for Visual Science, University of Rochester, USA*

Since Thomas Young first proposed that human color vision depends on three fundamental channels, the relationship between the cone mosaic and color experience has been controversial. The development of adaptive optics in the 1990's provided a new tool for addressing this issue in multiple ways. First, it enables the identification of the photopigment in individual cones in the living human eye. This technique has now been applied to a large number of eyes with different variations in the genes that code for the three cone photopigments, so that the organization of the mosaics of many kinds of color blind eyes as well as normal eyes is now understood. Perhaps the most striking conclusion from this work is how little impact the topography of the mosaic has on vision, illustrating the brain's cleverness in concealing variations in cone topography from our visual experience. Adaptive optics can also be used to microstimulate single cones in the human eye with flashes of light that are substantially smaller than the smallest flashes experienced in everyday vision. Repeated flashes of the same wavelength produce a surprisingly large variety of color experiences. One explanation for the variability of color from flash to flash in these unusual viewing conditions is that it is a natural consequence of neural mechanisms that conceal spatial variations in color appearance across the cone mosaic in everyday vision. I will describe a Bayesian model of the color appearance of small spots developed by David Brainard that is consistent with the data.

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## **Spectral sensitivity, photopigments and molecular genetics**

**Andrew Stockman**

*UCL Institute of Ophthalmology, London, UK*

A watershed event in human colour vision research was the isolation and sequencing of the long-, middle- and short-wavelength-sensitive (L-, M- and S-) cone photopigment opsin genes by Jeremy Nathans and his colleagues in 1986 (genes that are now designated OPN1LW, OPNL1MW, and OPNL1SW, respectively). OPNL1SW is positioned at 7q32 on chromosome 7, and OPN1LW and OPNL1MW are positioned at Xq28 in a head-to-tail tandem array on the X chromosome.

The head-to-tail arrangement of OPN1LW and OPNL1MW resulted from a relatively recent duplication of the ancestral OPN1LW gene. This duplication followed by mutation and DNA sequence divergence gave rise to trichromacy in our Old-World primate ancestors. Because the divergence was recent, the OPN1LW and OPNL1MW genes share a >98% nucleotide sequence identity. This similarity coupled with their adjacency make them highly susceptible to alterations during meiosis such as gene conversion, and equal and unequal homologous recombination. These events result in hybrid opsin genes, gene replacements, gene deletions and gene duplications, all of which can substantially alter red-green vision, particularly in male observers with only one X-chromosome.

Research linking the spectral sensitivities of cone photoreceptors in individuals to a molecular genetic analysis of their underlying opsin genes has led to an understanding of the genetic causes not only of most types of colour vision deficiency, but also of individual differences in normal colour vision. In general, the results of the gene alterations are either: (i) dichromacy (when one of the cone pigments is missing and colour vision is reduced to two dimensions); (ii) anomalous trichromacy (when one of the three cone pigments is altered in its spectral sensitivity but trichromacy is not fully impaired); or (iii) monochromacy (when two or all three of the cone pigments are missing and colour and lightness vision is reduced to a single dimension).

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## **Yves Le Grand's Legacy**

**Françoise Viénot**

*CRCC, CNRS USR3224, Muséum national d'Histoire naturelle, Paris,  
France*

Yves Le Grand was born in 1908. He entered the "Ecole Polytechnique" in 1926, a French academic institution in Paris where he was trained in Physics and Mathematics. He graduated in 1928.

In 1929, he entered Charles Fabry's laboratory. One facet of Charles Fabry's program was dealing with Photometry and the Optics of the eye. There, Yves Le Grand began studying the eye as an optical instrument. He obtained his PhD degree in 1937 with a thesis on the scattering of light in the eye.

Yves Le Grand's dual interests, in Physics and Biology, allowed him to enter the National Museum of Natural History, being appointed assistant to Jean Becquerel, Henri Becquerel's son. The scientific activity of the Becquerel family which has succeeded each other at the Museum, from generation to generation, since 1835, is a fascinating story. It had been exquisitely related by Yves Le Grand in his official "Leçon" when he was elected Professor of the Laboratory of Physics Applied to Biology to succeed Jean Becquerel.

