

# PERCEPTION

VOLUME 29

SUPPLEMENT



**23rd European Conference on Visual Perception  
Groningen, 27–31 August 2000**

**ABSTRACTS**

# Twenty-third European Conference on Visual Perception

## Groningen, The Netherlands

### 27 – 31 August 2000

## Abstracts

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### ECVP2000 would like to thank the following people, organisations and companies for their assistance, suggestions and contribution to the success of ECVP2000:

Tiziano Agostini	Fenna Fonck-Pot	Brian Rogers
Geoffrey Avrich	Walter Gerbino	Stella de Rooy
Jonathan Briggs	Jitty Jaarsma	Pieter Schiphorst
Tanja Coeckelbergh	Sijtske Klont	Mark Tant
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Iota AB EyeTrace Systems	Province of Groningen	University of Groningen (RuG)
Koninklijke Nederlandse Academie van Wetenschappen	Rotterdamse Vereniging Blindenbelangen	Visio
	School of Behavioral and Cogni- tive Neurosciences of the University of Groningen (BCN)	VisionScience.com

### ECVP

The European Conference on Visual Perception is an annual event. Previous conferences took place in:

1978 Marburg (D)	1986 Bad Nauheim (D)	1994 Eindhoven (NL)
1979 Noordwijkerhout (NL)	1987 Varna (BUL)	1995 Tübingen (D)
1980 Brighton (GB)	1988 Bristol (GB)	1996 Strasbourg (F)
1981 Gouvieux (F)	1989 Zichron Yaakov (ISR)	1997 Helsinki (FIN)
1982 Leuven (B)	1990 Paris (F)	1998 Oxford (GB)
1983 Lucca (I)	1991 Vilnius (LIT)	1999 Trieste (I)
1984 Cambridge (GB)	1992 Pisa (I)	
1985 Peñíscola (E)	1993 Edinburgh (GB)	

Next year's conference is planned to take place in Kuşadasi (Turkey)

ECVP2000 logo by Sjouke Heins

## SUNDAY

## SPECIAL SYMPOSIUM

## EYE MOVEMENTS AND ATTENTION

► **Visual attention: the active vision perspective**

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A frequently emphasised fact concerning visual attention is the ability to attend covertly to a location in the visual field without directing the eyes to that location. Based on this, the 'mental spotlight' metaphor has been widely prevalent and has given rise to much experimental work. However, an implied corollary of the suggestion is that covert attentional movements give rise to some form of mental scanning during visual tasks. It is argued that this account is not satisfactory. An alternative account, termed active vision, develops from the fact that overt eye scanning occurs several times each second. Detailed analysis of information intake during text reading and during visual search shows that no additional covert scanning occurs in these cases beyond what is involved in programming the eye movements. Attentional processes also permit pre-processing information in the visual periphery at the location to which the eyes are to be directed. This allows more rapid and efficient eye scanning. Covert attention to peripheral locations thus acts to supplement, not substitute for, actual movements of the eyes.

► **Neural correlates of inhibition of return in the monkey superior colliculus**

D P Munoz, M C Dorris, R M Klein¶ (Department of Physiology, Queen's University, Kingston, Ontario K7L 3N6, Canada; ¶ Department of Psychology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada; fax: +1 613 533 6840; e-mail: [doug@eyeml.queensu.ca](mailto:doug@eyeml.queensu.ca))

Inhibition of return (IOR) is a phenomenon whereby subjects are slower in responding to targets presented at previously cued locations. A number of studies have suggested that the superior colliculus (SC) is a necessary neural structure for the generation of IOR.

Our goal was to test this proposal by recording the extracellular activity of visual- and saccade-related neurons in the SC while monkeys performed an IOR paradigm. Visual stimuli were presented in the following sequence: a central location, a peripheral location, the central location, and a final peripheral location. The central fixation point, which required constant visual fixation, remained illuminated throughout the paradigm until the presentation of the final saccadic target. In this paradigm, final saccadic reaction time (SRT) was slowest when the first stimulus was presented at the same location as the final saccadic target (ie IOR) and this was correlated with reduced visual-related activity in the SC.

These findings suggest that oculomotor and visual history influence SRT through motor preparation and visual processing, respectively, at the level of the SC.

► **Inhibition of saccade return**

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Tasks such as reading or visual search consist of series of saccades. We have investigated to what extent saccades that are made within a series of self-paced movements are influenced by preceding movements. Here we present an analysis of the duration of the fixations that precede saccades.

We found that fixations before so-called 'return saccades' (saccades returning to the previously fixated position) are considerably longer (up to 40%) than other fixations. We have called this phenomenon 'inhibition of saccade return' (ISR) in analogy to 'inhibition of return' (IOR) of covert shifts of spatial attention. ISR is present when return and regular saccades are mixed in one trial, and seems to be reset after each saccade. The effect is strongest at the previously fixated target, and decreases gradually from there in a radial fashion. The radius of the area where ISR is found is about 4 deg. By studying responses to moving targets we found that ISR is encoded in head-fixed rather than in retinal coordinates.

ISR can be seen as a low-level short-term memory for locations already fixated. We discuss the relation between ISR and IOR (are they manifestations of the same phenomenon?), as well as the neurophysiological basis of ISR.

► **Attentional capture and oculomotor control**

J Theeuwes (Department of Cognitive Psychology, Vrije Universiteit, De Boelelaan 1111, NL 1081 HV Amsterdam, The Netherlands; fax: +31 20 444 8832; e-mail: [j.theeuwes@psy.vu.nl](mailto:j.theeuwes@psy.vu.nl))

Recently a new paradigm has been developed which makes it possible to study the relationship between top-down and bottom-up controlled attention and eye movements (Theeuwes et al, 1998 *Psychological Science* **9** 379–385; 1999 *Journal of Experimental Psychology: Human Perception and Performance* **25** 1595–1608). Observers were required to make a voluntary, goal-directed saccade to a colour singleton target while in some trials a new irrelevant object with abrupt onset appeared somewhere in the display.

Goal-directed eye movements towards the colour singleton were disrupted by the appearance of the visual onset. In many instances, before the eye reached the singleton target, it first moved to the visual onset. New findings show that eye movements with a short latency go to the onset while eye movements with a long latency go to the target. On the basis of inhibition of return, it is concluded that the onset always captures attention.

