Progress in solving the circuit for seeing black, white, and colour

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Abstract
We have successfully treated colour blindness in an adult primate using gene therapy. Our results raise the major question of what properties of the neural circuit make the addition of a new dimension of colour vision possible. To answer this, we probed the circuit for colour vision in the rodent using a gene therapy approach in which new long-wavelength sensitivity was targeted to either S-cone or M-cone pathways. Gene therapy using cone-class specific transcriptional regulatory elements enabled us to express human L-opsin in a mosaic of either M- or S-cones. Functional consequences of the expanded spectral sensitivity were explored after therapy, by measuring the neuronal response throughout the visual system with fMRI and behavioural tests of colour vision. Dramatic expansion of colour vision to include a red-green dimension of colour vision in these rodents was observed when L-opsin was targeted to S-cones but not when targeted to M-cones. This result indicates that the novel red-green colour vision observed in animals treated with gene therapy is served by a portion of the pre-existing circuit for blue-yellow colour vision involving the S-cone pathway. This implies that the gene therapy generates expanded colour vision with changes only at receptor level, without plastic neural changes in high-order cortical or subcortical circuitry. This presumably parallels the origins of the circuit for red-green colour vision in primates, which must have arisen from a pre-existing circuit serving blue-yellow colour vision rather than from evolution of a new circuit de novo.

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Neural correlates of lightness, brightness and colour

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Abstract
Single cell recordings from the lateral geniculate nucleus (LGN) of primates to related and unrelated light stimuli have led to a model of neural mechanisms responsible for the coding of surface colour, lightness and brightness (Valberg *et al.,* 1986; Valberg and Seim, 2008). Opponent LGN cells were modelled much like retinal ganglion cells, by opponent combinations of cone inputs. The multiplexed chromatic and intensity information in LGN opponent cells can be separated and recombined in several ways to form correlates to visual perception. The representation of blackness (NCS, 1982) of achromatic surface colours, for instance, can be conjectured as a sum of outputs of parvocellular decrement cells (PC OFF-cells) of opposite opponency (D_{L-M} + D_{M-L}). The magnitude of achromatic brightness perception (Glad *et al.,* 1976) as a percept of stimuli of high relative luminance follows a function similar to the sum of responses of increment cells (PC ON-cells) of opposite opponency (I_{L-M} + I_{M-L}). These facts suggest simple ways of combining LGN inputs to the cortex in order to obtain correlates of achromatic blackness and brightness (Seim *et al.,* 2007). In both cases the differential response to chromatic stimuli is largely neutralized, whereas the responses to achromatic stimuli are enhanced.

We shall discuss some implications of these results in view of the possibility that LGN cells have a higher threshold-firing rate than retinal ganglion cells (Seim *et al.,* 2008). For instance, how can one expect such nonlinear filtering of the retinal inputs to influence colour perception?

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Contribution of signals from magnocellular and parvocellular pathways to spatial vision

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Abstract

Most vision science textbooks state that it is signals from the parvocellular (PC) pathways that contribute to fine spatial vision, and not those from the magnocellular (MC) pathways. PC cells have much smaller receptive fields and higher sampling density than MC cells, which should make them suitable for processing fine spatial information. Direct physiological measurements, however, show little difference in visual resolution of PC and MC cells (Derrington and Lennie, 1984; Crook *et al.,* 1988). The optical blur and poor achromatic contrast sensitivity of PC cells effectively enlarges their centre size beyond the size of a single cone (Lee, 2003). The MC pathway appears to be primarily responsible for performance in hyperacuity tasks (Lee *et al.,* 1993; Rüttiger *et al*., 2002) and Vernier tasks for edges or gratings of mixed luminance and chromatic contrasts (Sun *et al.,* 2003; Sun and Lee, 2004). Previous studies have employed stimuli of high luminance and chromatic contrast.