Yves Le Grand had been admiring the capacity of the Becquerels to experiment manually, to produce experimental facts preliminary to providing theoretical explanation, to simplify at best the experimental methods in order to avoid artefacts. Being elected chair of the laboratory of Physics applied to Biology, his objective was to maintain the spirit of the Becquerel scientific creation. He chose to develop Physiological Optics. He supervised students and hired collaborators in order to cover the major visual functions. Besides, Yves Le Grand had to continue running a wide range of physics branches, in association with Biology, Earth Science, etc. He personally kept involved and published several contributions on the Optics of the sea. As he committed to developing scientific facilities for the Museum, he also introduced computer science at the Museum.

Teaching was one of his most productive activities. When he returned from captivity in Germany during the Second World War, Yves Le Grand was asked

by Professor Pierre Fleury, Director of the Paris Institute of Optics, to present lectures in Physiological Optics at that institution. These lectures were the bases for Yves Le Grand's outstanding treatises on Physiological Optics. The three-volume work (two volumes are available in English) was constructed after the organisation of Helmholtz's classic Handbook of Physiological Optics. Volume 2 entitled "Light, Colour and Vision" contains two sections. Section A consists of a report of purely experimental studies of the visual receptor, whereas section B gives a brief account of the principal theories of vision. In section A, Yves Le Grand carefully describes numerous ancient and modern experiments. Intentions are presented concisely, methods are explained in detail, mathematical demonstrations are exposed with pedagogy, and results are clearly described and given a personal interpretation.

Le Grand also devoted a considerable effort to applications of visual science to lighting techniques. He served as Honorary Secretary of the Commission Internationale de l'Eclairage (CIE) (1955-1967), and Vice-President of the CIE (1967-1971). He actively prepared the foundation of the International Colo(u)r Association and of the International Research on Colour Vision Deficiencies (IRGCVD). He was on the first editorial board of "Vision Research".

In 1971, he was chosen by his colleagues as Director of the Muséum national d'Histoire naturelle for a five year term.

He died on the 20 janvier 1986.

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## Cortical color vision

Thorsten Hansen

*Justus Liebig University Giessen, Germany*

The initial subcortical stages in color vision can be described by three cone mechanisms S, M, L that are transformed into three pairs of second-stage mechanisms, one achromatic pair of mechanisms ( $L + M$ ,  $-L - M$ ), one chromatic pair with S cone input ( $S - (L + M)$ ,  $-S + (L + M)$ ) and another chromatic pair that signal the difference between L and M cones ( $L - M$ ,  $M - L$ ). The further mechanistic description of cortical color vision is a topic of current research: how many mechanisms are needed to describe cortical color vision and what are their tuning properties? Physiological studies have found that neurons become more narrowly tuned to particular colors as one traverses up in the hierarchy of visual areas, and that the chromatic preferences of cortical neurons are approximately equally distributed in color space. Psychological studies have complemented these findings and provided data consistent with multiple mechanisms. However, some studies who specified their stimuli in a cone contrast color space failed to find evidence for multiple mechanisms. In a recent study we have shown that this failure was due to a restricted choice of stimuli. We ran experiments with a full set of stimuli in cone contrast space and found data consistent with multiple cortical mechanisms. We conclude that cortical color vision is governed by multiple higher-order mechanisms.

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## **Colour constancy: Colour perception in a world of illuminated surfaces**

Hannah E. Smithson

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The properties of the cone photoreceptors in the retinal mosaic impose a fundamental constraint on human colour perception. Metamerism – the prediction that two lights that evoke the same triplet of L-, M-, and S-cone quantal catches will be indistinguishable, even though they may differ in wavelength content – might imply that cone quantal catches are sufficient to predict colour appearance matches. But, this is true only under certain limited conditions of observation in which a small patch of light is seen in isolation against a black surround, as if through an aperture. In a world of illuminated surfaces, colour perception enters a different mode. The cone signals elicited from a collection of surfaces change when the illumination on them changes. Yet, the surfaces within a scene tend to remain constant in their apparent colour.

