Session: General ecology and evolution of primates

The evolutionary and ecological context of primate vision

Robert D. Martin

Most primates are either clearly nocturnal or clearly diurnal in habits. However, some exhibit an unusual pattern of activity that has been labelled cathemeral. There is a clear relationship between activity pattern and body size, with nocturnal species being considerably smaller than diurnal species on average. One hypothesis is that mammals tend to be nocturnal in the body size range shown by flying birds and that diurnal mammals are generally larger than flying birds. Nocturnal, cathemeral or diurnal activity patterns in primates impose quite different requirements on the visual system, and colour vision is essentially restricted to diurnal primates. There has been some discussion about the ancestral pattern of activity in primates. Although the predominant view is that ancestral primates were nocturnal, there is a minority interpretation that they were in fact diurnal. This controversy has been fuelled by molecular data reported for the opsin pigments of nocturnal primates. By using surrogate data from the skull such as the dimensions of the orbit and of the foramen for the optic nerve, it is possible to identify indicators of activity pattern that can be applied to the fossil record. This presentation will provide an overview of these data and re-examine the question of the likely activity pattern of ancestral primates. Evolution of visual capacity in primates is directly related to the evolution of the brain. so this aspect will also be considered.

Developmental Programs Robust to Variations in Scale and Niche: Examples in Primate Vision

Barbara L. Finlay, Luiz Carlos de Lima Silveira

New World monkeys offer an interesting opportunity to examine visual system design at varying body and brain sizes, for varying strategies for color vision, and varying niches. We can then turn to development to see how evolution modifies essential steps of retinal generation to produce retinas of different sizes and conformations. 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). These measures include rod, rod bipolar, cone, ganglion cell and optic nerve axon numbers and their distribution, and various aspects of eye conformation. Excluding the nocturnal owl monkey, Aotus azarae, whose ganglion cell number is approximately 65% of what would be expected for a diurnal monkey of comparable brain size, rods, cones and retinal ganglion cell numbers scale closely with brain size, but with rod number increasing at a much greater rate with brain size. Eye size scales with brain and body size at a lower slope in these (and all) primates than it does in other mammals; the constant absolute size of the fovea may serve as a constraint on eve enlargement. The owl monkey and the howler monkey. Alouatta caraya, show interesting variations. The howler monkey with its full trichromacy has an unusual fovea, with cone densities twice as high as those seen in both New and Old-World primates. Its total cone number is what would be expected for an animal of this size, however, so foveal cone density is achieved at the cost of peripheral cone density. Similarly, its total optic nerve axon count (1.1 million, n=3) is what would be expected for an animal of this brain size. Thus, its unusual visual system is produced by reconfiguring retinal topography within general primate numerical constraints, and not by generation of unexpected cell numbers. The owl monkey, by contrast, has fewer cones and ganglion cells than would be expected for its brain size, but many more rods, and has modified neurogenesis.We will argue that the conserved order of retinal neurogenesis is a likely cause of the different slopes of cone, ganglion cell and rod numbers with brain size and serves an adaptive consequence. This same order of neurogenesis is also permissive of a shift between characteristic nocturnal and diurnal retinal cell numbers. The different ratios of rods and cones produced may be the immediate cause of nocturnal/diurnal adaptations in eye conformation, such as presence of a fovea and eye size.

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Session: Photoreceptors

Origins of Primate Trichromacy: Is the Tuning of Primate Visual Pigments Optimal for Colour Vision?

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Primate L and M cone spectral sensitivities strongly overlap. Intuitive considerations and mathematical modelling shows that such an overlap generally decreases the number of colours that can be discriminated. One explanation for the overlap is that the spectral tuning of L and M cones reflects adaptation to spatial rather then colour vision. However, recent studies show that spectral positions of the L and M cones are close to the optimum for a specific task of detecting fruits and edible young leaves against a green leaf background. Surprisingly, the overlap of visual pigments is also beneficial for identification under varying illumination both of fruit and of flower spectra. An important lesson is that the benefits of trichromacy and optimal tuning of visual pigments depend critically on the noise of receptor mechanisms, and hence eye size and the visual ecology of a given species. In dim light noise in S cone mechanism is substantial, because reflected light in the short-wavelength part of the spectrum has a relatively low photon flux. Therefore, S - (L+M) chromatic signal is less reliable than the L - M signal. As trichromats may enjoy colour vision at the illumination levels where dichromats cannot, it is therefore possible that trichromacy appeared initially in animals active in relatively dim light. Finally, we look at the selective forces that act to maintain genetic polymorphism in the New-World and 'prosimian' primate lineages, where there is a single X chromosome L/M pigment gene, but the range of different alleles differs substantially between species.

Molecular Evolution of Primate Red and Green Cone Opsin Genes

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The trichromacy of primates has evolved from the dichromacy of an ancestral species in two distinct ways. In Old World primates, the longwave-sensitive (L) opsin gene on the X chromosome has duplicated to give two genes that encode pigments with max values around 530 nm (MWS) and 560 nm (LWS) respectively. In contrast, the trichromacy of New World primates is based on a single polymorphic L opsin gene; all males are dichromats and trichromacy is achieved only in those females that possess a different form of this gene on each X chromosome. The only exception to this system in New World primates is found in the howler monkey which also possesses an L gene duplication. In Old World primates, the duplicated L opsin genes are organised into a head-to-tail multi-gene array flanked on the upstream side by a single locus control region (LCR). An LCR is also present upstream of the single L opsin gene in New World primates, whereas it is duplicated along with the coding sequence in the howler monkey.A comparison of opsin gene sequences indicates that the MWS/LWS gene duplication in Old World primates is more ancient than that in the howler monkey. In addition, the amino acid sequences of the two howler monkey pigments show similarities to the pigments encoded by the polymorphic gene of other New World primates. It is likely therefore that the howler monkey gene duplication arose after the split between New and Old World primates and was generated by an unequal crossover that placed two different forms of the New World polymorphic gene on to a single X chromosome. In contrast, the lack of identity at certain sites between the New World opsin alleles and Old World opsin genes indicates that MWS and LWS genes in Old World primates diverged subsequent to L gene duplication.A striking feature of the pigments present in Old and New World primates is the use of a common set of substitutions at three amino acid sites to achieve the majority of the spectral shift between the middlewave- and longwave-sensitive pigments. The separate origin of the trichromacy in New and Old World primates would indicate that the selection of these substitutions is the result of convergent evolution, arising as a consequence of visual adaptation in both cases to foraging for yellow and orange fruits against a green foliage.

Photopigment and Color Vision Variations in Primates

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Although it has long been assumed that nonhuman primates have keen color vision, the nature of this key sensory capacity and the biology supporting it have come to be reasonably

understood only over the past two decades. Generalizations emerging from much work involving direct studies of color vision, photopigment measurements, and examinations of opsin genes include the following. Catarrhine primates have routine trichromatic color vision reflective of separate X-chromosome M and L opsin genes and retinal pathways that are favorably arranged to provide comparisons of signals originating in the three cone types. The color vision of most platyrrhine primates differs qualitatively from this pattern. These species have only a single X-chromosome opsin gene. The presence of multiple M/L alleles yields dramatic individual variation in photopigment complements and consequent polymorphic color vision that is characterized by uniform male dichromacy and by a mixture of trichromatic and dichromatic color vision among females. A complication to this picture is that there is some additional variation in the number of M/L opsin gene alleles across platyrrhine species and that animals from at least two genera fail to show opsin gene polymorphisms. The essential difference between the catarrhine and platyrrhine arrangements is believed to reflect the occurrence of an X-chromosome opsin gene duplication that occurred early in catarrhine evolution. Recently, a photopigment basis for trichromacy has been detected in a few strepsirrhine species that is seemingly similar in nature to that of the platyrrhines. This discovery raises questions about the evolution of color vision and its relationship to photic habitats. Despite all of this recent accomplishment, many questions about primate color vision remain open. Among these, for instance, is the issue of why trichromacy has emerged in primates, but not in any other eutherian mammals. One answer often proposed is that the development of M/L opponency, and hence a second dimension of color vision, is predicated on the presence of a retinal midget cell system. Attempts to engineer M/L color vision in species lacking a midget cell system can potentially provide a test of that assumption.