In line with neurophysiological evidence it is suggested that there are two parallel pathways involved in the generation of saccades: a subcortical pathway depending on the superior colliculus, and a cortical pathway depending on the frontal eye field.

► **Saccades, attention, and subjective gaze**

H Deubel, W X Schneider (Institute of Psychology, Ludwig Maximilians University, Leopoldstrasse 13, D 80802 Munich, Germany; fax: +49 892 180 5211; e-mail: [deubel@psy.uni-muenchen.de](mailto:deubel@psy.uni-muenchen.de))

It is now well established that saccadic eye movements are preceded by shifts of attention to the saccade target. Considerably less is yet known about the precise spatiotemporal properties of these attention shifts and about their subjective consequences.

In the first part of this presentation, we focus on the dynamics of the attentional deployment before saccades. In dual-task experiments, subjects had to discriminate between letters presented at various temporal intervals before goal-directed saccadic eye movements. The data show that the time course of the attention shifts depends on the type of task and on whether saccades are triggered endogenously or exogenously.

In the second part we demonstrate a stunning illusion. Subjects were presented with a brief test stimulus at various points in time before or after a saccade and had to report where they were looking when the test stimulus was presented. They reported they were fixating the saccade target location already long before the actual saccade occurred. We conclude that the perceived direction of gaze shifts a long time before the eyes actually move; subjects mistake shifts of visual attention for shifts of the eyes.

## SPECIAL SYMPOSIUM

### COMBINING CUES

► **Combination of cues and priors in depth perception**

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A large number of visual cues may be used to estimate distance, depth, surface orientation, surface shape, and so on. In this talk I survey recent behavioural work on depth cue combination, emphasising questions in four overlapping areas:

(i) *Representation*. Is 3-D scene geometry represented in terms of depth, surface orientation (the first derivative of depth), surface curvature (the second derivative)? Does the representation depend on the task or available cues?

(ii) *Combination rule*. Are depth estimates from these multiple cues combined linearly (a weighted average)? Are there more complicated cue interactions?

(iii) *Scaling and constancy*. To what extent do observers display constancy (of depth, slant, curvature, etc) with changes in viewing distance and gaze direction? What are the signals observers use to compute distance and gaze direction? Are these (retinal and extra-retinal) signals combined on the same principles as the depth cues?

(iv) *Optimality*. Does the combination rule satisfy an optimality constraint? For example, are cue weights chosen to maximise the reliability of the final estimate? Is the combination rule implementing a Bayesian decision rule, and does a Bayesian analysis help us to understand the prior constraints brought to bear on the problem of depth estimation?

[Supported by NIH grant EY08266 and AFOSR grant 93NL366.]

► **Are cues really averaged?**

M A Hogervorst, E Brenner¶ (Perception, TNO Human Factors, Kampweg 5, NL 3769 DE Soesterberg, Netherlands; ¶ Department of Physiology, Erasmus University Rotterdam, PO Box 1738, NL 3000 DR Rotterdam, The Netherlands; fax: +31 34 635 3977; e-mail: [hogervorst@tm.tno.nl](mailto:hogervorst@tm.tno.nl))

When several cues provide information about a single property of an object of interest, the information from the different cues has to be combined in some manner. One possibility that has gained considerable support is weighted averaging.

Assuming that discrepancies between cues are due to errors, weighted averaging can provide the best guess about the property of interest. In this process, information about discrepancies between cues is lost. We examined whether we can demonstrate such loss of information in subjects' settings in a matching task.

Subjects set pairs of cues that were considered to provide information that was likely to be averaged: texture and binocular disparity for judgments of slant; expansion and changing disparity for judgments of motion in depth. We reasoned that the loss of information should manifest itself in a negative correlation between the cues, and in more variability within each cue when both had to be set than when only one did. Neither of these predictions was confirmed by the data.

► **Texture and motion in depth perception**

J M D O'Brien, A Johnston (Department of Psychology, University College London, Gower Street, London WC1E 6BT, UK; fax: +44 20 7679 7576; e-mail: [ucjtjmo@ucl.ac.uk](mailto:ucjtjmo@ucl.ac.uk))

Both texture and motion can be strong cues to depth, and estimating slant from texture cues can be considered analogous to calculating slant from motion parallax.

A series of experiments was conducted to determine the relative weight of texture and motion cues in the perception of planar surface slant when both texture and motion convey similar information. Stimuli were monocularly viewed images of planar surfaces slanted in depth, defined by texture and motion information that could be varied independently. Slant discrimination biases and thresholds were measured by a method of single-stimuli binary-choice procedure. When the motion and texture cues depicted surfaces of identical slants, the depth-from-motion information neither reduced slant discrimination thresholds, nor altered slant discrimination bias, compared to texture cues presented alone. When there was a difference in the slant depicted by motion and by texture, perceived slant was determined almost entirely by the texture cue. The regularity of the texture pattern did not affect this weighting.

Implications for models of cue combination with different types of motion and texture stimuli are considered.

► **Motion from structure: the graceful construction of 3-D percepts from 'conflicting' motion parallax and stereo cues**

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The visual system is able to recover the shapes of 3-D objects from changes over time in the retinal image, by assuming object rigidity (structure from motion). In an artificial display, stereo signals can be added that indicate some other shape. Faced with such a stimulus, what is a poor visual system to do? Since there is a nonrigid object that is consistent with all of the signals, the visual system could choose to construct a percept of that object. In other words, the stimulus contains a conflict only to the extent that the Bayesian prior for rigidity is stronger than the visual system's faith in its own stereo measurements.

If faith in stereo is low, modified weak fusion (Landy et al, 1995 *Vision Research* **35** 389–412) applies, and the percept is something like a weighted average. But if faith in stereo is high, the visual system very sensibly interprets the motion as nonrigid: motion from structure. The latter is an instance of strong fusion [Clark and Yuille, 1990 *Data Fusion for Sensory Information Processing Systems* (Boston, MA: Kluwer)]. The transition from weak fusion to strong fusion can be used to predict how often objects in the real world are rigid.