The transformation imposed on the cone signals by a change in illumination dictates what the visual system must ‘undo’ to achieve constancy of surface colour appearance. The problem is mathematically underdetermined, and can be solved only by exploiting regularities of the visual world. We discuss how the illuminant colour transformation might be simplified, and how the parameters of the inverse transformation might be set by elements of a complex scene.

We consider both the information that is, in principle, available and empirical assessments of what information the visual system actually uses. A recurrent finding in our experiments is that information about the illumination that is available at any one instant is not sufficient to predict surface colour appearance. Instead, in addition to using information that is distributed over space, the visual system uses information that is distributed over time to parse the visual world into coloured surfaces and lights that illuminate them.

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## **Colour categories**

**Valérie Bonnardel**

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Human colour perception is categorical and subject to categorical perception (CP) effects. Defining aspects of CP are qualitative and quantitative. Qualitative aspect is evidenced by the identification in the physical continuum of the visible spectrum of a colour on one side of a category boundary and of another colour on the other side. Quantitative aspect is appreciated by a peak of discrimination occurring at the boundary of adjacent categories.

Language, as a normative process of colour space segmentation, influences the way colour samples are grouped based on their perceptual similarities. There is higher within- compared to cross-language agreement when the number of basic colour terms differs between these languages. Similarly, subjects are more accurate to report as different two colours presented successively if they are associated to two different colour terms compared to the condition where they are associated to the same colour term. These results are interpreted as the expression of a CP effect with colour categories essentially determined by language.

Evidencing a CP effect in colour discrimination tasks is more complex. The inspection of 400-700 nm visible spectrum indicates category boundaries approximately located at 470, 490, 510, 575, 595, and 610 nm. Yet, with three minima (440, 490, and 590 nm) the wavelength discrimination curve gives only a partial support of enhanced discrimination at category boundaries.

Emulated bluish and greenish samples on a monitor have been repeatedly used to detect a PC effect. In a visual search task, a PC effect occurs if a green target is detected faster when presented among blue distractors (or vice versa) than if it is presented among distractors of a different shade of green. Results vary across studies. A PC effect limited to the right visual field has been reported, but PC effect in the two visual fields, and absence of PC effect were also reported. The validity of these results is based on the assumption that supra-threshold colour-differences between pair of stimuli (Blue-Green vs. Green-Green) for a given observer are equal. If this assumption is not met,

inequality in stimuli discriminability can be a confounding variable leading to inconsistencies across studies.

Only few studies on PC effect have directly measured just noticeable differences (JNDs) thus avoiding the difficulty of supra-threshold colour scaling. In one of these studies, stimuli were defined in a cone-excitation space, and discrimination was probed along the unique blue-unique yellow line. The smallest JNDs were found to be located at the boundary between greenish and reddish colours, that is, not between two adjacent categories, but rather close to the centre of a category. In a different study, stimuli were Sinusoidal Spectral Power Distributions, defined by their phase, frequency ( $c/300$  nm) and amplitude. JNDs measured along a full hue ellipse (i.e. in all colour directions), revealed two minima of discrimination corresponding to perceived yellow/orange and blue/magenta boundaries.

In summary, studies addressing the quantitative aspect of PC fail to provide consistent results and the existence of an enhanced discrimination at category boundaries remains an empirical question.