Session: Retinal anatomy and physiology

Anatomy of Colour Pathways in the Primate Retina

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Three types of cones, sensitive to short (S), medium (M) or long (L) wavelengths are present in the retinae of trichromatic primates. Cone opponent signals from these cone types are transmitted to the brain by at least two parallel pathways, the midget-parvocellular pathway and the blue cone pathway. Here the anatomical components of the blue cone pathway were investigated in the retinae of New World and Old World monkeys using immunocytochemical and intracellular injection methods in combination with electron microscopy. The S or blue cones make up about 10% of the entire cone population. In the outer plexiform layer, S cones provide input to blue cone bipolar cells and horizontal cells. The blue cone bipolar cells transfer the S-cone signal to the inner plexiform layer where they contact the small bistratified (blue ON/yellow OFF) ganglion cell. Two sources of chromatic opponent input to this blue-on signal can be identified. First, a diffuse bipolar cell type contacting M and L cones provides synaptic input to the small bistratified ganglion cell. Second, one class of horizontal cell (H2) could provide inhibitory feedback from M and L cones to S cone bipolar cells. These components of the S cone pathway are a consistent feature of the retina in both New World and Old World primates.

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The human visual system is very accurate in localizing and estimating the trajectory of moving objects. For example, relative location of moving vernier targets can be localized, in the fovea, to an accuracy of seconds of arc, independent of movement speed. Is this accuracy inherent in the signals of ganglion cells or, must it de developed by cortical mechanisms which combine and integrate ganglion cell signals? We have analyzed the spatial variance of ganglion cell responses to moving targets (bars/gratings) and found that the spatial accuracy of signals of the cells of the magnocellular (MC) pathway is highest at low drift rates/temporal frequencies, despite the transient nature of this pathway. Accuracy closely matches human performance on vernier tasks with the same stimuli. This suggests that central mechanisms are able to make good use of the ganglion cell signals. However, closer comparison of ganglion cell signals and human performance may help constrain models of central motion mechanisms. For example, the stochastic nature of impulse trains complicates the way central mechanism can sample from the ganglion cell array. Also, the neurometric analyses used to derive the results assumes that central mechanisms are able to integrate over long periods of time (> 1 sec), yet the critical duration for such judgements is much shorter (50-100 msec). This and other features of the data suggest that central motion mechanisms must operate as sophisticated, flexible spatiotemporal filters in order to make optimal use of ganglion cell signals.

A review of comparative aspects of the m and p ganglion cells of diurnal and nocturnal anthropoids

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The retina of all mammals is organized in similar layers, possesses the same gamut of neurons, which are distributed throughout the retinal extension following the same basic rules. One has to go deep into details of retinal morphology and physiology to first find and then understand the differences in retinal organization among mammals. A considerable knowledge of retinal structure and function is necessary to grasp the subtleties of the primate retina, and it seems ironic that trichromacy, a feature reserved to primates among all mammals, depends on such a minute structural change in the photoreceptor array that it can only be anatomically demonstrated using the modern, very sophisticated adaptive optics retinal imaging. In this work, the main aspects of the retinal anatomy and physiology of anthropoid primates are reviewed, emphasizing those topics that can be related to adaptation to their diurnal or nocturnal behavior. The findings supporting the present view of primate retinal organization were obtained by careful observation followed by quantitative analysis of retinal flat mounts and retinal sections stained with classical stains, such as Nissl, Golgi or Gros-Schultze, or modern immunocytochemistry and neurotracing. For some species, there is also information available about the electrophysiology of retinal neurons, which was obtained by in vivo or in vitro retinal recording. The M and P ganglion cells have been identified in all primates so far studied, including man, other catarrhines (Pan, Papio, Macaca), diurnal platyrrhines (Saimiri, Cebus, Callithrix), nocturnal platyrrhines (Aotus), and prosimians (Galago). M cells have large cell bodies, thick axons, and large dendritic trees with a radial branching pattern, whereas P cells have small cell bodies, thin axons, and small dendritic trees with a more bushy and dense branching pattern. The M and P cells occur in two morphological varieties, one ramifying in the outer half of the inner plexiform layer, the outer cells, and the other ramifying in the inner half, the inner cells. The outer cells correspond to the off-center and the inner cells to the on-center varieties. Every point of the photoreceptor matrix is connected with at least one inner and one outer ganglion cell of the two cell classes, M and P. In Macaca, it was estimated that M and P cells correspond, roughly, to 10% and 80% of the total ganglion cell population. For platyrrhines, the total M cell population was estimated in 140,300 and 74,000 for the Cebus and Aotus retinae, respectively, corresponding to about 10% and 15% of the total retinal ganglion cell population in these primates. There are regional differences in the retina in the proportion of these two cell classes and these differences might be species specific. Both cell classes increase in density towards the fovea, but the proportion of M cells increases in the nasal guadrant in diurnal catarrhines and platyrrhines such as Macaca and Cebus, and in less proportion in the nocturnal Aotus. Only recently, it has become possible to record M and P cells from in vitro retinal preparations and then label the same cells by intracellular injection of neurotracers. With this technique, it was directly demonstrated for the first time that M cells are the phasic, broad-band cells, and that P cells are the tonic, red-green color opponent cells, previously described by

electrophysiologists. The direct correlation between morphology and physiology has so far been achieved only for *Macaca*, but it is largely assumed that it also holds for other primates, both anthropoids and prosimians. There is anatomical and physiological evidence indicating that both cell classes, M and P, are a general feature of the primate visual system with primary functions that are not related to the color vision phenotypes. This is consistent with the hypothesis that the P pathway evolved before red-green color opponency and thus was primarily involved in achromatic vision.

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Session: The lateral geniculate nucleus

Specificity and Destination of Chromatic Signals in the Primate Visual Pathway.

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Signals from spectrally distinct receptor classes enable colour vision, and also contribute to other visual sub-modalities such as form and motion perception. We measured single-neurone responses in the subcortical visual system of marmosets, a species with polymorphic colour vision. The goal of these experiments was to discover the specificity with which spectral signals are segregated in the early stages of vision. We found that signals originating in shortwavelength sensitive (S or "blue") cones are carried predominantly in the koniocellular division of the lateral geniculate nucleus (LGN) in all marmosets. Signals from S cones showed a high degree of functional isolation. The 'blue-on' and 'blue-off' cells received strong functional input from S cones, but the majority of parvocellular and magnocellular neurons received no functional input at all from S cones. In marmosets expressing two pigments in the medium-long wavelength sensitive (ML or 'red-green') range, neurons showing red-green opponent responses were predominantly encountered in the parvocellular layers of the LGN. No differences in the receptive field dimensions or achromatic contrast sensitivity of the centre mechanism were seen on comparing parvocellular neurons in dichromatic and trichromatic animals. These data suggest that signals for the redgreen dimension of colour vision are carried in the parvocellualr pathway without compromising other aspects of this pathway's functional role in spatial vision.

Spatio-temporal properties of the retino-geniculate pathway and the significance for vision

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The receptive fields (RFs) of primate retinal ganglion and LGN cells have spatially coextensive centre and surround regions, which have antagonistic Gaussian responsivity profiles. This linear representation seems to fail under certain circumstances. We investigated the interaction between the RF centre and surround and its significance for human visual perception. Responses of neurones in the marmoset LGN were measured to stimuli that were spatially build of a centre region, which optimally matched the RF centre, and an annulus which mainly stimulated the RF surround. The centre and surround regions were either selectively or simultaneously modulated. The relative phase between the centre and surround stimuli was varied in the combined stimuli. It was found that the cells responded minimally when the surround stimuli were phase advanced relatively to the centre stimuli, indicating the presence of phase lag in the responses of the RF surround. In psychophysical experiments, it was found that the perceived flicker strength in the centre stimulus is similarly modulated by the relative phase between centre and surround stimuli and that it was minimal when the surround stimulus led the centre stimulus. The similarities between the physiological and the psychophysical data suggest that the physiological basis of the perceived flicker strength in the centre stimuli, is already present in the retino-geniculate pathway. But the perceived flicker is most probably determined by a the responses of an array of cell, the majority of which are, unlike in the physiological experiments, not aligned with the stimulus. We therefore studied the influence of a spatial displacement between stimulus and RF on the responses of the cells. In this manner, the response of an array of cells could be approximated. Assuming a cortical peak to trough detector on the responses of this cell array, the output of which is proportional to the difference between the maximal and minimal cell responses in the array, can explain the similarities between the physiological and the psychophysical results. On the basis of the responses to the combined stimuli, the contributions of the RF centre and surround in the the combined stimuli could be extracted and compared the responses to selective centre and surround stimuli. These comparisons showed that the centre responses were relatively similar in the combined and the selective stimuli. From this we concluded that the centre response is not altered by the presence of a simultaneous response in the surround. However the surround response is phase advanced in the combined stimuli when compared with the responses to the selective surround stimuli. This suggests that the presence of a response in the centre interacts with the response in the surround making it phase advanced.