► **Visual, haptic, and vestibular cue integration**

H H Bühlhoff (Department of Psychophysics, Max Planck Institute for Biological Cybernetics, Spemannstrasse 38, D 72076 Tübingen, Germany; fax: +49 7071 601-616; e-mail: [heinrich.buehlhoff@tuebingen.mpg.de](mailto:heinrich.buehlhoff@tuebingen.mpg.de))

In the past we have studied the integration of different visual cues for depth perception. Recently we have begun to study the interaction between cues from different sensory modalities. In a recent paper (Ernst et al, 2000 *Nature Neuroscience* **3** 69–73) we could show that active touch of

a surface can change the visual perception of surface slant. Apparently, haptic information can change the weights assigned to different visual cues for surface orientation.

In another multisensory integration project we could show that visual and haptic information about the shape of objects can lead to a common representation with cross modal access [Bülthoff et al, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) 398].

Now we are investigating another input into our spatial representation system. Using a 6-DOF Motion Platform we are studying the interaction between the vestibular and the visual system for recognition. I report on first experiments that show that we can derive reliable information about position and velocity of a moving observer from the vestibular system. This information could be used for spatial updating in recognition tasks where the recognition of objects or scenes is facilitated by knowing the position and viewing direction of the observer.

► **Combining retinal and extra-retinal signals in the perception of depth from motion**

T C A Freeman (School of Psychology, Cardiff University, PO Box 901, Cardiff CF10 3YG, UK; fax: +44 29 2087 4858; e-mail: [freemant@cardiff.ac.uk](mailto:freemant@cardiff.ac.uk))

Because smooth-pursuit eye movements add a component of motion to each point in the image, they physically alter some retinal motion cues to depth. For instance, a slanted plane moving at right angles to an observer produces a gradient of retinal motion that is the sum of relative motion (eg shear) and translation. If the eye tracks the plane, the translation disappears. This raises the question of how the visual system judges the tilt and slant of the plane during eye pursuit. Estimating relative motion alone cannot suffice because the sign of relative motion must be compared to the sign of translation to recover tilt. Similarly, its magnitude must be compared to the speed of translation to recover slant. Retinal estimates of relative motion are therefore combined with extra-retinal estimates of translation to judge depth during pursuit. I discuss two consequences of this signal combination. First, tilt is correctly perceived when relative motion is presented during eye pursuit, but appears ambiguously tilted when the eye is stationary. Second, perceived slant increases during pursuit. The latter finding is the result of the well-known mismatch between retinal and extra-retinal estimates of object speed.

► **Individual differences in cue integration**

D Buckley (Department of Ophthalmology and Orthoptics, University of Sheffield, 'O' Floor, Royal Hallamshire Hospital, Glossop Road, Sheffield S10 2JF, UK; fax: +44 114 276 6515; e-mail: [d.buckley@sheffield.ac.uk](mailto:d.buckley@sheffield.ac.uk))

We have argued that monitor-displayed stimuli contain conflicts that are not present in equivalent real-world stimuli and this can give rise to different patterns of cue integration for the two types of stimuli (Buckley and Frisby, 1993 *Vision Research* **33** 919–933). One such conflict is that between vergence and accommodation. For example, for a stereogram of a depthful scene the vergence changes required for stereo fusion may be at odds with accommodation, which will be determined by monitor distance in order to prevent image blur. I show that this vergence/accommodation conflict may explain why an observer's tonic accommodation level is a very good predictor of her/his cue reliance in cue conflict stereograms and also their latency in seeing complex stereograms. In an object-recognition experiment it has also been found that how much an observer relies on motion, stereo, texture, and outline cues in monitor displays can predict his/her recognition performance.

Most cue-integration models are actually models of cue integration in monitor-displayed stimuli. These models do not take into account oculomotor factors or individual differences in such factors. Many applications that use monitor displays, such as endoscopy and virtual reality, would benefit from more inclusive models.

► **Cross-cue-interaction and the motion correspondence process**

M F Bradshaw, P B Hibbard (Department of Psychology, University of Surrey, Guildford GU2 5XH, UK; fax: +44 148 325 9553; e-mail: [m.bradshaw@surrey.ac.uk](mailto:m.bradshaw@surrey.ac.uk))

Image motion is a primary source of visual information about the world. Before this information can be used, however, the visual system must establish which image features originate from the same physical object in space. This is known as the motion correspondence problem.

We investigated whether cross-cue matching constraints contribute to the solution of this problem, which would be consistent with the fact that many directionally selective cells in the visual cortex also respond to additional visual cues. We measured the maximum displacement limit ( $D_{\max}$ ) for 2-frame apparent-motion sequences.  $D_{\max}$  increases as the number of elements in such sequences decreases. In the displays used here, however, the total number of elements was always constant while the number of a subset of elements, defined by a difference in contrast polarity, binocular disparity, or colour, was varied.  $D_{\max}$  was found to increase as the number of elements distinguished by a particular cue was decreased.  $D_{\max}$  was affected by contrast polarity



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for all observers, but only some observers were influenced by binocular disparity, and others by colour information.

These results demonstrate that the human visual system exploits local, cross-cue matching constraints in the solution of the motion correspondence problem.

## THE PERCEPTION LECTURE

### ☛ Let there be motion ...

W A van de Grind (Department of Neuroethology and Comparative Physiology,  
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A single photoreceptor can measure temporal contrast, two of them can measure spatial contrast and ... motion. No doubt, motion is the most informative of these elementary measures and it might have been instrumental in the evolution of visual systems. There is not an aspect of highly evolved vision that does not benefit from motion and several visual capacities only exist because 'everything flows' (panta rhei).

The importance of motion for vision first became apparent after scientists in the nineteenth century succeeded in generating convincing motion stimuli in the laboratory. Natural motion information is still difficult to bring to the laboratory, since all exploratory movements of the subject would have to be fed back instantaneously to the virtual-reality device. Simple motion stimuli, with names from alpha to omega and each in first to  $n$ th order varieties, have already uncovered some of the principles underlying motion-based vision (heading, shape-from-motion, etc). No doubt a lot is yet to come and a final insight is not in sight.

I review in biased fashion what has been accomplished in the previous millennium and attempt to illustrate basic findings with flows on a flat screen. I hope the visuence (= visual equivalent of 'audience') is moved by this and prepared to transform screen-flow into mindflow. That would be a great start for a new millennium of research on motion vision or derived-from-motion vision (the rest).