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## **Animal colour vision at night: the case of a tree frog**

Marc Théry<sup>1</sup>, Doris Gomez<sup>1</sup>, Christina Richardson<sup>2</sup>,  
Thierry Lengagne<sup>2</sup>

<sup>1</sup> CNRS UMR 7179, Muséum National d'Histoire Naturelle, Brunoy,  
France

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Nocturnal frog species rely extensively on vocalization for reproduction. But recent studies provide evidence for an important, though long overlooked, role of visual communication. In many species, calling males exhibit a conspicuous pulsing vocal sac, a signal bearing visually important dynamic components. Here, we investigate female preference for male vocal sac coloration—a question hitherto unexplored—and male colour pattern in the European tree frog (*Hyla arborea*). Under nocturnal conditions, we first conducted two-choice experiments involving video playbacks of calling males with identical calls and showing various naturally encountered colour signals, differing in their chromatic and brightness components. We adjusted video colours to match the frogs' visual perception, a crucial aspect not considered in previous experiments. Females prefer males with a colourful sac and a pronounced flank stripe. Both signals probably enhance male conspicuousness and facilitate detection and localization by females.

We then conducted two mate choice experiments under controlled scotopic light conditions. These experiments involved static male models with identical calls but different vocal sac colouration combining chromatic (red/orange) and brightness (dark/light) information. We found that females preferred dark red over light orange, evidencing for the first time a visually-guided mate choice in nocturnal diffuse light conditions. Conversely, females did not discriminate between dark orange and light red. The preference for dark over light in the first but not in the second experiment suggested that females had not only access to brightness cues but also to chromatic cues. The absence of preference may originate from females choosing at random in a situation where colour and

brightness cues may convey contradictory information about male quality or from individual heterogeneity in the type of cues used for mate choice.

Overall, these experiments provide the first support for the use of colour vision in a nocturnal amphibian.

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## Le Grand (1949): "Les seuils différentiels de couleurs dans la théorie de Young"

J. D. Mollon

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In a powerful paper of 1949 (*Revue d'Optique*, 28, 262-278), Yves Le Grand re-analysed the discrimination ellipses that MacAdam had obtained at different positions in the CIE chromaticity diagram. Estimating the spectral sensitivities of the retinal cones using two different theories of deuteranopia, Le Grand calculated how the cone signals were modulated as chromaticity was varied along lines of different directions passing through the centre of each ellipse. He concluded that colour discrimination depended on two independent signals. These signals correspond, in modern terms, to the two axes of the MacLeod-Boynton chromaticity diagram:  $S/(L+M)$  and  $L/(L+M)$ , where L, M, S are the excitations of the long-, middle- and short-wavelength cones respectively. In the case of the first signal, Le Grand suggested that thresholds increase with the log of  $S/(L+M)$ . In the case of the second signal, the discrimination depends on the ratio of L and M excitations, and thresholds are lowest at the L/M ratio of the adapting white.

Many subsequent studies (e.g. Boynton, Nagy, Olson, 1983, *Color Research and Application*, 8, 69-74; Krauskopf & Gegenfurtner, 1992, *Vision Research*, 32, 2165-2175) have asked how far the discrimination of colours does depend on two independent signals of the type identified by Le Grand. Danilova and I have found that thresholds for foveal discriminations parallel to the horizontal axis of the MacLeod-Boynton diagram – discriminations that should depend only on the ratio of L and M – are strongly affected by the level of S excitation (Danilova & Mollon, 2012, *Journal of the Optical Society of America*, A29, 157-164). Thresholds were at a minimum in the vicinity of the 'yellow-blue' line. The latter is the locus of chromaticities that appear neither reddish nor greenish under the adaptation conditions of our experiments (the background was metameric with Illuminant D65). This yellow-blue locus does not correspond to the vertical axis of the MacLeod-Boynton diagram but runs obliquely across the diagram with negative slope. What is of interest beyond the humble realm of

colour psychophysics, is that thresholds are minimal at a boundary between two subjective categories, the boundary between redness and greenness. Is this true for the boundaries between other hue categories? Does it require explanation in terms of neural channels that do not map on to either axis of the MacLeod-Boynton diagram?

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Boynton, Nagy & Olson, 1983, *Color Research and Application*, **8**, 69-74

Danilova & Mollon, 2012, *Journal of the Optical Society of America*, **A29**, 157-164.