The Role of the Lateral Geniculate Nucleus and Parallel Pathways in a Dynamic System

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The LGN in primates has been long regarded as a relay station for visual signals that are passed on from the periphery to cortex for conscious vision. Signals that are sent from the retina via the LGN to primary visual cortex (V1) presumably serve the purpose of maintaining the integrity of messages that are inherently incompatible or that can only be combined at later stages of processing. In spite of decades of study, however, controversy still exists over the role of the LGN in visual processing, as well as, how many parallel pathways exist and over the function of these pathways in vision. Why bother relaying messages without changing them appreciably? We know, for example, that the receptive field properties of the LGN neurons are very similar to those of their retinal ganglion cell inputs. We also know that the LGN, like other thalamic sensory relay nuclei, receives most of its synaptic input *not* from the periphery (the retina), but from other cortical and subcortical sources. Why? In answering these questions, this talk will provide data to support four main points. First, focus on primate vision has blinded us to lessons learned from the visual systems of other mammals where parallel processing involves not only the retino-geniculo-cortical pathways but retino-subcortical pathways. Together these pathways are likely to operate in parallel, even in primates, to control complex visual behaviors. Second, parallel visual pathways carry more than a single message. Parallel pathways cannot be linked to specific complex visual or visuomotor functions either subcortically or cortically but can carry non-visual signals including cognitive and motor information even at the level of the LGN; each pathway is multipurpose. Sensory messages carried by parallel retinal pathways also are utilized in a variety of ways. Third, coding within parallel visual pathways must involve more than transmission of spike rates in individual neurons to avoid ambiguity. Evidence indicates that additional information exists in form of a temporal code either within single cells or. more likely, across populations of cells. What these codes are and whether the codes are the same at different levels of the system remains an open question. Finally, vision is not a unidirectional process that goes from sensation through perception to action. Instead the system is dynamic such past experience and future expectations literally "color" or change sensory messages carried by parallel pathways from the LGN to cortex.

Session: Primary Visual Cortex

Retinotopic Organisation of Space in the Primary Visual Cortex of the Common Marmoset Revealed by Optical Imaging

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Retinotopy, the fact that nearby cells in the visual cortex encode nearby positions in visual space, is perhaps the most fundamental characteristic of the visual system. Even species such as rodents, that seems to possess little in the way of organisation for orientation, possess a rough retinotopic organisation of space within their primary visual cortex. Recent studies have shown that optical imaging of intrinsic tissue properties can be used to measure local retinotopy in a variety ofspecies and in particular can be used to analyse anisotropies in cortical magnification factor (CMF) as noted in earlier electrophysiological and anatomical studies. We examined the retinotopic mapping of the visual world in the primary visual cortex of the marmoset monkey using differentialoptical imaging. Two sets of complementary stripe-like locations were visually stimulated in turn. Their difference depicts the cortical representations of continuous bands of visual space. By rotating the sets of stripe-like locations it is possible to map different spatialaxes. Analogous to the macaque we found that the V1/V2 border represented the vertical meridian while horizontal, 45, and 135degree angled stripes of space were also represented in a continuous manner. We developed a new automatic method of calculatinglocal measures of cortical magnification from our optical retinotopic maps. Using this method we found no evidence of any localanisotropies in cortical representation. Overall our results indicate that space is mapped isotropically in the primary visual cortex of the common marmoset.

Color Vision of Dichromats and the Evolution of Trichromacy

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Human dichromats, despite lacking one type of cone photoreceptors, use all the color terms "red", "green", "blue", and "yellow", to describe their color percepts. Most color vision models fail in this respect; for protanopes or deuteranopes, where L- or M-cone inputs, respectively, are absent, a reduced number of color qualities is predicted. Based on results of hue scaling experiments with protanopes and deuteranopes, we developed a new model for the color percepts of these dichromats. We assume a combination of signals from S cones and the single longer-wavelength sensitive cone type (M or L), yielding a third channel that mimicks a second longer-wavelength sensitive cone type. The model employs weak nonlinearities, gain control, and opponency in the processing of cone signals, physiological mechanisms known to play a role in vision. These transformations correspond to an embedding of the two-dimensional cone input space in a threedimensional perceptual space. Thus, perceptual axes of "red" vs "green", "blue" vs "yellow", and "light" vs "dark" can be represented. With two modifications, our dichromat model can easily be expanded to describe trichromatic color vision: Firstly, by taking into account the X-chromosomal opsin gene duplication, resulting in both M and L cones; secondly, by assuming that a Hebbian-type meachanism leads to separation of M vs L wiring during development. We hypothesize that this dichromat model is also valid for our dichromatic simian ancestors who may have taken advantage of a pseudo-trichromatic representation for image segmentation and categorization of colors. This implies that the perceptual color axes of "red"-"green" and "blue"-"yellow" may have evolved even before retinal trichromacy.

Effects of Acetylcholine on Length Integration in Primary Visual Cortex

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Recent evidence from slice studies suggests that Acetylcholine (ACh) modulates the balance between intracortical/feedback and afferent thalamocortical/feedforward information processing. This re-balancing decreases the efficacy of lateral and feedback cortical processing, and might thereby increase the relative efficacy of thalamo-cortical/feed-forward processing. We hypothesized that such rebalancing would affect centre-surround integration in primary visual cortex. We predicted that application of ACh should alter V1 neurons' length tuning preferences inducing a shift towards shorter length preference. We recorded single neuron activity from V1 neurons in 6 anaesthetized Marmosets (Callitrix jacchus) under control conditions and while applying ACh iontophoretically (pulsed and/or continuous application). We presented bars of preferred orientation in the centre of the receptive field. Bar length was varied from 0.5, 0.75, 1, 1.5, 2, 3, to 5 times the receptive field diameter. Neurons exhibiting changes in firing rate upon ACh application mostly showed an increase in firing rate during spontaneous and stimulus driven activity. Additionally, responses to flashed bars generally became much more tonic when ACh was applied. In line with our prediction we found that ACh induced a shift of preferred length towards shorter stimuli in the majority of neurons. These data suggest that ACh modulates the flow of information in a dynamic fashion -- decreasing effects of lateral/feed-backward connections while increasing the impact of information coming in from the eye. ACh has been associated with mechanisms of attention. In line with this we hypothesize that ACh may aid in eliminating information from the surround of the classical receptive field in order to emphasize local information currently in the centre of the attentional spotlight.

Session: Higher Cortical areas

The Evolution of Complex Visual Systems in Primates

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Most of what we know about brain evolution is based on inferences from observations on the brains of extant species. A comparative approach involves examinations of the brains of the most relevant species, determining shared features, and evaluations the probabilities of inheritance from a common ancestor or independent evolution. Primates share a number of features of the visual system with non-primate relatives, including a laminated lateral geniculate nucleus (LGN), a pulvinar complex, and primary (V1) and secondary (V2) visual areas. Primates differ from other mammals in having paired magnocellular and parvocellular layer in the LGN, and superior colliculus with an expanded retinotopy restricted to the contralateral visual hemifield, a pulvinar complex with a number of nuclei, and an expanded number of cortical visual areas. Early primates appear to have had visual areas V3, DM, MT, DL(V4), and several subdivisions of temporal and parietal cortex, as well as a frontal eye field. V1 was subdivided into blob and non-blobmodules, while V2 had band-like modules across its width. Less is known about specializations that occurred with anthropoid primates, but visual regions of the temporal and parietal lobes expanded, and the addition of visual areas is likely. The evolution of the human brain is characterized by a huge increase in size over the last 3 million years, and a decrease in the proportion of cortex occupied by visual areas V1, V2, and MT. Scaling problems posed by this increase in size have been reduced by limiting the sizes of these visual areas, increasing the number of smaller areas, and decreasing the connections between distant visual areas, including those in the two hemispheres. A further understanding of the differences in the visual systems of humans and the African apes is both needed, and it is just starting to emerge.

Cortical Representation of Moving Objects for Perception and Action

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In primates, motion processing represents a cortical phenomenon established in areas MT and MST of the extrastriate cortex. Here, we focus on area MST which has previously been shown to be involved in motion perception as well as in the generation of smooth pursuit eye movements. Firstly, we further elucidate the contributions of area MST to the generation of pursuit. Second, we demonstrate the contributions of area MST during perception of multi-modal moving stimuli and paradoxical motion stimuli. The fact that the neuronal activity observed during pursuit of an imaginary target was similar to the activity during pursuit of a real target indicates that neurons in area MST not only responded to visual stimuli, but also responded to eye movements. These extra-retinal response properties were also demonstrated by the responses during anticipation-based pursuit. The results of our experiments consisting in combined eye-head movements of our monkeys as well as in a combination of a pursuit task with vestibular stimulation indicate that the neuronal activity in areas MST coded for the target movement in space. This finding is further supported by the results of intracortical microstimulation in area MST.To address the contributions of area MST to motion perception, we used paradoxical motion and multi-modal moving stimuli. The latter consisted in either a moving visual object or a moving sound source. In case of the paradoxical motion stimuli, second-order motion stimuli (drift-balanced and theta motion) were opposed to first-order motion (fourier motion) and luminance-defined moving stimuli. Our monkeys were able to report the direction of all applied stimuli correctly. However, the recorded single-unit responses from area MST did not encode the moving stimulus in all conditions. In case of a moving sound source, the neurons did not change their activity at all. In case of the theta stimulus, the neurons coded the direction of the retinal image motion, not the direction of the object movement. Taken together, our results strengthen the view that area MST is directly involved in the generation of smooth pursuit eye movements elicited by a moving object as well as by the perception of a moving object. However, there are situations in which the neuronal activity in area MST could not be directly linked to the processing of a moving stimulus.