Here, the role of signals from the MC and PC pathways in spatial vision were investigated near detection thresholds. Detection thresholds for a hybrid luminance-chromatic grating (one greenish bar next to one reddish bar, both of sinusoidal modulation) were measured from three human observers and compared to detection thresholds of traditional luminance and chromatic gratings. Psychophysical performance was then compared with macaque MC and PC ganglion cell response to the same set of stimuli (Lee *et al.,* 2005). MC ganglion cells gave similar responses to luminance gratings and hybrid gratings, while PC ganglion cells gave similar responses to chromatic gratings and hybrid gratings. If signals from the MC and PC pathways can support the detection of fine spatial gratings equally well, the psychophysical detection thresholds for the hybrid grating should follow the detection envelope for luminance and chromatic gratings. To be able to discriminate between the hybrid and luminance gratings, or the hybrid and chromatic gratings, information from both PC and MC pathways must be utilized. The results showed that detection thresholds did follow the envelopes of the detection thresholds for luminance and chromatic gratings; discrimination thresholds between the hybrid and luminance gratings followed the detection curve for the chromatic grating, while discrimination thresholds between the hybrid and chromatic gratings followed the detection curve for the luminance gratings. This suggests that information from both MC and PC pathways must be utilized to elucidate fine spatial structure of objects.

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Modelling neural mechanisms for colour vision

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Abstract
It is thought that different cells types in visual cortex provide neural correlates for the perception of the colour, lightness and brightness of a surface. Using data from the lateral geniculate nucleus (LGN) of the primate, we have discussed possible neural mechanisms for achieving this goal (Seim *et al.,* 2007; Valberg and Seim, 2008). Most cone-opponent ON- and OFF-cells of the LGN can be modelled, much like retinal ganglion cells, by opponent combinations of cone inputs. Using this model, we have shown how multiplexed chromatic and intensity information in opponent increment and decrement LGN cells (ON- and OFF-cells) can be separated and recombined to give a physiological account of colour discrimination (Valberg *et al.,* 1986).

However, simultaneous recordings of 1) pre-potentials originating in retinal ganglion cells (Lee *et al.,* 1983) and 2) of the firing of the targeted LGN cell have revealed an unusual high threshold non-linearity before the LGN cell starts to fire. At LGN threshold, a pre-potential firing rate of approximately 30 impulses/s was not uncommon. The old model assumed proportionality between retinal and geniculate outputs and thus did not take this "clipping" or "cut-off" into account. A modified model will be presented that improves the modelling of the responses of LGN cells, includes the cut-off firing frequency as an important parameter, and allows us to successfully predict colour discrimination.

If clipping or cut-off is a common phenomenon related to the level of anaesthetics, as might be anticipated, one would be better off allowing the model-response to a black stimulus to take a value that, in the case of some LGN cells, would appear as a "negative" firing rate (because it happens to be below the threshold firing rate of the LGN cell). This new conjecture implies a more realistic model simulation, and it promises to improve our understanding of primate colour vision.

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Curing colour blindness with gene therapy

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Abstract

We are developing gene therapy methods aimed at targeting cone photoreceptor based disorders using a non-human primate model system. Among members of the New World primate species, Saimiri sciureus (squirrel monkey), a subset of females are trichromatic while males have dichromatic colour vision. The dichromats are an ideal model of red-green colourblindness in humans that results from the absence of either the long- (L) or middle- (M) wavelength-sensitive photopigment genes. Important components of the technology required to ultimately treat cone-based disorders in humans include: 1) primate cone targeting and efficient therapeutic transgene expression in cones, 2) non-invasively monitoring physiological function of the transgene product, and 3) assessing therapeutic effects of vector treatment using behavioural measures of visual capacity.

Here, adult male squirrel monkeys were behaviourally trained and then treated subretinally with an adeno-associated virus vector containing a human long-wavelength-sensitive opsin gene under the control of a cone-specific enhancer and promoter. Successful L-opsin expression and modified cone physiology were demonstrated in living monkeys using a custom-built, wide-field colour multifocal electroretinogram system. Comparisons of pre- and post-therapy colour vision test results obtained using an adapted version of the Cambridge Colour Test indicated that the animals gained a new sensory capacity, red-green colour vision, in response to gene therapy. The successful treatment of adult monkeys that had a colour vision defect from birth is encouraging for the possibility of using gene therapy to treat a variety of inherited vision disorders that involve cone photoreceptors in humans.