Krauskopf & Gegenfurtner, 1992, *Vision Research*, **32**, 2165-2175

Le Grand Y., Les seuils différentiels de couleurs dans la théorie de Young. *Revue d'Optique*, **28**, 262-278)

## **Development and Aging of Human Color Vision**

**John S. Werner**

*University of California, Davis*

The human visual system undergoes continuous change from infancy to old age at the molecular, cellular and systems levels. The consequences of most of these changes for color vision have not been widely studied. Yet, age-related variations in color vision could provide fertile ground for understanding mechanisms that subserve detection, discrimination and appearance.

Throughout life, the density of the crystalline lens increases, resulting in a change in the intensity and spectral composition of the light reaching the photoreceptors. To separate changes in sensitivity due to optical and neural factors, it is essential to measure ocular media density in individual subjects. Such measurements reveal losses in short-wave transmission of light reaching the retina by a factor of ~25 (at 400 nm) from infancy to old age. When ocular media density is taken into account in evaluating sensitivity, continuous changes in sensitivity of the cone pathways (i.e., neural losses) can be seen from infancy, when all cone classes are functional, to adolescence, when sensitivity reaches a peak. After adolescence, there is a progressive loss in sensitivity across the life span. We have described these changes after adolescence as linear with age, and have obtained evidence that they are due to both receptor and postreceptor mechanisms. These results are important for both scientific understanding as well as for applications. Age-based norms are essential for clinical diagnoses, understanding low vision, and implementation of universal design.

Variations in color vision across the life span may also be used as a probe for identifying neural substrates. For example, our recent study demonstrated different rates of aging for detection of increments and decrements mediated by short-wave sensitive cones (i.e., putative S-cone ON- and OFF-pathways). This dissociation implies that different pathways mediate the detection of increments and decrements.

Results obtained from threshold studies of aging, however, do not predict color appearance. For example, changes in unique hues, color naming, and the

stimulus that appears achromatic, all reveal a surprising degree of stability in color appearance across the life span. To achieve stability in color perception while early stage mechanisms are changing, however, raises new questions about how the visual system compensates for these changes over the life span. By studying color vision changes following removal of a brunescent lens (i.e., cataract), we find strong support for the view that the visual system continuously renormalizes itself to maintain constancy of color perception. These mechanisms have a more protracted time-scale than typically engaged by adaptation experiments in the laboratory. Thus, an elderly person may call the same stimulus “white” as he or she did 70 years ago, even though it must be based upon a markedly different retinal stimulus and ensemble of neural activity.

In summary, studies of early development and aging may identify neural processes that are fundamental for understanding color vision, revealing processes that may be less apparent when studying the system at a single age.

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## **Psychophysics conducted above the threshold**

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Psychophysical experiments are typically based on analyzing observer choices as a function of a (or some) stimulus dimension(s) in order to make inferences about the underlying sensory and/or decision processes. Modern psychophysical theory derives from Signal Detection Theory (SDT) in which the observer's performance depends on a noise contaminated decision variable that in association with a criterion determines the rates of both successful classifications and errors (Green & Swets, 1966; Knoblauch & Maloney, 2012). The largest body of psychophysical work is based on discrimination of small (threshold) stimulus differences, however, yielding measures of perceptual strength that do not obviously (or easily) extrapolate to predict performance for large (supra-threshold) differences nor for appearance. Some recent techniques do permit extensions of SDT to the supra-threshold domain, however. For example, Maximum Likelihood Difference Scaling (MLDS) is a psychophysical method and fitting procedure that involves scaling of large stimulus differences based on paired-comparisons of stimulus intervals (Maloney & Yang, 2003; Obein, Knoblauch & Viénot., 2004; Knoblauch & Maloney, 2008, 2012). Maximum Likelihood Conjoint Measurement (MLCM) can also be shown to depend on comparing stimulus intervals, but across stimulus dimensions (Ho, Landy & Maloney, 2008; Knoblauch & Maloney, 2012). The resulting scales have interval properties, i.e., equal differences along the scales are perceptually equal. The decision rules underlying discrimination, MLDS and MLCM are all based on the same equal-variance Gaussian model. I review studies that evaluate the coherence of the scale measures obtained by these three different approaches using as an example the quantification of the strength of the long-range filling-in color of the Watercolor effect (Pinna, 1987; Devinck & Knoblauch, 2012). I argue that the results support a unified theory of psychophysics that extends from threshold to appearance.