Chromatic Sensitivity of Silent Surrounds in macaque V1 and V2

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Cortical neurons receive input from regions of space outside their classical receptive field (CRF). Stimulation of this otherwise silent surround usually reduces the responses of the CRF to its optimal stimuli, but little is known about the chromatic properties of the silent surround or how this may interact with the chromatic tuning of the CRF. To address this guestion, we recorded from 218 neurons in V1 and V2 of macagues prepared for acute electrophysiological experiments. We measured responses to grating patches of optimal spatial frequency and orientation, but varying size, that were modulated along achromatic or isoluminant (L-M and S-cone) color directions. We found that the surrounds of all V1 cells were relatively insensitive to chromatic modulation, regardless of the strength of chromatic inputs to the CRF. This lack of correlation meant that the preferred color direction often depended on the size of the test patch: many cells preferred achromatic gratings for small patches and chromatic gratings for large patches. In V2 the strengths of chromatic inputs to CRF and surround were well correlated, and the preferred color directions of cells were largely independent of patch size. Further, in V1, the weights and signs of different cone inputs were not stable against changes in patch size, with the exception of cells that had well balanced L- and M-cone inputs, or significant S-cone input (about 14% of cells). In V2, the relative weights of cone inputs to all types of receptive fields were more stable. The stability of chromatic signature against variations in the sizes of stimuli is important if neurons in early visual cortex are to represent the chromaticity of objects. Our results suggest that only a small fraction of V1 cells, though perhaps most V2 cells, meet this requirement.

Session: Applications of primate research

The clinical applications of primate vision research

Eberhart Zrenner

Session: Perceptual correlates of physiological processes

Neural Substrates of Coherent Visual Perception in the Human and the Monkey Brain

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The question of how local image features on the retina are integrated into perceived global shapes is central to our understanding of human visual perception. However, the neural mechanisms that mediate unified shape perception in the primate brain remain largely unknown. Our recent fMRI studies on both monkeys and humans addressed this question by using an adaptation paradigm, in which stimulus selectivity was deduced by changes in the course of adaptation of a pattern of randomly oriented elements. Accordingly, we observed stronger activity when orientation changes in the adapting stimulus resulted in a collinear contour than a different random pattern. This selectivity to collinear contours was observed not only in higher (occipitotemporal) visual areas that are implicated in shape processing, but also in early (retinotopic) visual areas where selectivity depended on the receptive field size. These findings suggest that unified shape perception in both monkeys and humans involves multiple visual areas that may integrate local elements to global shapes at different spatial scales. Further human fMRI studies showed decreased detection performance and fMRI activations when misalignment of the contour elements disturbed the perceptual coherence of the contours. However, grouping of the misaligned contour elements by disparity resulted in increased performance and fMRIactivations. These studies provide evidence for the role of early perceptual organization processes and their interactions with higher stages of visual analysis in unified visual perception in the primate brain.

Colour in the Cortex and the Significance of Multimodal Interactions

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Colour is the product of a sequence of computations involving the retina and the cortex. Whereas we understand relatively well what happens with respect to colour at the first stages (i.e. the separation of luminance and chrominance by means of spatially and chromatically opponent processes), the emergence of colour from cortical processes still contains many open questions. One major topic that has arisen recently is the relationship between the processing of colour and that of the other submodalities of vision (form, depth, motion). This challenges the segregated pathway hypothesis which states that the different modalities are being processed in parallel pathways and specialized centres in the brain (Ungerleider & Mishkin, 1982; Livingstone & Hubel, 1988; Zeki, 1990). Colour, according to this hypothesis, is filled into the processed form at a later stage, much like colouring a book. A problem with this view is to find a stage where the visual attributes do actually recombine in order to form a unified percept. Recent advances in physiology and psychophysics however, challenge this view and advocate a coupled analysis of the different dimensions of vision (Lennie, 1999; Werner, 2003), even going so far as to guestion the existence of a colour center at all (Gegenfurtner and Kiper, 2003). In my talk I will present recent psychophysical evidence for interactions between colour, form, depth and motion that take place during the central processes of chromatic adaptation and will outline their significance for the chromatic analysis and colour constancy in natural scenes.

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Response Times and Achromatic and Chromatic Contrast Coding

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Experiments aimed at determining how response time (RT) reflects the physiological characteristics of different pathways are described. Stimuli are luminance modulated, sinusoidal gratings, or chromatically modulated Gaussian spots located in different regions of colour space. Simple RTs are obtained by pressing a button in response to the appearance of the stimulus. For many, but not all conditions, a linear function accounts for the data when RTs are plotted in terms of 1/contrast. This linear relationship allows us to draw RT-based spatial tuning functions and to derive a measure of gain at different luminances, which matches that obtained from single unit electrophysiological studies. In the spatial domain, the data provide an interesting insight in to classical contrast sensitivity functions and readily reveal the activity of the magno- and parvo-cellular pathways. In the chromatic domain, RTs are highly sensitive to departures from subjective isoluminance. Processing for blue/yellow stimuli appears to be much slower than that for red/green. This difference, suggesting the activity of cone opponent mechanisms, remains when stimulus intensity is scaled in terms of equal supra-threshold increments, rather than cone contrast. The experiments suggest that RTs are triggered at a relatively early, probably pre-cortical stage, along the visual pathway.

Functional MR Investigation of the Saccadic System

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Recent evidence indicates that primary visual cortex (V1) is activated during voluntary saccadic eye movements and that on-going stimulus-evoked activity in V1 can be enhanced by attention. Since a saccade is preceded by a shift of spatial attention, we asked whether saccade-related responses in V1 can be distinguished from those caused by voluntary shifts in attention. Using functional MRI together with eye-movement recording, we have examined cortical responses evoked while subjects performed visually guided saccades and compared these responses to a) those elicited by saccades to instructed locations in the absence of visual targets, or b) those measured when the subjects shifted their attention while maintaining central fixation. Robust and replicable BOLD responses were found in frontal and parietal eye fields of six subjects in all examined conditions. Primary visual cortex was only consistently activated when saccades were performed, but not during covert shifts of attention, suggesting that V1 is part of the cortical circuit of eye-movement control.

Posters

Spatiochromatic Properties of Natural Images in Kibale Forest, Uganda

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The human visual system (hvs), as well as that of other trichromatic primates, has different contrast sensitivity functions for chromatic and luminance stimuli. The spatial filtering is low-pass for chromatic stimuli and band-pass for luminance. Previous results have shown that a subset of natural scenes, namely those with red objects (e.g.fruit) on a background ofleaves have spatial properties that correspond to this physiological spatial filtering (Parraga, Troscianko and Tolhurst; Current Biology 12, 483-487;2000). Our original dataset on which these conclusions were based wasconsisted of English natural scenes. Here we analysed the spatiochromaticproperties of a dataset of natural scenes obtained in Kibale Forest. Uganda, which is a natural habitat containing large numbers of wild trichromatic primates. We used the same calibrated digital camera as in the previous study, which delivers L,M,S cone responses, and opponent-channel responses, for each pixel. We obtained 270 images of scenes, many of them containing red fruit, red leaves, red flowers and green leaves corresponding to the primate visual environment as seen from the ground and from the canopy. All the red fruit and leaves were confirmed as forming a significant part of the diet of trichromatic primates. Our results support the English plants), namely that the luminance and chromatic Fourier spectra of earlier finding (with pictures containing reddish objects on a background of leaves correspond well to the spatio-chromatic properties of the luminance and red-green systems in human vision, at viewing distances of the same order of magnitude as the grasping distance.