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Inherited tritan colour-vision deficiencies are rarely congenital

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Abstract

Tritan colour-vision deficiencies are inherited in an autosomal dominant manner. Affected individuals have a mutation on the S-opsin gene that give rise to different single amino acid substitutions, and five mutations are known (L56P, G79R, S214P, P264S, R283Q) (Weitz *et al.*, 1992a, Weitz *et al.*, 1992b, Gunther *et al.*, 2006, Baraas *et al.*, 2007). Those who are heterozygotes for a mutation are not always affected, whereas homozygotes always are (Weitz *et al.*, 1992a).

Tritan colour-vision deficiencies usually show incomplete penetrance and worsening colour vision with increasing age. There are, however, also reports on families where younger members have a colour-vision deficiency that is stronger than what is seen among some of the older members of the family (Kalmus, 1955).

Recent discoveries made with adaptive optics retinal imaging of two related individuals who were heterozygote with the same mutation (R283Q), but different phenotypes, have revealed that tritan phenotypes with S-opsin mutations are associated with a progressive loss of S-cones and a disruption in the regularity of the cone mosaic (Baraas *et al.*, 2007). This pattern is similar to what is seen in autosomal dominant retinitis pigmentosa (adRP), and S-opsin gene mutations are analogous to rhodopsin mutations that cause adRP. Heterozygosity for rhodopsin mutations gives rise to dominant negative interactions between normal and mutant pigments expressed in the same photoreceptor, which lead to the death of the affected rod photoreceptor (Hwa *et al.*, 1997). Henceforth, heterozygosity for S-opsin gene mutations will cause both normal and mutant S-opsins to be expressed in the same S-cone photoreceptor. This is predicted to interfere with folding, processing, or stability of the encoded opsin causing S-cones to die and subsequently a progressive S-cone dystrophy accompanied by a disruption in the regularity of the cone mosaic.

Such a mechanism can explain the seemingly contradictory reports on tritan phenotypes. Individuals that are heterozygous for the mutation are expected to exhibit normal trichromatic colour-vision until S-cones give in to the negative interactions of the mutant opsin. Congenital and stationary colour-vision deficiencies, on the other hand, are expected only in individuals that are homozygous for the S-opsin mutation. Some new results will be presented in support of this.

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Large individual differences in simultaneous colour contrast

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Abstract

A major problem in the theoretical treatment of simultaneous contrast and other context effects in colour vision is that results from different psychophysical studies are notoriously difficult to relate to each other. Accordingly, many different models have been proposed which differ not only in minor quantitative detail, but also with regard to basic questions, such as whether colour vision is fundamentally contrast-based or not (Whittle, 2003). The most frequently discussed reasons for these difficulties are critical differences in experimental variables such as stimulus size, viewing conditions, psychophysical measurement techniques and observer instructions. Much less frequent are discussions of individual differences in the susceptibility to context effects. One reason why this issue is rarely considered is presumably the more or less implicit assumption that the effects are due to hard-wired mechanisms, which are largely identical for all "colour normal" observers. If true, this assumption would seem to justify the common practice of using a relatively small number of observers. If not, however, it is quite conceivable that the differences between studies are also due to individual differences, precisely because of the small number of observers. An overly optimistic view of the inter-observer agreement appears to have survived for decades in the related research on unique hues, where common experimental practice is similar (Kuehni, 2004).

While there seems to be plenty of anecdotal evidence for large individual differences (often related to parts of a larger audience failing to see any contrast effects in demonstrations which the majority experience as striking), systematic experimental evidence is scarce (but see Cataliotti and Becklen, 2007; Bosten and Mollon, 2008). Here I present data from an asymmetric colour matching experiment similar to those reported in Ekroll *et al.* (2004) but with a larger sample of colour normal observers (no errors on Ishihara plates). While the general trend in the data is similar to that reported previously, there are also quite dramatic differences between observers. The differences are not likely to stem from different judgmental modes, since all observers were given precise instructions and were carefully debriefed afterwards. A particularly interesting feature of the data is that not only the amount of the induction effect varies, but also the shape of the matching curves. In Ekroll *et al*. (2004) we interpreted the highly nonlinear shape of the matching curves as an indication of multiple contributing mechanisms. I tentatively interpret the present data as independent inter-individual variations in the quantitative characteristics of each of the contributing mechanisms, and delineate general ideas about how this variation might be used to tease the contribution of different mechanisms apart.