## MONDAY

### VISIO LECTURE

#### ☛ Deficits of visual perception in children with cerebral visual impairment due to early brain damage

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Since the CT studies of van Nieuwenhuizen et al (1983 *Lancet* **I** 868–869; 1984 *Behavioural Brain Research* **14** 143–145) on the cerebral basis of visual disabilities in persons with neonatal complications, the interest in cerebral visual impairment has grown steadily. However, research on visual perception in these children has lagged behind considerably compared to the study of visual acuity, fields, etc. This is not in the least part due to a lack in methodology and instruments applicable to children who exhibit multiple disabilities. Particularly, the fact that non-verbal intelligence seems more vulnerable to early brain damage than verbal intelligence obscures interpretation, because this results in lower performance on visual perceptual tasks as well as on non-verbal intelligence subtests.

I discuss how to disentangle these disabilities, and show that visual perceptual and non-verbal intelligence impairment co-occur as separate deficits. I show that early brain damage causes selective impairments in visual perception and that the damage must be bilateral. Frequently, the accompanying visual acuity and field reductions are too mild to qualify as low vision. In fact, at least a third of children with physical disabilities without a diagnosis of visual handicap suffer from visual perceptual impairment.

### ORAL PRESENTATIONS

#### FACES

##### ◆ Why is the eye–mouth distance overestimated by more than 30%?

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Several previous studies have stressed the importance of configural information in face recognition. In this study we investigated the *perception* of configural information in faces. The task consisted in adjusting the length of a line in order to match the inter-eye distance or the eye–mouth distance of a simultaneously presented face in 0°, 90°, 180°, and 270° of planar rotation.

Experiment 1 revealed that the eye–mouth distance was overestimated by more than 30% and the inter-eye distance by about 15%. The superposition of a white line on the facial distances led to a substantial reduction only for the adjustments of the perceived eye–mouth distance (experiment 2). In both experiments the adjustments for the inter-eye distance were dependent on orientation following the pattern of the horizontal–vertical illusion (HVI) which was measured in experiment 3. In experiment 4 we revealed that removing the eyes and the mouth did reduce the large overestimations found in experiments 1 and 2. This effect was additive to the pattern of the HVI. In contrast, removal of the nose led to even larger overestimations.

Possible relations to perceptual illusions are discussed (Müller-Lyer, Oppel–Kundt, surface information, and effect of the oval context).

##### ◆ Configural face processes use high spatial frequencies

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When the top and bottom halves of different familiar faces are aligned, each half is more difficult to identify owing to configural interference from the other (Young et al, 1987 *Perception* **16** 747–759). We manipulated the visual medium of the face to ascertain the information used by configural processes.

Observers viewed gray-scale images of the top half of one of six famous male faces paired with the bottom half of a different face. The bottom half-image was (a) gray scale, (b) low-pass filtered, (c) high-pass filtered, (d) contrast inverted, or (e) two-tone. Face halves were either aligned or misaligned. Observers pressed one of six keys to identify the face in the top half. Response times and error rates were measured. When the bottom half of a face was gray-scale, observers were indeed slower to identify the top half of a face if it was aligned—configural interference. Similar interference was observed with high-pass-filtered faces, whereas it was absent when the bottom half of the face was low-pass filtered, two-tone, or contrast inverted.

These results suggest that configural information for face processing is carried by high spatial frequencies.

◆ **Perception of facial expressions: A relationship between affective attributes and configural measures**

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How do components of the face work together to be recognised as emotional expression? We explore one possible explanation—that affective attribution is mediated by facial configuration.

Stimuli were prototypes of seven basic expressions [Ekman and Friesen, 1976 *Pictures of Facial Affect* (Palo Alto, CA: Consulting Psychologists Press)] and photographic-quality morphs interpolated between them. They were quantified according to the FACEM system (Pilowsky and Katsikitis, 1994 *Journal of Affective Disorders* 30 61–71). Subjective affective attributes were derived by applying multidimensional scaling to dissimilarity data, elicited with a sorting procedure.

Values along four dimensions were obtained: D1 distinguished positive from negative expressions; the other three dimensions were interpreted as attributes differentiating ‘Surprise/Fear’, ‘Anger’, and ‘Disgust’. Multiple and bivariate regression analyses were used to relate the dimensional values (coordinates) for the stimuli to their FACEM properties. D1 (‘Valence’) appeared to be primarily a ‘lower face’, or mouth dimension. D2 (‘Surprise/Fear’) was associated with measures of eye openness and mouth curvature; D3 (‘Anger’) with lip thinness and lowered eyebrows; and D4 (‘Disgust’) with lip thickness and eye closing.

The findings support the view that decoding of affective attributes of facial expressions is founded on configural (ie relational) information.

◆ **Judgments of facial expressions studied with the use of band-pass-filtered morphed photographs and eye movements**

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I investigated the effect of global and local features of the face on the judgments of facial expressions using band-pass-filtered morphed photographs. I recorded eye movements by the method of corneal reflection while subjects were viewing the photographs of morphed faces. Upright or inverted morphed faces were shown under three conditions with different spatial-frequency ranges. A 2AFC task was employed to judge the facial emotions, ie happy versus neutral, surprised versus neutral, sad versus neutral, or disgusted versus neutral.

High-spatial-frequency components played an important role in the recognition of surprised faces under both upright and inverted conditions; local features were effective in judging the faces. The performance dropped for the inverted version of happy faces; subjects used local features as well as facial lines in judging happy faces. There were great differences in the performance between the upright and inverted versions of happy faces in the low-spatial-frequency range. Subjects demonstrated a considerable amount of fixation on facial lines (furrows, wrinkles, and subtle creases of the face) to judge facial expressions.

These results suggest that facial lines have low-spatial-frequency components, ie global features.

## EYE MOVEMENTS AND SPATIAL (MIS)LOCALISATION

◆ **Localisation during smooth-pursuit eye movements: different retinal areas are integrated with gaze signals from different moments in time**

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To localise an object in space, the object’s retinal location has to be integrated with the gaze direction from the same moment in time. It is usually assumed that all retinal input is integrated with a single gaze signal. During smooth-pursuit eye movements, the images of static objects move on the retina. Mateeff et al (1991 *Vision Research* 31 2235–2237) showed that in this situation perceptual latencies are shorter for motion toward the fovea than for motion away from it. Such differential latencies should disrupt position constancy during pursuit. Nevertheless, everyday experience tells us the visual world is stable.