Visual encoding stability of green leaves in primate vision

Tom Troscianko, Roland Baddeley, C Alejandro Párraga, Ute Leonards, David Tolhurst, Jolyon Troscianko

It is known that primate red-green color vision is efficient at encoding the presence of red or yellow fruit or leaves against a background of green foliage. Separately, we have shown that images of red fruit and red leaves have Fourier spectra that appear to be optimally encoded by the spatio-chromatic properties of primate vision. However, our observations of monkey foraging behavior in Kibale Forest, Uganda during the dry season suggested that monkeys frequently ate green leaves on trees lacking any red object. They also showed preferences for specific trees. We asked whether the neural encoding of the green leaves of such trees allows discrimination from other trees, across marked differences in illumination due to time-of-day and weather effects. We obtained 80 images of two scenes, each containing several types of tree, throughout two days at intervals of 10-20 minutes, using a calibrated digital camera system described elsewhere (Párraga, Troscianko, and Tolhurst (2002) Current Biology 12, 483-487). The camera calibration allowed the decomposition of each pixel into L,M,S cone responses, and also luminance, red-green, and yellow-blue opponent responses. We averaged the values of these responses in five separate patches for images from Day 1, and six patches for Day 2. Our first analysis replicated the approach of Nascimento, Ferreira, and Foster (2002) JOSA A 19, 1484-1490, who suggested that ratios of cone responses across different patches should be invariant against changes in illumination. This turned out not to give a stable representation, especially when one of the patches was plunged into shadow. However, if similar ratios are taken of the opponent-channel responses, these ratios are more invariant across illumination changes by an order of magnitude. In particular, the red-green system gives a particularly stable ratio. We therefore conclude that the red-green opponent system provides information about scenes containing green leaves which is strongly invariant across changes in illumination direction, spectral composition, and intensity. In other words, for scenes containing foliage, the colour constancy problem is solved at the level of the retina.

S-cone topography in Old world primate species: Man, Chimpanzee, Mandrill and Barbary Ape.

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While Mammalian M-cone topographies are usually arranged concentrically around the visual axis, S-cone topographies show considerable variability correlated to the tiling of the visual field in specific environments. We studied eyes from Old world monkeys with different ecologies for comparison with human samples. Primate eyes were obtained from autopsy specimens from Zoos and animal parks and Human retinas were obtained from corneal donor eyes. The isolated retinas were labeled for S-opsin using JH455 antibody (provided by J.Nathans) to obtain density maps. For comparing the weighting of visual field sectors between species the density values were integrated along 50% and 100% meridional lengths. Foveal Slope: Tissue quality limited precise mapping of some foveal centers, yet all four species have central S-cone density minima and concentric maxima. However, in humans at least, variability of deficits implies individual states ranging between tritanopic and tritanomal conditions. General topography: Topographic and polar plots demonstrate S-cone densities in Chimpanzee (max. 2000/mm²) are concentric with a slight weighting at the inferior hemisphere while those in Man show a slight stretching at the superior hemisphere. The Mandrill, a semi-terrestrial rainforest species and the mountaineous Barbary Ape have similar foveal densities (ca. 1600-1800/mm²) but the overall patterns deviate clearly. Both species maps have horizontal extensions especially in the nasal retina where values above 600/mm² are maintained towards the far periphery. Nasal horizontal elongations of S-cone densities are likely advantageous in more open habitats for spotting/tracking predators and foraging group members (in Mandrill with coloured skins parts). Thus, the more concentric pattern in Man resembles that of forestal/arboreal species rather than those of guadrupedal terrestrial monkeys, rising guestions on the role of different habitat scenarios and bipedism during hominization.

Fruits, Flowers and Origins of Primate Trichromacy

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While most animals have non-overlapping cone sensitivities, we and other Old World primates have long-wavelength (L) and middle-wavelength (M) cones whose sensitivities strongly overlap. Intuitive considerations and mathematical modelling show that the non-overlapping receptors of a majority of animals are well suited for discriminating of a variety of colours. However, recent studies have shown that spectral positions of primate L and M cones are close to the optimum for detection of fruits and edible red, young leaves against a background of mature green leaves. This may indicate that primate trichromacy appeared as an adaptation for finding food. Plants use fruits to attract birds and mammals dispersing their seeds, while flowers are used to attract pollinators, mostly insects. These two types of advertisements of plants generally differ in their spectra. We show that the overlapping L and M cones in primates are nicely adjusted for reconstruction of spectra of both fruits and flowers. Our finding indicates that primate trichromacy may be beneficial for identification of many colourful objects, not just of edible ones.

Colour Discrimination in Golden-headed Lion Tamarin.

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With exception of primates and some Australian marsupials, dichromacy is the basic condition for all mammals. In stem anthropoids or in the ancestor of platyrrhines a polymorphic trichromacy probably evolved. This polymorphism, found in many New World monkeys and present in some prosimians, allows the existence of dichromatic or trichromatic females but only dichromatic males. In contrast, human beings, apes, Old World monkeys and howler monkeys have habitual trichromatic colour vision. Trichromatic colour vision has long been thought to be the result of an adaptive process involving the detection of targets (i.e., ripe fruits and/or young leaves) against a foliage background. To our knowledge only two genera and five species of the family Callitrichidae from a total of five genera, 39 species and 61 subspecies have already had their colour vision capability investigated. Callitrichids feed on three primary types of food items, tamarins, however, seem to include more fruit in their diet then do marmosets. Because of their diversity of feeding behaviours, marmosets and tamarins are of great interest for colour vision research. Among these animals, the genus Leontopithecus depicts attention because of their low distribution and population densities. Basic research can help us understand why these animals are endangered, while other species that inhabit the same environments are not. The colour abilities of six (three males and three females) golden-headed lion tamarin (Leontopithecus chrysomelas) in discriminating Munsell colour chips were assessed through a discrimination learning paradigm. The animals were kept in semi-natural conditions, being tested in their own home cages, using a Plexiglas version of the Wisconsin General Test Apparatus. Pairs of chips were chosen from an early experiment with humans. The monkeys were tested with stimuli of the same hue but different brightness in order to make sure that discriminations were based on colour rather than brightness cues. The results show that all subjects had an above chance performance in pairs that are easily discriminated by human dichromats and trichromats. On the other hand, pairs that were of easy discrimination by trichromats but of difficult discrimination by dichromats produced a random performance in all subjects. Contradicting what would be expected, the present study does not indicate the presence of a visual polymorphism as found for other species of callitrichids. However, additional experiments are been conducted in order to enlarge the sample size and to determine the genetic basis of colour vision found in this specie.

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Physiological Evidence for Fully Developed Trichromacy in Howler Monkeys

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ERG recordings have shown that the retina of both male and female howler monkeys have three cone photopigments. However, the retinal organization underlying colour vision in these animals is not well understood. Since the M and L opsin genes each have a locus control region, there is a possibility that the howler monkey retina co-expresses M and L opsins in one cone. The purpose of this work was to test this possibility. One adult male Alouatta caraja was used. Extracellular recordings were obtained from parafoveal retinal ganglion cells. We used three different stimuli: luminance or chromatic flashes to classify the cell in transient or sustained: narrow-band heterochromatic stimuli modulated with different relative phases or in counterphase at different contrasts at six different temporal frequencies to study cells' spectral sensitivity. Post-mortem microspectrophotometry (MSP) was performed on the same retina to obtain rod and cone spectral sensitivities. The temporal properties of Alouatta ganglion cells were similar to those of another New-World primate, the Cebus apella (Lee et al., 2000). P-cell responses showed strong opponency, resembling those of trichromatic female Cebus. The MSP data are consistent with only a single opsin being expressed in each cone. These results argue against the hypothesis that in the howler monkey two different opsins are expressed in the same cone. It appears that this primate expresses full trichromacy, and has a very similar retinal organization to Old-World monkeys. Cone-specific opsin expression in the presence of a locus control region for each opsin may call into question the hypothesis that this region controls opsin expression.

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Just another Difference – the Variance of L/M-ratio in Women and Men

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Three cone types provide the input signals for human color vision. Their spectral sensitivities are highest at wavelengths of about 420 nm (S), 530 nm (M) and 558 nm (L). L- and M-cones make up the majority in the retina of color normal humans. Due to their similarity, differentiation of those two cone types is difficult in intact retinae. Using direct (mRNA-analysis, Hagstrom et al. 1998) and indirect (Roorda et al. 1999) methods, the distribution of cones in color-normal human retinae has been assessed: the large majority of cone types are L- and M-cones with an averaged ratio of L- to M-cones of about 2 (Cicerone et al. 1994, Walraven 1974). Averaging L/M-ratios is based on the assumption, that they are independent of gender. We tested this assumption with 50 subjects, 25 women and 25 men, aged between 20 and 58, whose normal tri-chromatic color vision was assessed with the Farnsworth Hue 100 test. These subjects viewed a colored square of 2° side length imbedded in, and alternating with, a white background at a frequency of 15 Hz. Observers changed the chromatic appearance of the colored square by attenuating the gain of each of the three guns (RGB) of a calibrated color monitor. Settings at which the color was perceived as non-flickering were taken for 16 colors evenly distributed over the gamut of available colors. The data obtained were transformed into cone excitations using the Stockman (1993) fundamentals and fitted to a plane in cone space, which yields the respective contributions of cone types to perceived brightness. Results show that the variance in the ratio of the number of L-cones divided by that of M-cones as well as the mean L/M-ratio in women significantly differs from that in men. The genes encoding L- and M-cone pigments reside on the X-chromosome (Nathans et al. 1986) and hence are present twice in the genome of women, but only once in men. The specificity found for the L/M-ratio may be a bias for L-cone pigments to be built into cones when two copies of the X-chromosome can be accessed during ontogenetic development.