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Predicting distortions of perceived distance when a scene changes size

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Abstract

Using immersive virtual reality, distortions of visual space have been explored in an expanding room paradigm (Glennerster *et al.,* 2006; Rauschecker *et al.,* 2006). Here, the centre of expansion was the cyclopean point, so all objects in the scene remained the same retinal size and position, and no single monocular image could be used to determine whether the room had changed. This paradigm creates opposing cues, some signal an expansion of the scene while others signal that the scene remains stable. It is widely accepted that the visual system combines available cues to produce a percept. Cue combination theories based on the weighted average of the reliability of each individual cue are strongly supported, particularly in the domain of surface slant (Knill and Saunders, 2003) and shape (Johnston *et al.,* 1993). However, to our knowledge these have not been applied to distance estimation and space representation.

In our experiments we used immersive virtual reality to explore the relationship between different cues to distance in an expanding environment. Physical and relative cues were manipulated to give different information about distance, thus providing conflicting signals. The "physical" cue is here defined by stereopsis and motion parallax while the "relative" cue is described as the relationship between the target and its surroundings rather than specifying a particular distance, and is thus unaffected by the expansion of the scene. In our experiments we specifically asked whether biases in a distance-matching task could be predicted from a weighted combination of the physical and the relative matched distances.

Observers wore a wide field of view head mounted display. They were surrounded by a virtual brick room and judged the change in distance of a floating object presented in two intervals. The scene changed in size between intervals (by a factor of between 0.25 and 4). When the target was presented close to the observer, the pattern of biases suggested the use of physical cues, and when the target was close to the walls observers matched the distance more in terms of relative cues. In separate experiments we explored whether biases in this distance-matching task could be predicted. We determined the relationship between physical and relative cues by measuring thresholds, and hence reliability, for detecting a change in object distance where these cues were separated. Thresholds for the physical task were best when the target was close to the observer and, as expected, relative thresholds improved with proximity to neighbouring objects.

We show that biases in distance judgements change significantly according to proximity to other objects and that biases can be predicted by measuring thresholds from a physical and a relative task. Our results lead to interesting implications that may challenge traditional views of space perception.

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Spatial resolution in responses of single units in the LGN of cat changes dynamically during brief visual stimulation

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Abstract
Sharpness of vision depends on the resolution of details conveyed by individual neurons in the visual pathway. In the dorsal lateral geniculate nucleus (LGN) neurons have receptive fields with centre-surround organization, and spatial resolution may be measured as the inverse of the centre width.

We studied dynamics of the centre width of single LGN neurons in anaesthetized cats during the response to light or dark spots presented with durations (400-500 ms) corresponding to natural inter-saccadic fixation periods. Centre width was estimated from a series of spatial summation curves made for successive 5 ms intervals during the stimulation period.

In nonlagged neurons the centre was wide at the start of the response, but shrank rapidly over 50-100 ms after stimulus onset, whereupon it widened slightly. Thereby, the spatial resolution changed from coarse-to-fine with average peak resolution occurring transiently ~70 ms after stimulus onset. The changes in spatial resolution did not follow changes of firing rate; peak firing appeared earlier than maximal spatial resolution. We suggest that the response initially conveys a strong but spatially coarse message that might have a detection and tune-in function, followed by transient transmission of spatially precise information about the stimulus. Experiments with spots presented inside the maximum but outside the minimum centre width suggested a dynamic reduction in number of responding neurons during the stimulation, from many responding neurons initially to fewer ones as the centres shrink. This implies a coarse-to-fine change also in the recruitment of responding neurons. Lagged neurons, which get their initial visual response suppressed by intrageniculate inhibition, lacked the dynamic changes in receptive field organization.

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Mathematical models for spatiotemporal receptive fields in cat LGN cells incorporating dynamic receptive-field-centre shrinkage

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Abstract
The difference-of-Gaussians (DOG) model is a simple and popular descriptive model for the spatial receptive field organization of retinal ganglion cells and LGN cells, and used in combination with an appropriate temporal function, may account for many features of the spatiotemporal receptive field properties of these cells (Rodieck, 1965; Dayan and Abbott, 2001). The model can be refined by allowing for different temporal functions for the DOG centre and surround terms, typically assuming a delayed or a more slowly activating surround term (Dayan and Abbott, 2001). The parameters of such models have typically been determined by comparison with experiments based on drifting-grating or "white-noise" stimuli (DeAngelis *et al.,* 1995).