To find out how position constancy is maintained during smooth pursuit, we studied where subjects localised visual targets presented either ahead of or behind the fovea. We presented either static targets, which have different latencies in these two zones, or flashed targets, which

do not. Our results show that static stimuli are localised correctly irrespective of their retinal location. Flashes ahead of the fovea, however, are perceived too far ahead, whereas flashes behind the fovea are localised correctly. This suggests that the brain maintains position constancy by integrating different retinal areas with gaze signals from different moments in time.

◆ **Prior knowledge influences the mislocalisation of a flashed target during smooth pursuit**

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Human subjects misjudge the position of a target that is flashed during a pursuit eye movement. They mislocate it in the direction in which the eyes were moving.

We investigated whether prior knowledge about when the flash will appear helps subjects judge its position. We compared three conditions. In the first condition, subjects pursued a moving target which flashed somewhere along its trajectory. After the presentation, they indicated where they had seen the flash. The second condition was the same as the first but now the subjects judged after seeing the whole stimulus twice, with the flash at the same position. In the third condition, again a single target flash was shown, but now at 500 and at 1000 ms before the target flash two flashes of a different colour were shown. The mislocalisation was considerably smaller when the subjects judged after seeing the stimulus twice. This was not so when the target flash was preceded by two coloured flashes.

We conclude that prior knowledge can influence the perceived position of a flashed target, but we still do not understand the underlying mechanism.

◆ **Mislocalisation under flash-stimulus retinal-stabilisation condition**

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In previous studies, mislocalisation of a brief flash stimulus presented temporally near a saccade was explained with the cancellation theory (Honda, 1993 *Vision Research* **33** 709–716). That is, mislocalisation is caused by the mismatch of the sluggish extra-retinal eye position signal (EEPS) and the quick displacement of the stimulus image on the retina (retinal signal, RS).

In the present study, the effect of the absence of retinal stimulus displacement was investigated. The subject was asked to make a rightward saccade (8 deg). In the retinal- and space-stabilisation conditions, the flash stimulus was presented at the same positions on the retina and in space throughout the saccade, respectively. In the retinal-stabilisation condition, the time course of mislocalisation showed its displacement from the right to the left (backward phase) near the saccade in time as seen in the previous space-stabilisation studies. The size of the backward phase was larger than in the space-stabilisation condition.

This result suggests that the backward phase is caused by the EEPS rather than the RS.

◆ **Perisaccadic visual stimulation changes perceived target positions**

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Two types of perisaccadic localisation errors for flashed objects have been described: first, a uniform shift in the direction of the saccade [Cai et al, 1997 *Nature (London)* **386** 601–604] and, second, a compression of space around the saccade goal [Ross et al, 1997 *Nature (London)* **386** 598–601]. Compression occurs only when a visual reference is available after a saccade [Lappe et al, 2000 *Nature (London)* **404** 892–895]. Here we show a third effect: when presented briefly, the saccade target itself may appear shifted towards a subsequently flashed object.

Subjects viewed a dark screen displaying a horizontal white line. During rightward saccades (12.8 deg) towards a briefly (50 ms) flashed target, a vertical luminous bar was flashed (8.3 ms) at one of four locations around the saccade goal. In blocked trials, subjects reported the perceived position of the bar or the perceived position of the saccade goal. Even though saccade amplitudes were always the same, perceived location of the saccade goal was shifted towards the subsequently flashed bar. Likewise, the position of the bar appeared shifted towards the saccade goal. This suggests that perisaccadic compression should be interpreted as a misperception of the relative position of the flashed bar and the saccade target.

[Supported by HFSP]

## BRIGHTNESS, LIGHTNESS, AND SPATIAL STRUCTURE

### ◆ The appearance of brightness and lightness

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In simplest terms, brightness is the appearance of illumination and lightness is the appearance of objects. The aim of the experiment reported in this paper was to measure the appearance of three visible faces of a real cube in outdoor illumination. Three faces of the cube were painted white and the other three were painted different shades of gray. When the observer sees three white faces, the appearance of illuminations is being measured. When the three visible faces have different reflectances, then the appearance of objects and illuminations is being measured.

The results of matching experiments show that humans make the same match for radiance changes caused by illumination as for those caused by reflectance. The results are consistent with the hypothesis that maxima in the field of view change slowly with radiance and that all areas darker than the maxima change rapidly with radiance.

Humans can successfully identify changes in whites due to illumination. They also can identify changes due to reflectance of darker objects. However, they cannot discriminate between dark appearances caused by either illumination or reflectance.

### ◆ Brightness differences in an illusory cube

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It has been shown that subjective contours of the Kanizsa type go along with measurable differences in brightness (Dresp, 1993 *Vision Research* **33** 759–766). There has been a longstanding debate whether simultaneous contrast is the cause of this brightness change. In the case we are presenting here there cannot be any form of simultaneous contrast.

We measured brightness differences in a 3-D picture resulting from two flat, homogeneously illuminated 2-D forms. The outlines of two disparate hexagons give rise to the clear perception of a 3-D cube, which is even clearer and more stable if the cube is rotating. The perception of the 3-D picture goes along with a clear distinction of the three planes forming the visible path of the cube. We measured the luminance threshold at the three planes with a very refined threshold measurement procedure: MUEST. The threshold of the upper plane is indeed different from the thresholds of the side planes. Furthermore, a control condition in which the outlines were presented stationarily and without disparity led to equal thresholds in the three areas.

### ◆ No lightness induction emerges from real objects

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As shown by Adelson (1993 *Science* **262** 2042–2044) lightness induction is affected by spatial arrangement. A wall of blocks depicted in two slightly rearranged ways produces very different effects. When looking as if viewed through transparent light and dark filters, the effect is much stronger than in textbook demonstrations. However, without apparent illumination differences between blocks, the effect is considerably reduced. Still, it is not clear why such a residual lightness induction effect still remains. We suggested that, if the same wall of blocks were made real, the effect would, probably, disappear completely. This hypothesis was tested in the following experiment.