Dichromacy and Duality

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For a trichromat, chromaticity is represented within the two-dimensional chromaticity diagram as a point; for a dichromat, it is represented as a straight line belonging to a pencil of straight lines. This corresponds to the interpretation of the chromaticity diagram as a projective plane, a structure possessing two sorts of elements, points and straight lines. Between points and straight lines, the so-called incidence relation may exist. An example is the dichromatic neutral zone: achromatic colours fulfil the incidence with it, while chromatic colours do not. When the incidence relation is formulated algebraically, this statae of affairs is a reflection of antagonistic colour opponency. The projective duality has its counterpart in associating the dual vector space with the vectorial colour space. This leads to simple transformational properties between dichromatic systems.

Receptive Field Properties and Laminar Organization in the Lateral Geniculate Nucleus of the Gray Squirrel (Sciurus carolinensis)

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Anatomical and physiological studies of carnivores and primates over the last decades have identified three major classes of relay cells in the retina and lateral geniculate nucleus (LGN) of mammals, called X, Y, and W cells in carnivores and parvocellular (P), magnocellular (M), and koniocellular (K) cells in primates. Relationships among X, Y, and W cells and P, M, and K cells remain unclear. Some have suggested that X and P and Y and M cells are homologous because X and P cells show sustained firing while Y and M cells are both transient. Others have suggested that linear M cells and non-linear M cells are related to X and Y cells, because, unlike P cells, M, X, and Y cells show high contrast gains. To better understand the relationships among LGN cells in mammals, we have characterized receptive field properties of single neurons in the LGN of a highly visual diurnal rodent, the gray squirrel. On the basis of laminar organization, receptive field organization, response latency, and response variability, we divided the cells into three groups, called P-like, M-like, and K-like. P-like cells show sustained firing, center-surround organization, and are almost exclusively linear in spatial summation. M-like cells are transient, have short response latencies and centersurround organization, and can be either linear (75%) or non-linear (25%) in spatial summation. The K-like cells are a heterogenous class and are generally transient, vary widely in response latency, can be either linear (76%) or non-linear (24%), and show less vigorous and more variable responses than P-like or M-like cells. P-like, M-like, and K-like cells had relatively linear response curves and showed low contrast gains, and the relationship between receptive field center size and eccentricity was very weak for all cell types. Our data are consistent with the idea that all mammals contain three basic classes of LGN neurons, one showing reliable, sustained responses and centersurround organization, another showing transient but reliable responses, short latencies, and center-surround organization, and a third, highly variable and heterogeneous class of cells. Other properties such as dependence of receptive field size on eccentricity, linearity of spatial summation, and contrast gain appear to vary from species to species.

Calbindin Immunocytochemistry Labels the Retina of Diurnal and Nocturnal New World Anthropoids Differently

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To identify the pattern of labeling by anti-calbindin immunocytochemistry in the retinae of diurnal and nocturnal New-World anthropoids, Cebus and Aotus.: All animals were maintained and treated in accordance with current national and international regulations for animal welfare. Most animals were used in other anatomical or physiological studies that did not interfere with the present study. The animals were killed by a lethal dose of sodium pentobarbital and subsequently perfused transcardially with 4% paraformaldeyde/ phosphate buffer 0.1 M, pH 7.2. The cornea and lens were removed and after three hour in fixative, the eyes were transferred to PBS at 4°C until they were further processed. Vertical 20 µm sections were obtained by cutting on a freezing microtome (Leica, Jung CM3000). Calbindin-positive immunoreactivity was detected with anti-calbindin (C-8666, 1:3.000, Sigma) and revealed using avidin-biotin complex and the 3,3' diaminobenzidine (DAB) reaction. The calbindin-positive cells were visualized using optical microscopy. In the Cebus retina, calbindin labeling was present in the outer nuclear (ONL), inner nuclear (INL) and ganglion cell (GCL) layers. The labeling was present in the outer segments, inner segments, cell bodies, and axonal pedicles of the cones. Rods were calbindin-negative. In the Aotus retina, anti-calbindin immunocytochemistry was restricted to a few bipolar and amacrine cells in the INL and a few neurons of the GCL. No immunoreactivity was found in the ONL: The absence of calbindin in cones of nocturnal (Aotus) and the presence in cones of diurnal (*Cebus*) New-World anthropoids suggests a different role of the calbindin calcium binding protein in the two species, possibly related to different states of photoreceptor adaptation at similar illuminance levels in the two species as was proposed recently by Chiquet et al. (Neuroscience 115: 1323-1333, 2002). Supported by CNPg and CAPES. We are grateful to the National Primate Center (Ananindeua, Brazil) for providing the animals used in this study.

Is Monkey Contrast Sensitivity Optimised for Prior Knowledge of the Distribution of Contrasts in Natural Scenes?

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The problem faced by an animal using noisy sensory information to find out about its environment may be suited to Bayesian analysis. The animal will be most accurate if it guesses that the event occurring is the event for which the probability of event given neural responses, p(e|r), is maximum. In order to estimate p(e|r), an organism must know the probabilities of occurrence of events p(e) (the priors), and the probabilities of neural responses given events p(r|e). Given these, one can apply Bayes' formula: $p(e|r) = p(r|e) \cdot p(e)/p(r)$ We examined the problem, developing a computer model of contrast identification in which 16 simplified V1 neurons must infer, from their noisy responses (variance = 2.mean, Tolhurst et al 1983), the value of stimulus contrast presented. The contrast response function is modelled by the Naka-Rushton equation (Albrecht and Hamilton 1982). An important parameter is the level of contrast at which the neuron attains half of its maximum response (c_{50}). We ran simulations in which the c_{50} distribution was taken from monkey (D. Ringach, personal communication) and cat (D.J. Tolhurst, unpublished observation) neurophysiology and found performance in contrast identification to be different from that of a control population with a uniform c_{50} distribution. For the animal c_{50} simulations performance peaked at the mid contrast range, corresponding to the peak in the distribution of contrasts in natural scenes, as estimated by an equivalent contrast method (Peli 1990). This would give the animal the advantage of being best at coding the contrasts most frequently occurring in the natural world. This observation was supported by calculations of mutual information (1) between a set of natural contrasts and model contrast estimates, which found I to be greater for cat and monkey populations (2.4 and 2.2 bits, respectively) than the control set (2.1 bits). Modelling of priors made no difference to *I*, but did shift the peak accuracy of the control population closer to the peak of the natural contrast distribution – an effect analogous to making the c_{50} set more like that of the animal populations. So, although the model used explicit probability distributions, we found that the effect of one of these distributions, the priors, could be mimicked by adjusting c_{50} . This suggests that by setting c_{50} values, either genetically or developmentally, V1 is able to encode prior information. Albrecht, D.G. & Hamilton, D.B. (1982). J. Neurophysiol. 48, 217-237.

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Rod Inputs to Retinal Ganglion Cells in two New-World Primates, the Diurnal Cebus and the Nocturnal Aotus

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Rod input to magnocellular projecting retinal ganglion cells (M-cells) is stronger in Cebus than in macaque. Similar differences were also found in LGN M-cells of Callithrix. Other than in Old-World anthropoids, rod inputs are observable in the responses of ganglion cells or thalamic cells of New-World primates even at relatively high illuminance levels. In the present work, this issue was further investigated by comparing rod driven signals in the M-cell responses of diurnal and nocturnal New-World primates. Two species were studied: the diurnal Cebus apella and the nocturnal Aotus infulatus. Only results from dichromatic Cebus were used to allow direct comparisons with those from the monochromatic Aotus, since M-cells receive input from only one M-/L-cone type in both animals. In vivo recordings were obtained from parafoveal M-cells using tungsten-in-glass microelectrodes. Three stimuli were used: luminance pulses to classify the cells as phasic or tonic; two narrow-band heterochromatic modulating lights at different relative phases, or at counterphase with different relative amplitudes. The measurements were repeated at different temporal frequencies and retinal illuminances. As previously described, Cebus M-cell responses were dominated by cone input. However, some cells showed small rod driven signals even at relatively high illuminance levels. Aotus M-cell responses were heavily dominated by rod input even at very high illuminance levels. The presence of a very strong rod driven signal in the Aotus retina is in agreement with the high rod to cone ratio as was found in morphological studies (e.g. Franco et al., 2000). The ganglion cell responses of diurnal anthropoids are less rod dominated than those of nocturnal anthropoids. However, the generally stronger rod input to ganglion cells in platyrhines when compared with catarrhines supports the hypothesis that New-World anthropoids went through a nocturnal stage during evolution (Lee et al., 2000).