Ruksenas *et al.* (2007) recently performed a thorough investigation of the temporal development of the receptive field of cat LGN cells following stimulus onset. They used flashing spot stimuli, and a striking finding was that the receptive-field-centre width of nonlagged neurons was large at the start of the response, but shrank rapidly over 50-100 ms after stimulus onset, whereupon it widened slightly.

Here, we investigate various new descriptive models for the spatiotemporal receptive field accounting for the observations by Ruksenas *et al.* (2007) as well as new unpublished data. These descriptive models consist of a phasic part essentially describing the receptive field shrinkage and a tonic part describing the "steady-state" response with a constant receptive-field-centre size. The tonic part is modelled as a slowly onsetting DOG, while two variations are considered for the phasic part: In the first model a sum of two spatial Gaussians with different temporal functions is used (Gazeres *et al.,* 1998), while in the second model a novel function type with the time-dependent receptive-field-centre size as an explicit model parameter is considered. Example results from fitting the candidate receptive field models with experimental data will be presented, and the pros and cons of the suggested models will be discussed.

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Feedforward and feedback contributions to temporal signal processing in LGN: A modelling study

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Abstract
We derive and investigate a firing rate model describing feedforward and feedback effects on temporal signal processing for relay cells in the lateral geniculate nucleus (LGN). The model for LGN relay ON-cells includes (i) feedforward excitation and inhibition (via intrageniculate interneurons) from retinal ON-cells and (ii) feedback input from cortical ON- and cortical OFF-cells. The model incorporates both direct excitatory cortical feedback effects and indirect inhibitory feedback effects via inhibitory neurons in the thalamic reticular nucleus (TRN) or LGN (Einevoll and Plesser, 2002; Yousif and Denham, 2007).

After constructing a general model system in terms of Volterra integral equations (Nordbø *et al.,* 2007) we derive a single differential delay equation with absolute delay governing the dynamics of the system. This simplification of the resulting differential equation model is allowed for by our choice of temporal kernels in the feedback loop, as well as, but to a lesser extent, nonlinear firing rate functions.

We investigate both the impulse-response of the model and the response to drifting gratings, but we find the impulse-response to be better suited than the drifting-grating frequency response to differentiate between feedforward and feedback contributions to the temporal signal processing in LGN. Exploration of the parameter space of the model shows that both purely feedforward and feedback models can account for the values of the specific measures of the impulse-response waveform reported in the literature (Cai *et al.,* 1997; Usrey *et al.,* 1999). That is, the normalized rebound magnitude, the biphasic index, and the time of maximal response. However, we find that feedforward and feedback contributions can be separated by the value of the cross-correlation between the biphasic index and time of maximal responses. For the pure feedforward model we find a strong anti-correlation between these two measures ($|r| > 0.9$) in contrast to the lack of correlation in the case of models including feedback ($|r| < 0.1$).

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Sensory receptors in human extraocular muscles and their potential role in oculomotor control

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Abstract
Previous publications have promoted the view that the precise gradations in motility of the eyes, which are a prerequisite for development of binocular vision, rely on the complement of sensory receptors in the extraocular muscles (Steinbach and Smith, 1981; Kim *et al.,* 2006). This notion is supported by the large number of various specialized nerve endings which can be observed either within the bulk of the muscle (Ruskell, 1989) or at the musculotendinous interface (Sodi *et al.,* 1988). The presence of these receptors suggests that extraocular muscle activity can be monitored and readjusted, matching the system of motor control in skeletal muscles. However, the structural organization of extraocular muscle receptors departs to such a degree from their somatic counterparts that it is legitimate to question whether they have the same functional role.

There are large variations in the complement of sensory receptors throughout the animal kingdom (Ruskell, 1978; 1979), but in the extraocular muscles of humans there seem to be only two potential sources, the muscle spindle and the tendon receptors. The latter type of receptor has been found at the myotendinous junction of several species and consists of a sensory axon terminating on a multiply innervated slow contracting muscle fibre (Bruenech and Ruskell, 2000). Recent publications have argued that some of the neural elements may represent motor endplates (Blumer *et al.,* 2001), yet some uncertainty remains. Muscle spindles are also present in the extraocular muscles, but due to certain peculiar features their proprioceptive capacity has been questioned (Bruenech and Ruskell, 2001). Again, some uncertainty remains.