Thirty-five observers were presented with (i) Adelson's pictures, and (ii) a 3-D wall of blocks made from cardboard so that one of the pictures was an exact 2-D representation of it. Observers were asked to evaluate lightness of the same diamond-shaped targets inserted in all three displays using a Munsell grey scale. The cardboard wall of blocks was found to produce no significant lightness induction effect, whereas the picture of the same blocks produced a strong lightness illusion. We conclude that lightness induction is, perhaps, a pictorial phenomenon which does not occur in natural vision.

### ◆ Influences of motion and depth on lightness induction—an illusory transparency effect

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We investigated how lightness induction is affected by motion and depth differences between the test surface and its surrounding. The task was to adjust and match the lightness of two vertically

separated stationary grey test disks, which were presented against a textured background of numerous inducing disks arranged on a uniform grey field. Inducers in upper field were white or black, those in lower field were black or white, respectively. Across trials, inducers were either stationary or moving horizontally. In experiment 1, test disks had either zero or crossed disparity relative to inducers; in experiment 2, they had zero or uncrossed disparity, but the test disks occluded inducers in each monocular image.

In experiment 1, lightness induction was weakest when the test disks were segregated by both motion and disparity, strongest when there was no motion nor disparity, and intermediate with either motion or disparity alone. However, not all observers conformed to this ordering. In experiment 2, lightness induction was strongest when the test disks were segregated by both motion and disparity. Lightness induction is thus clearly affected by motion and depth. The difference between the results of the two experiments can be explained by what we term 'illusory transparency': the textured background appeared to extend transparently over the test disks.

## VISUAL SEARCH AND EYE MOVEMENTS

### ◆ Visual search in depth

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We present three experiments investigating eye-movement responses during visual search for orientation, stereo depth, and their conjunction. In all experiments subjects searched for a rectangle situated in one of eight points equidistant from fixation. Eye movements were labelled as correct if they fell in a 45 deg sector centred on the target.

In the first experiment, subjects searched for a vertically oriented rectangle in the presence of horizontal distractors. In the second experiment, subjects searched for rectangle which appeared at a different depth plane to the distractors. In the third experiment, subjects searched for a target defined by both orientation and depth, eg a vertical target in front of the fixation plane. It was found that 75%, 49%, and 35% of initial eye movements were made to the target in search for orientation, depth, and their conjunction respectively. The results show that the information provided in these three experiments was not sufficient to program accurate eye movements to the extent that they can be said to have popped out. These results suggest that the information used to generate target-elicited eye movements in a search task may differ from that used in target detection.

### ◆ Accumulation of information across saccades during visual search depends on how far the first saccade lands from the target

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An ideal-observer analysis has shown that task information increases from the first to the second saccade during search (Eckstein et al, 1999 *Perception* **28** Supplement, 111a). Is this increase caused by longer processing of the initial-fixation retinal image or by new information from the fixation image after the first saccade? To address this, we measured the accuracy of second saccades (for incorrect first saccades) in two subsets of trials: those in which the first saccade decreased target retinal eccentricity and those in which it increased it.

Three observers searched for a bright disk (SNR: 11.5) among dimmer disks (SNR: 8.4) in white noise within a 10AFC task (task SNR: 3.1). The disks were equally spaced at 5.9 deg eccentricity from an initial central fixation. Saccadic accuracy was determined by using a closest-distance criterion. The accuracy of second saccades was significantly ( $p < 0.05$ ) higher for trials in which the first saccade landed closer to the target than those in which it landed farther away: 0.599 vs 0.388, 0.620 vs 0.458, 0.493 vs 0.275, for the three observers. This result suggests that a new image, sampled after the first saccade, contributed to the increase in second-saccade information, with the added information a function of target retinal eccentricity.

### ◆ Visual search of heading direction

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When we move along we frequently look around. How quickly and accurately can we gaze in the direction of heading? We studied temporal aspects of heading perception in expanding and contracting patterns simulating self-motion. Center of flow (CF) eccentricity was 15 deg. Subjects

had to indicate the center of flow by making a saccade to it. A temporal constraint on the response time was introduced, because stimuli were presented briefly (1 s).

On average, subjects needed two saccades to find the CF. Subjects underestimated the eccentricity of the CF. The systematic radial error ranged from  $-2.4$  to  $-4.9$  deg. The systematic tangential error was small (about 0.5 deg). The variable radial error ranged from 2.7 to 4.6 deg. We found a relation between saccade onset time and saccade endpoint error. Saccade endpoint error decreased with increasing saccade onset time, suggesting that saccades were often fired before the heading processing had been completed.

From the saccade onset times, saccade endpoint errors and an estimate for the saccadic dead time (interval prior to the saccade during which modification is impossible: 70 ms) we estimated the heading processing time as 0.43 s.

[This work was supported by HFSP RG 34/96B and ALW-805-33.171-P]

◆ **‘Attentional landscapes’ and phasic changes of fixation duration in picture perception**

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Visual search is commonly thought to consist of two stages: a preattentive, automatic, parallel stage, and an attentive, controlled, serial stage. The preattentive stage is considered to be data-limited. The attentive stage is capacity-limited: only few aspects or objects are processed. During this stage only, fixation durations can be voluntarily controlled.

In various experiments on picture perception, a number of stimuli irrelevant to the actual perceptual activity was found to prolong the current fixation duration. This prolongation is phasic in nature and largely independent of the type of task.

In a study on selection as a function of the search task, subjects viewed paintings in three conditions: free viewing, object-naming, and interpreting social relations between the shown characters. Visual and auditory distracting stimuli led to instantaneous increases in fixation duration, without affecting the scan path. On applying a filter rule based on the dissociability of preattentive and attentive fixations, the distribution of attention over the picture—‘attentional landscape’—showed significant differences for type of task but not for the presence or type of distracting stimulus.

The results show that switching between preattentive and attentive processing is reflected in oculomotor behaviour. This has important implications for the interpretation of eye-movement data as indices of attention in perceptual tasks.