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Ganglion cell arrays in the primate fovea

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In previous experiments we studied interactions between the centre and the surround of receptive fields of neurons in the retino-geniculate pathway and their consequences for human visual perception. To be able to correlate the physiological and the psychophysical data, it is important to consider that a visual stimulus is encoded not by one cell, but by a cell array, the receptive fields of which have different locations relative to the stimulus. We have developed an algorithm with which the spatial distribution of the receptive fields of retinal ganglion cells within the primate fovea can be simulated. To calculate the positions of central points of the receptive fields, the model uses Delaunay triangulation with a superimposed jitter (Zhan and Troy, Visual Neuroscience 17, pp. 23-39). The resulting array is subsequently stretched according to the cell density variation with retinal eccentricity. Our model considers the literature data on the anatomical structure of the primate central retina. However, the model simulates the positions of the receptive fields rather than the locations of the ganglion cells' bodies, which in the fovea might be different owing to the lateral displacement of the ganglion cells. For the macaque retina, the simulated patch has a diameter of approximately 3 degrees and contains about 3400 ON- and 3400 OFF-centre magnocellular cells. Other cell subpopulations and other primate species (marmoset, human) were also considered. Any array size can be chosen depending on the visual stimulus projected on the retina.

Effect of Spectral Separation of Cone Pigments on Red-Green Opponent Responses of Primate Lateral Geniculate Cells

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Red-green (RG) opponent responses in the retina and lateral geniculate nucleus (LGN) of macaque can be accounted for by vector summation of medium- (M) and long- (L) wavelength sensitive cone mechanisms with fixed temporal delay (1). We measured the effect of M and L cone pigment spectral separation on RG opponent signals in parvocellular (PC) cells. Female marmosets (Callithrix jacchus) carrying the 543/563 nm or 556/563 nm pigment combination were identified by RFLP-polymerase chain reaction. Animals were anaesthetised with 6µg/kg/hr Sufentanil i.v., and artificially ventilated with a 70/25/5% N₂O/O₂/CO₂ mixture. Extracellular single-unit recordings were made during temporal modulation between red (639 nm) and green (554 nm) LEDs, in a two-channel Maxwellina view system. The contrast, temporal frequency, and relative phase of the LEDs were varied. Response amplitude was compared to predictions of the vector summation model. A total of 35 cells in the 543/563 and 36 in the 556/563 phenotype was analysed. Cells' response amplitude and contrast gain was compatible with the model, with a fixed temporal delay of 3-11 msec between opponent cones for both phenotypes. Our results show that RG opponent response strength increases in a linear way with spectral separation of ML pigments, and also suggest a common basis for opponent responses in different pigment phenotypes. In a separate analysis, the responses of 26 PC cells to RG gratings of varying spatial frequency were compared between 543/563 and 556/563 phenotypes. Cells in the 543/563 phenotype displayed spatial low-pass responses characteristic of those in the macaque, whereas responses in the 556/563 phenotype were spatially band-pass. This suggests that one effect of increased spectral separation between M and L cones is to broaden the response spatial bandwidth for chromatic signals in PC cells.

(1) Smith, VC, Lee, BB, Pokorny, J, Martin, PR, and Valberg, A. (1992) J.Physiol. 458:191–221.

Saccadic System is Insensitive to Static Background, but Sensitive to changes in Background

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Since the number of axons in our optic nerve is limited, the spatial resolution of our visual system displays a strong anisotropy. We constantly perform saccades, fast and ballistic eye movements, to bring certain details of the visual environment into the foveal field of vision characterised by its high spatial resolution. We asked in this study whether the preparation and the execution of saccades directed towards visual targets were affected by different conditions of structured backgrounds. The IR tracker recordings of 6 healthy subjects revealed that target position (5° or 10° towards the left or right) did not affect saccade latency significantly. The latencies obtained when the target was presented onto a homogeneous dark background (grand average 201 ms) were not significant different from the latencies obtained if the target was presented on a structured background (197 ms) (2-fact. ANOVA: factor subject p<0.0001, factor background p=0.08, interaction p=0.712). The post saccadic error and the dynamic saccade parameters constituting the main sequence were also not affected by the background condition. However, if either the luminance or the orientation of the background elements was changed at the same time the saccade target was presented, we observed a statistically significant increase of saccadic reaction time (luminance: 124 %; orientation: 119 %). Note that the change in background was absolutely irrelevant for the task. In contrast, the post-saccadic position error as well as the main sequence of the saccades was not affected by the background change. We conclude that the preparation of a saccade was only affected by a sudden, unexpected change occurring simultaneously to the presentation of the target in the background, which most likely allocated reflexively computational resources of our subjects. In all other background conditions, the saccade system was perfectly able to filter relevant information concerning target appearance and localisation from irrelevant background information.

Müller Cells in Human Macula: Implications for Macula Degeneration

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Despite of much research in the field, the cellular constitutents and the histological organization of the primate fovea are still a matter of debate. This concerns the role of the specialized macular Müller (glial) cells in macula generation and degeneration including macula hole formation, as well as the gualitative and quantitative relationships between Müller cells and retinal neurons. Human retinae (from donor eyes) and retinae of Maccaca fascicularis were fixed as soon as possible. Transmission and scanning electron microscopy, including the freezefracture technique, as well as (confocal) light microscopy including immunocytochemistry and Dil labeling, were applied. We confirmed that in the non-macular retina the Müller cells form a framework of rather uniform, straight 'props', aligned orthogonal to the retinal surface and associated with columnar units of neuronal cells. In the fovea, however, two different types of Müller cells were found. A first small population of cells is confined to the foveal area; the processes of these cells fail to show any peculiar relationship to retinal neurons, and run towards the inner retinal surface where they form large endfeet. Another population of Müller cells extend their processes in parallel to the Henle fibers of the photoreceptor cells; thus, the major part of these cells (including their somata) is located outside the fovea. These cells are very long and thin, and 'Z- shaped', with two parts of their processes being aligned orthogonal to the retinal surface (in ONL and OPL-INL-ILM) and one part in parallel to the surface (in the Henle fiber layer). The average diameter of the retinal area in which the Müller cells display this 'Z shape' is the same as that of full-thickness macular holes. Within this area, the number and composition of the neurons constituting a columnar unit, changes considerably dependent on the distance from foveolar center. In another series of experiments, the mechanical properties of enzymatically dissociated Müller cells were studied. The available data suggest that the peculiar morphological (and, thus, mechanical) properties of the local Müller cells may be involved in the ontogenetic mechanisms of fovea generation, and in the pathomechanism(s) of macula hole formation.

Functional consequences for the primate visual system after photodynamic therapy (PDT)

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PDT is a two-step ophthalmic procedure: Photosensitizing drug is first administered to the patient, usually i.v. After a delay (to allow for accumulation and selective binding), the central retinal area is illuminated with light corresponding to the absorption peak of the drug. It is assumed that minimal damage is present in non-pathologic tissues. To identify the changes in the primate visual system after photodynamic therapy. As part of a larger study, PDT (Diode laser 689 nm, 50 J/cm2, 600 mW/cm2, 83 sec, 4 mm spot size) with Verteporfin (Visudyne®) 6 mg/m² i.v. infusion was performed on 2 Cynomolgus monkeys (4 yrs old, F). The times of testing were: pre-PDT baseline, 1, 3, 7, 14, 22, 28, 43 days after PDT. Changes in macular reflectivity with RPE proliferation were observed. They were accompanied by hypo-perfusion of the choroidal vasculature with gradual recovery. Transient foveal thickening followed by foveal thinning and reduced function on the multifocal electroretinography (mfERG) occurred. The later was accompanied with a functional deficit in the non-treated area with gradual recovery and changes in the ratio of the signal coming from the treated area compared to the non-treated area. In a primate model, under standard clinical parameters, almost a complete block of the choroidal circulation in the treated area is observed which persists for a period of at least 6 weeks. In addition, accumulation of subretinal fluid and subsequent foveal thinning were observed. All this resulted in marked decrease in the activity of second-order neurons (as measured by mfERG), that underwent gradual recovery. The topography of the mfERG response underwent significant changes during the observed period, probably reflecting retinal functional plasticity.