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## **Color in Space, Time and Motion**

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Color is a feature not seen alone. In the natural world, colored objects have a size, location, orientation, shape, and sometimes a direction of motion. In laboratory studies of color vision, however, non-chromatic features are frequently disregarded or minimized, for example by using large fields, blurred edges or a display seen in a two-dimensional plane rather than three-dimensional depth. Control experiments can be designed to show that the size, spatial sharpness, or duration of a light does not alter a conclusion about color vision; failing that, non-chromatic features sometimes are compensated by rigorously determined “correction factors.” The main point of this paper is to cast doubt on this approach to studying color. Instead, non-chromatic features should be harnessed and exploited to reveal fundamental neural processes that mediate the colors we see.

Changes in color appearance from a chromatic surround were known to Chevreul more 170 years ago. Since then, color shifts often were studied with a uniform surrounding light, but more complex chromatic surrounds—for example, a mosaic of many different chromatic patches—can induce color shifts unlike those from any uniform background. For example, a surrounding mosaic composed of a broad range of chromaticities compresses the perceived saturation of chromatic lights. More broadly, the theoretical importance of chromatic variation within a surround is revealed by a surrounding pattern composed of just two different chromaticities, which can induce a larger color shift than a uniform surround at either one of the chromaticities alone. In general, spatial chromatic variation within a scene makes a unique, cortically mediated contribution to the colors we see.

It may seem paradoxical, but introducing spatial patterns provides the leverage to isolate a neural signal for color uncoupled from any shape or location. When one colored spatial pattern is presented to the left eye and a different pattern to the right eye, binocular rivalry suppresses one of the spatial patterns but not that pattern’s color. This surviving “disembodied” chromatic neural representation subsequently is expressed somewhere in the dominant pattern in

the opposite eye! This example highlights the problem of color feature binding: how does color stay correctly connected to an object? Experiments with chromatic patterns that change over time, or are in motion, expose failures of the visual system to maintain the correct correspondence between an object and its color, thereby revealing a neural process that, normally, correctly links an object's chromatic and non-chromatic features.

Finally, the influences of chromatic and non-chromatic features are reciprocal. Shape affects color perception, but also color affects perceived shape. The direction of motion of a chromatic object can alter its perceived color, but also the color similarity among objects can change their perceived direction of motion. In sum, studying color in isolation, even if possible, fails to reveal basic neural processes that mediate the colors we normally see, and misses the full contribution of chromatic coding to visual percepts other than color.

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## **Spectral Properties of Melanopsin Photosensitive Ganglion Cells**

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For nearly 200 years the human retina was thought to contain only two classes of photoreceptors, rods (~90 million) for low light scotopic vision and cones (~5 million) mediating photopic, color vision. Recently however, a new photopigment called melanopsin was discovered in retinal ganglion cells (ipRGCs) that are directly sensitive to light. Melanopsin represents only a small fraction of ganglion cells (<3,000) evenly distributed across the retinal surface. The maximum sensitive of melanopsin is to short wavelength blue light with a spectral absorbance that peaks at approximately 480 nm. ipRGC responses to light are strikingly different from those of rods or cones and require relatively high light intensities, are slow to respond at light onset and exhibit sustained intensity dependent responses that can persist long after light offset. Because of these properties, melanopsin is considered an “irradiance detection system”. Surprisingly, melanopsin closely resembles invertebrate photopigments and, like fly or squid rhodopsin is “bistable” and can use light to drive both sensory responses and chromophore regeneration.