## POSTER SESSION 1

### (ELECTRO)PHYSIOLOGY AND NEUROTRANSMITTERS

● **Decoding of visual stimulus features from the intrinsic activity of retinal-ganglion-cell populations**

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Information processing in the visual system is a parallel process. The message that ganglion cells communicate to the brain is highly contextual: features that a ganglion cell encodes are meaningful only in the context of signals produced in other ganglion cells.

We studied how turtle retinal ganglion cells encode simple patterns of retinal illumination using a 100-microelectrode array. It was inserted into the ganglion cell side of the retina, which was stimulated periodically with spatial-, intensity-, and colour-modulated light. Simultaneous single-unit and multi-unit activity was recorded from all electrodes.

Bitmap snapshots of the population activity within given time intervals were used as input vectors for a perceptron neural network. The perceptron was trained and tested to classify the stimulus features. The external stimulus trigger (external information) or the maximum of the estimated population spike density function (internal information) were used to determine starting points for the bitmaps. Stimulus features could be estimated reliably from the bitmaps obtained by both methods. Stimulus estimation ranged from 65% to more than 95% correct, depending on the exact procedure. Larger bitmap time intervals gave better results. We conclude that it is possible to reliably decode stimulus features by using exclusively the intrinsic activity of ganglion cell populations.

- **A VEP study on the processing of the representation of shape**

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We studied the characteristics of transient visual evoked potentials (VEPs) associated with the figure salience by manipulating the spatial alignment of Gabor patches. The components P1 (120–130 ms), N1 (160–190 ms), and P2 (220–260 ms) obtained in the experiments were largely influenced by the spatial alignment. The results showed that closure figure affected N1 and P2 components and that figure salience in the closed patterns affected the latency and amplitude of N1 component.

These results might reflect the intermediate level of bottom–up (symmetry computation) and top–down (cognitive operation) processes.

- **Benzodiazepine effects on primed picture-fragment completion**

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Contour versions of line drawings of everyday objects were developed in which all interior features were removed. Contours could be built gradually, starting from different curvature singularities: maxima ( $M^+$ ), where positive curvature is strongest, minima ( $M^-$ ), where negative curvature is strongest, or inflections ( $I$ ), where curvature goes through zero when changing from positive to negative. Identification thresholds were determined for 66 contours (22 in each condition). In general, they were lowest when starting from  $I$  (44.5% of the contour needed), highest when starting from  $M^-$  (54.8%), and intermediate for  $M^+$  (46.9%).

In a previous study (Wagemans et al, 1998 *Psychopharmacology* **138** 326–333), we discovered that lorazepam but not diazepam (both benzodiazepines and thus GABA-agonists) caused an increase in all of these thresholds. In the present study, the thresholds were lower because all subjects saw all pictures before (with or without the name). However, the priming effects did not differ in these two conditions and they did not interact with drug group or singularity condition.

This suggests that the benzodiazepine effects on picture-fragment completion are to a large extent caused by their effects on implicit and explicit memory and much less due to perceptual contour integration as such.

## ATTENTION, TEXTURE, AND VISUAL SEARCH

- **A new powerful method for the study of feature binding in conjunction visual search**

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A new method is proposed which reveals how different perceptual attributes (colour, orientation, size, etc) of an object are bound together after they have been separately identified. The basic idea of this method is to present information about separate features such as colour and orientation that conjunctively define the target at different instants of time.

Presenting information about two features one before another provides advance partial information and consequently extra time for processing the visual feature that has been presented earlier. All changes in the search time can be explained by a simple growth-processes (accumulator) model according to which a target is identified when two separate neural activities embodying the recognition of the defining features have both reached a fixed activation level.

A paradoxical situation has been found in which processing of a visual attribute (orientation) in isolation is slower than when the second attribute (size) is processed at the same time.

- **Time course of asymmetric visual search**

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The efficiency of visual search, where an observer looks for an object within a scene, may depend on which of two elements is the target and which is the distractor. These search asymmetries are seen as revealing the underlying nature of feature dimensions in visual system. The less efficient target–distractor mapping often shows large increases in response time over display size, a pattern that has been interpreted as evidence for a serial visual-attention mechanism.

The serial model of search has recently been challenged by a signal detection model of visual-search accuracy in which decreases in detection accuracy reflect increased sources of errors,



not serial processing. We directly compare the two models using a procedure that measures the full time course of processing for an easy search for a C among Os or a more difficult search for an O among Cs with display sizes of 4 or 12 items. Target detection was measured at processing times between 0.05 s and 1.9 s.

In brief, in displays without eye movements, the time course of both kinds of search is little affected by display size. Parallel models provide a parsimonious account of these data without assuming asymmetry of processing.

- **Visual search when targets and distractors are connected or unconnected**

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Subjects searched for simple targets among heterogeneous distractors, roughly half of which were similar to the targets, and the remainder were dissimilar. The parts were either separated ('separate' condition), or the target and each similar distractor (relevant shapes) were joined to a dissimilar distractor ('joined' condition).

In experiment 1, we manipulated the relative sizes of the stimuli: in one condition all three shapes were the same size, whereas in the other the dissimilar distractors were bigger than the relevant shapes. When all shapes were the same size, search slopes (the cost of adding each distractor) were the same for the separated and joined conditions. When the relevant shapes were smaller than the dissimilar distractors, however, search was more efficient in the separated condition than in the joined condition. In experiment 2 we introduced a new condition where each relevant shape appeared to occlude a portion of the irrelevant distractors. Performance was as slow as in the joined condition, and again slower than in the separated condition.

These results show that redundant information around regions of interest sometimes (experiments 1 and 2) but not always (experiment 1) impairs visual-search efficiency. Implications for models of visual search are discussed.

- **Ocular behaviour analysis for the interpretation of seismic images**

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To detect presence of oil in the underground, geologists need to analyse seismic images. Seismic images are an echography of the underground; the examination needs training and experience to interpret the images. Geologists have to analyse a large volume of seismic data in a short time. We study human visual perception during scanning of seismic images in order to help specialists to perform some of their tasks faster.

We compare the visual behaviour of experts with that of less-skilled geologists. We are also interested in image regions that attract the gaze of the geologists. In order to detect these seismic zones automatically, we aim to establish a correlation between ocular index (fixation durations – zone) and image index. The best-fitting image attribute in our case is the texture feature. This attribute codes both the energy and the geometry of the structure.