The Nasotemporal Overlap of Ganglion Cells in the Human Retina

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Along the vertical retinal meridian, a zone of overlap of ipsi- and contralaterally projecting ganglion cells has been found in monkeys by retrograde labelling techniques. In the foveal region, a widening of this zone was observed and was thought to produce a 'foveal sparing' in the central visual field in humans with hemianopia. However, the functional consequences of these morphologic findings were unclear because they cannot be proven by conventional perimetry due to insufficient spatial resolution, light scatter effects and insufficient fixation control. It was the aim of this study to investigate the vertical border of the absolute field defects in patients with hemianopia by a perimetric method that does not have these shortcomings. We used a Scanning Laser Ophthalmoscope (SLO) to perform a specialized microperimetry¹ with 0.5° spatial resolution and with simultaneous fundus control to exclude eve movement artefacts. The absolute field defects of 20 patients (36 eyes) with hemianopia and without macular sparing were determined. For this purpose, vertical triplets of dots (20 arcmin diameter) were scanned onto the retina at various eccentricities from the vertical meridian and varying inter-dot distances. Altogether, a grid comprising 241 locations in each eye was tested. In 34 of 36 eyes, the seeing area extended into the blind hemifield and formed a concave field of perception. In the macular region, in 12 eyes a continuous strip of perception on the hemianopic side along the vertical meridian occurred. In none of the eyes, an additional foveal sparing was found.² A vertical strip of perception along the vertical meridian was observed in 34 of 36 eves. These results show that the nasotemporal overlap exists also in humans. The concave shape of the strip can be explained by the size and the distribution of the receptive fields of the retinal ganglion cells.

¹Trauzettel-Klosinski S, Reinhard J. The vertical field border in hemianopia and its significance for fixation and reading. Invest Ophthalmol Vis Sci 1998;39:2177–2186. ²Reinhard J, Trauzettel-Klosinski S. Nasotemporal overlap of retinal ganglion cells in humans: a functional study. Invest Ophthalmol Vis Sci 2003;44:1568–1572.

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Comparative Analysis of the Ultrastructural Characteristics of the RPE cells in Normal and Pathological Conditions

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Retinal pigment epithelial cells (RPE) are known to be the key element for the normal functioning of the photoreceptor cells. Their damage usually leads to severe disruption of the retinal functions resulting in conditions like Retinitis Pigmentosa. Expecting to find how to restore the normal functions of the RPE cells in disease affected patients, scientists are still trying to explore the ultrastructuaral characteristics of these cells. The aim of our study was to compare the electronmicroscopical characteristics of the RPE cells in normal and in pathological conditions. We used enucleated human eyes with normal retina and proliferative tissue of patients with PVR and vitreous hemorrhages, taken during vitrectomy surgery. The materials were then processed for transmission and scanning electron microscopy according to the routine techniques. The results of our investigation showed that the normal retinal pigment epithelial cells are usually polygonal in shape, with big eccentrically situated nucleus, apical microvilli and numerous in shape and size pigment granules. Very typical for the RPE cells are the specialized intercellular junctions of the zonulae occludens type. In the proliferative tissue of the PVR patients the RPE cells alter their characteristics. They retain their shape and specific type of junctions but the pigment granules disappear and a concentration of mitochondrial complexes in the perinuclear zone is seen. The cells resemble mesenchymal ones. In the cases with vitreous hemorrhage some of the RPE cells of the proliferative tissue change their characteristics further and in some of them particles of phagositosed erythrocytes can be seen. The RPE cells are cells with pluripotent characteristics. In abnormal conditions they rapidly change their ultrastructural characteristics and functions. All agents changing in some way the normal conditions in which these cells develop may be responsible for irreversible alterations in their morphology.

The Ocular Fundus Observed by Scanning Laser Ophthalmoscopy in a Patient with Enhanced S-Cone Syndrome

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To present the ocular fundus images in a patient with enhanced S-cone syndrome (ESCS) by scanning laser ophthalmoscopy (SLO). PATIENT: A 34 year-old Japanese woman whose parents were consanguineous. The patient showed mismatched electroretinogram responses to photopically balanced single flash stimuli with a larger signal to blue than red light. The central macula lacked the foveal reflex and the surface was dull. Yellow flecks and pigment epithelial atrophy were evident in a ring both at and around the vascular arcades. A deposition of faint black pigmentation was seen in the mid-peripheral retina. The ocular fundus of the patient was observed by SLO with the use of an argon blue laser (wavelength, 488 nm), a helium-neon laser (633 nm), and an infrared laser (780 nm). Argon blue laser revealed numerous black pigment spots, which were ambiguously found as a faint pigmentation by conventional ophthalmoscopy. They were enhanced with argon blue laser than with helium-neon laser. The white spots, which corresponded with the yellow flecks in a ring at and around the vascular arcades, were enhanced with helium-neon laser than with argon blue and infrared lasers. The atrophy of the retinal pigment epithelium was best shown with infrared laser. An abnormality of the retinal structure in ESCS might exist throughout the entire retina in at least some patients.

PIII and Derived PII Analysis in a Patient with Supernormal and Delayed Rod Electroretinogram Syndrome

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Supernormal and delayed rod electroretinogram (ERG) syndrome shows features of cone dystrophies. However, its rod ERGs suggested a form of cone dystrophy unlike those previously reported. The pathophysiological mechanism of this disease still remains unknown. To present ERG findings in a patient with supernormal and delayed rod ERG syndrome, and to analyze rod and cone PIII components and rod inner nuclear layer (derived PII) responses. A Japanese 11year-old girl complained of a poor visual acuity. No family members complained nyctalopia and hemeralopia. There was no parental consanguinity in her family. The corrected visual acuity was 0.7 in both eyes. No nystagmus was observed. The cornea, lens, and vitreous were clear. No abnormal finding was observed in both fundi. Kinetic visual fields measured with a Goldmann perimeter showed mild constriction to V and I targets at intensity 4e. Color vision was abnormal with no specific axis (Farnsworth D-15). Dark adaptometry showed the elevated final threshold (about 1 log unit). Full-field ERGs were recorded under ISCEV protocol. Rod and cone a-waves were analyzed using a fitting model by Hood and Birch [1, 2], and the responses of the derived PII were analyzed using a technique described by Hood and Birch [3]. In photopic ERG, responses to bright flash and 30-Hz flicker were attenuated. In scotopic ERG, b-wave was supernormal in amplitude in response to intense flashes, but smaller than normal and markedly delayed over a lower range of flash intensities. By PIII analysis. phototransductions (values of S) of both rod and cone were below the normal range. The derived PII responses for this patient were larger than the responses for normal subjects, and the onset of the responses in this patient are significantly delayed compared to those in normal subjects. The ophthalmological findings in this patient are consistent with previous publications of this disease. Although Hood et al [4] reported that the sites of disease action were beyond the outersegment (values of S were within the normal range) and involved a delay in the activation of inner nuclear layer activity, our results suggest that photoreceptors could be involved in sites of disease action in at least some patients with this disease.

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Content of kynurenic acid and activity of kynurenine aminotransferases in the human eye

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Kynurenic acid (KYNA) is the only known endogenous antagonist of glutamate receptors and neuroprotectant synthesized by kynurenine aminotransferases (KAT I and II). KYNA was identified and guantified in the rodent and avian retinas, and KYNA synthesis was suggested to play a neuromodulatory role in retinal ontogeny (Rejdak et al. Graefe's Arch. 2002; Rejdak et al. Vision Res 2003) and neurodegereration (Rejdak et al. Vision Res 2003). This study investigated KYNA contents and KAT I and II activity in structures of the human, monkey, rabbit and bovine eye. Adult human, monkey, Albino rabbit and bovine eyes were used for the study. KYNA levels were investigated with HPLC and detected fluorimetrically. The activity of KAT I and II was assayed as quantitative analysis of newly synthesised KYNA in vitro. (KYNA concentration is expressed here in pmol/g wet tissue weight.) Mean KYNA levels (± SD) in the human retina and vitreous body were 36.8±7.6 and 33.1 ± 6.2, respectively. KAT activity is expressed as KYNA synthesis in pmol/g wet tissue weight/hour. In human eyes, KAT I activity in the vitreous body was 0.57 ±0.28, KAT II – 2.56 ±0.69. KAT I activity in the retina was 3.42 ±1.17 and KAT II – 10.75±9.2. The values of KYNA and KAT observed in other mammalian species tested were in the same range. The present study found that KYNA and KAT activity are present in the structures of the human and other mammalian eyes. It is conceivable that findings in animal retina are important for studies on the role of KYNA synthesis in the development and pathology of the human visual system.

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