The purpose of this study was to analyse the structural organization of the receptors in human extraocular muscles in order to obtain a better understanding of their functional role in oculomotor control and/or in the development of binocular vision anomalies.

Samples of human extraocular muscles were selected from stock and all sections containing muscle receptors were selected for further analysis. The age of the subjects ranged from 2 months to 90 years and both sexes were included. An image analysis system (Imaris Imageaccess) was attached to a light microscope (Nikon Optiphot) in order to obtain a more detailed analysis. Digital three-dimensional reconstructions of the most prominent morphological features were obtained from serial sections of several spindles. These features included narrow periaxial spaces, fragmented intrafusal fibres and other peculiar features which could potentially interfere with the functional principals upon which this type of mechanoreceptor is based. The digital reconstruction provided additional information about variations in spindle shape, which most likely would have been missed by conventional light microscopic observations.

The proprioceptive capacity of the muscle spindles in human extraocular muscles has previously been questioned based on the presence of several peculiar morphological features. The current study confirmed these observations and the preliminary results have added credence to the notion that the muscle spindles in human extraocular muscles are not the main source of proprioception. Further analysis of the spindle and tendon receptors is now in progress.

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Reduced eye blinking during VDU work: Does it matter, and what can be done?

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Abstract
Visual discomfort has a high prevalence among VDU workers (Horgen and Aarås, 2003). According to Sheedy *et al*. (2003) eyestrain is the most frequent symptom reported by computer users. Many studies have found a reduced eye blink rate when performing VDU work compared with other less visually demanding tasks (e.g. Acosta *et al.* 1999; Patel *et al.* 1991). The eye blink rate at rest as reported in the literature typically varies widely (12-19 blinks per minute). Tasks such as listening, talking, arithmetical exercises and silent rehearsal increase the blink rate. The blink rate while working with computers has been shown to fall below that of resting conditions (e.g. Patel *et al.* 1991).

Here, we evaluate eye blink rate in presbyopes and young adults during VDU work. Eye blink rate was evaluated with normal and small text size, both under ideal visual conditions and under conditions with glare sources in the vicinity of the VDU. We performed laboratory and field studies on presbyopes and young adults to investigate whether the luminance levels in the vicinity of a VDU and the size of the characters on the screen had any influence on the eye blink rate (Helland *et al.,* 2007), and to compare eye blink rate in a lab situation with real life situations (Helland *et al.,* 2008a, 2008b). All studies were performed on groups of healthy experienced VDU users. A digital video camera (Sony DCRTRV22; 25 frames per second) and a video-editing program (Pinnacle Studio DV 8) were used to record and investigate the eye blink rate. The videos were later analysed by visual inspection, and the frequency of eye blinks was measured using a mechanical counter.

The laboratory studies show a marked reduction in eye blink rate for VDU work compared with a typical rest situation. This applies both for young adults and presbyopes. A reduction from approximately 21-24 blinks per minute (group mean) during easy conversation to approx. 5-10 blinks per minute during visually demanding VDU work was found. This was true whether the character size on the screen was "normal" or "fairly small", and whether the work was done under ideal visual conditions or with glare sources in the vicinity of the screen.

The results from our studies confirm a marked reduction in eye blink rate for VDU work. The reduced blink rate is likely to be one of several possible causes of dry eye symptoms and visual discomfort experienced by VDU workers. Possible problems due to a reduced blink rate and prophylactic actions to avoid problems will be discussed, and brief details on ongoing and possible future research will be given.

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A multi-level framework for measuring perceptual image contrast

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Even though several previous studies have been carried out (Peli, 1990; Tadmor and Tolhurst, 2000; Michelson, 1927; King-Smith and Kulikowski, 1975; Burkhardt *et al.,* 1984; Whittle, 1986), the problem of measuring perceptual contrast in complex images or natural scenes is not solved (Pedersen *et al.,* 2008).