Melanopsin ipRGCs mediate a wide range of “non-visual” functions (as opposed to conscious visual perception) including the photic synchronization of circadian rhythms and sleep wake cycles, pupillary constriction, rhythmic hormonal secretions, metabolism, heart rate and core body temperature, alertness and cognitive functions. Animals (or humans) that have lost all rods and cones are visually blind but conserve “non-visual” functions whereas if melanopsin ipRGCs are absent, animals have normal vision but are blind for non-visual functions and suffer from disturbed sleep and circadian rhythms. Recently, a subclass of ipRGCs has been found to project to the lateral geniculate nucleus, to activate visual cortex and to promote arousal in higher cortical regions. This functional diversity suggests that among the visual photopigments, melanopsin has the broadest role in light detection.

Yves Le Grand significantly contributed to establishing human photopigment sensitivity functions. In comparison, the current state of knowledge of melanopsin photobiology is in its infancy and the “melanoptic” sensitivity function is not fully characterized. This is further complicated by the fact that ipRGCs also receive photic inputs from rods and cones, such that the neural output is a composite, integrated signature consisting of the combined intrinsic melanopsin photosensitivity and the rod- and cone-driven signals. Light responses are also strongly influenced by previous light exposure history. As a consequence, specifying the composite spectral efficiency functions of different melanopsin dependent functions remains a major challenge in the field.

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# **From neuroprotection, studying the spectrum of retinal phototoxicity based on Yves Le Grand's eye/light source model, towards visual restoration**

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When staring at the sun during eclipse, light can damage photoreceptors irreversibly. However, light can also damage photoreceptors under more subtle daily conditions. For instance, several studies indicated that light exposure is a risk factor in the pathogenesis of age-related macular degeneration (ARMD). In causing ARMD, light appears as a major cause of blindness in industrialized countries. Apart from age and tobacco, antioxidant deficiencies have been identified as risk factors in ARMD. Among antioxidants, taurine was considered very important during the 70s because its deficiency induced photoreceptor degeneration in cats, rats and primates. However, since that time, no retinal pathology was attributed to taurine deficiency.

The presentation will introduce two neuroprotective strategies as well as a new optogenetic approach to restore vision using photosensitive proteins.

Recently, we discovered that the retinal toxicity of an antiepileptic drug, vigabatrin, is related to a taurine deficiency (Jammoul et al., 2009; Jammoul et al., 2010). This drug-induced retinal toxicity was relying on a phototoxicity as it was prevented by darkness and reduced by taurine supplementation. The clinical relevance of these studies was indicated by the similar decrease in plasma taurine observed in both vigabatrin-treated patients and animals. To investigate further the spectrum of phototoxicity at a cellular level, we implemented with the company ESSILOR a light generator to expose retinal cells to 10 nm illumination bands. Light intensities were normalized to light intensities reaching the retina in vivo. Irradiances were normalized to the ocular media filtering and to the daylight radiance, based on Yves Le Grand's eye/source model. We first investigated light toxicity on an ARMD model, constituted by A2E-loaded retinal pigment epithelium (RPE) cells. Based on our

definition of the phototoxicity spectrum (Arnault et al.), the ESSILOR Company is proposing new glasses as a neuroprotective strategy.

When it is too late to prevent photoreceptor degeneration, different strategies were proposed to restore vision in blind patients. These strategies not only include retinal prostheses but also optogenetic tools such as photosensitive ionic channels or ionic pumps. Using this later approach, we showed in collaboration with Dr Roska that dormant cone photoreceptors could be reactivated in blind mice and even in the postmortem human retina (Buskamp et al., 2010). OCT images have already confirmed the presence of such non-photosensitive cones in blind patients affected by retinitis pigmentosa (Buskamp et al., 2010).

These studies could thus lead to a prevention of phototoxicity or to a visual restoration strategy when phototoxic events have already induced the complete degeneration of the photosensitive part of photoreceptors.

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