Here, we propose and discuss a novel approach for a multi-level contrast measure in images. It addresses the problem of multi-level measure recombination of the computational pyramid of previous algorithms with different local spatial measures of contrast, including a parameterized way of recombining local contrast maps with chromatic channels. In particular, we have focused on two previous contrast measures proposed by Rizzi *et al.* (2004; 2008). The RAMMG measure (Rizzi *et al.,* 2004) works in the following steps: 1) It sub-samples the image to various levels in the CIELAB colour space. 2) For each level, local contrast is calculated by calculating the average difference between the lightness channel value of each pixel and the surrounding eight pixels, thus obtaining a contrast map of each level. 3) A recombination of the averages for each level results in the final overall measure.

Rizzi et al. (2008) proposed a new measure, RSC, which works with the same concept of pyramid levels as previously (Rizzi *et al.,* 2004), but it executes Difference-of-Gaussians (DOG) (Tadmor and Tolhurst, 2000) neighbourhood-contrast calculation for every pixel in each level, rather than from the surrounding eight pixels. The computation of DOGs is applied not only to the lightness channel, but also to each of the chromatic channels separately. For both algorithms, the analysis has focused on the following four points: pyramid construction in CIELAB colour space, neighbourhood local contrast calculation, local contrast maps, and global measure.

In order to obtain only one contrast measure as default for each image, the problem of how to recombine the various levels has to be considered. In fact, as default, the averages of all the planes are averaged again, with uniform weights, in order to obtain a unique number. According to the literature (Meur *et al.,* 2005; Rizzi *et al.,* 2008), some spatial frequency channels may contribute more than others to the final perceived contrast. We propose an automatic way to recombine the levels according to the image content. In order to test the soundness of the new method, a subjective test has been carried out, and the results have been compared with algorithms proposed by other researchers. Tests and results are presented and discussed in detail.

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Motion sensitivity across the visual field in ageing and in patients with visual field loss

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Abstract

The World Health Organization indicates that as many as 180 million people are blind or visually impaired, and that this number is expected to double in the next 20 years due to the increase in the ageing population. A leading problem for people with low vision is the visually-guided task of mobility, which gets steadily worse with advancement of visual field loss (e.g. Turano *et al.,* 2004). The primary causes of irreversible visual loss in industrialized countries are age-related macular degeneration (AMD) and primary open angle glaucoma (POAG). In AMD high-resolution central vision is lost with spared peripheral vision, whereas in POAG peripheral vision is lost and central vision is generally spared. Self-motion and the motion of objects in the real world give rise to characteristic patterns of retinal motion, known as optic flow (e.g. Koendrink, 1986). The perception of optic flow is important for self-motion, estimating time until collision with other objects or persons, and for safe navigation in our surrounding environment. We have previously shown that patients with peripheral visual field loss show impaired sensitivity to complex optic flow patterns (Falkenberg and Bex, 2007). This study investigated the sensitivity to motion and radial optic flow dot patterns as a function of retinal location in normal ageing and in patients with central or peripheral field loss, with a view to determine functional deficits in relation to mobility.

Apparent speed, speed discrimination sensitivity and global motion coherence thresholds (MCT) were measured as a function of retinal eccentricity, with random radial Gaussian dot patterns. In the MCT task observers were required to discriminate the direction of motion (expansion or contraction). In the speed discrimination task observers discriminated which of two intervals contained the fastest moving stimulus, and in the apparent speed matching task the observers adjusted the speed of a central target to match that of a peripherally-viewed target.

The results showed that MCT and speed discrimination sensitivity were invariant of retinal eccentricity and location for all observers, however there was a reduction in sensitivity with age. Patients with POAG showed reduced MCT compared to age-matched normals and patients with AMD. Speed discrimination was impaired in both patient groups. The speed matching experiment showed that expanding and contracting dot patterns were perceived as moving significantly faster in the periphery than centrally, and that this effect increased with age and with central visual field loss.

The observation that moving dot patterns containing the same distribution of element speed can appear to move at different global rates suggests that distinct mechanisms process different patterns of complex motion. In spite of this, motion coherence thresholds and speed discrimination sensitivity were invariant across the field and both were relatively constant for different global motion patterns. This implies that patients with central or peripheral visual field loss would not be expected to show selective impairment in optic flow-based tasks (such as mobility), simply on the basis of the location of their scotoma.

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