Our results show that the ocular behaviour of experts is different from that of less-skilled geologists. Experts have longer fixations and are less attracted by the energy of the seismic region. These results confirm that texture analysis represents a good first visual exploration for seismic images.

- **Effect of attention on the detection and identification of masked Gabors**

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The present study is related to recent ideas that the classical paradigm of orientation and spatial-frequency channels should be complemented with an attentional mechanism (Foley and Schwarz, 1998 *Journal of the Optical Society of America A* **15** 1036–1047; Lee et al, 1999 *Nature Neuroscience* **2** 375–381).

The effect of attention on the detection and identification of vertically and horizontally oriented Gabors superimposed on obliquely oriented masking Gabors with the same spatial frequency was studied. Attention was manipulated by varying the set size in a visual-search experiment. The psychometric functions were measured for two tasks (detection and identification) and for two set sizes (1 and 8). In the detection task the set size had little effect on the performance. In the identification task increasing the set size from 1 to 8 resulted in a large decline in performance. It is concluded that in the conditions of divided (low) attention direct access to labelled

orientation-selective channels is lost or greatly reduced. The detection task in this condition is probably mediated by some other (luminance- or texture-discriminating) mechanism.

- **Visual-search and attention shifts between layers in the 3-D environment defined by linear perspective**

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We studied visual-search task in superimposed and overlapping 2-D (frontoparallel) and 3-D (perspective) layers. The items on the layers were on invisible grid surfaces, which were immediately perceived as distinct 2-D and 3-D subjective surfaces. The subjects' task was to search for a feature or conjunction target object appearing in either of the layers. The number of distractors in the layers was manipulated. The target objects in the 3-D layer appeared in four different sizes (distances). Experimental sessions differed in the information provided to the subjects before search as to the relevant layer.

During conjunction search with the target always in the 2-D layer, subjects successfully ignored the 3-D layer. With target in the 3-D layer, the superimposed 2-D layer was not disregarded, and its impairing effect was negatively related to the number of items. Search with target in either layer elicited longer detection RTs, but not their sum. Rather, increased RTs were related proportionally to those elicited by single-layer search in the layer where the target happened to be located. For feature search, there was also a cost to search in both layers. Taken together, the results suggest that layer segregation precedes both feature and conjunction search.

## BINOCULAR AND SPATIAL VISION

- **The time course of hierarchical grouping in discrete periodic patterns**

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Perceptual grouping of spatially dispersed elements is an essential precondition for making sense of visual scenes. This process was isolated in psychophysical experiments involving perceptually multistable dot lattices (Kubovy and Wagemans, 1995 *Psychological Science* **4** 225–234). After 300 ms presentations of two-dimensional dot arrays, participants indicated the perceived orientation of dot clustering by selecting one out of four alternatives. A similar procedure was used to investigate perceptual organisation of dot lattices with an intrinsic hierarchical organisation (Kubovy et al, 1998 *Cognitive Psychology* **35** 71–98).

The stimulus set was extended to include particular discrete periodic patterns [Grunbaum and Shephard, 1989 *Tilings and Patterns* (New York: W H Freeman)]. Response items were chosen so as to reflect the grouping clusters emerging from the dot patterns. These are situated on several hierarchical levels. The dot fields were shown in 300 ms and 600 ms presentations. The goal was to examine how the ratio of grouping strengths of several mutually exclusive responses would vary for different stimuli and how they would evolve through time. The complexity level of the organisation did not interact with the presentation duration. This suggests that the selection of an interpretation in these stimuli does not depend on a gradual build-up from parts to wholes.

- **The combination of disparity and motion information and perceived shape**

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Through the combination of binocular disparity and retinal motion cues veridical shape information can be recovered (Richards, 1985 *Journal of the Optical Society of America A* **2** 343–349). Although most evidence is inconsistent with this model (eg Tittle et al, 1995 *Journal of Experimental Psychology: Human Perception and Performance* **21** 663–678; Brenner and Landy, 1999 *Vision Research* **39** 3834–3848), there is some empirical support (eg Johnston et al 1994 *Vision Research* **34** 2259–2275). However, the latter study featured only horizontally oriented cylinders rotating about vertical axes. This may be a special case, as disparity and motion are related by the same image transformation.

We investigated whether veridical shape can continue to be recovered under more general conditions using an ACC task. In five conditions, cylinders were defined by disparity, and/or two-frame or multi-frame motion (presented at 30 cm, 90 cm, and 150 cm). Horizontally or vertically oriented cylinders were rotated about horizontal or vertical axes to vary the relationship between disparity and motion. Observers' settings were biased for the disparity and two-frame motion stimuli although veridical shape judgments were made under all conditions for combined-

cue stimuli. Therefore disparity and motion can be combined to recover veridical shape and this is not restricted to the particular stimulus conditions used by Johnston et al.

- **Comparison at a distance: orientation and luminance**

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We investigate how precisely the visual system can compare the attributes of stimuli presented at large separations in the field. Previously we have shown that neither contrast discrimination nor spatial-frequency discrimination deteriorate as the separation of stimuli is increased up to 10 deg—even though in primary visual cortex the lateral connections become systematically sparser with distance.

We report here analogous investigations of orientation discrimination and luminance discrimination. The stimulus patches were sectors of an annulus (1.5 deg width) centred on the fixation point. The centres of the two stimuli on each trial lay on an imaginary circle of 5 deg radius; the separation between their centres was varied in different blocks. Stimulus duration was 100 ms for orientation discrimination and 150 ms for luminance discrimination. Orientation discrimination showed rather little change with separation of the patches and, as in the case of spatial frequency, we are led to question whether the comparison is performed at a level where orientation is represented by the activity of individual neurons. In the case of luminance, performance is superior when the stimuli are abutting, and here the subject may be using a difference signal that is generated at a retinal level.

- **Binocular vision and transparent depth layers**

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Transparent images are becoming more and more common owing to new technologies such as head-mounted, head-up displays and screen reflections. Such displays are only comfortable in use when the gaze direction and depth are at the voluntary control of the user.

We have investigated the ability to maintain steady convergence at a particular depth plane in the presence of a transparent distractor image. The test consists of a dynamic task that requires the exact convergence, accommodation, and fusion of the target object—a disparity-defined pacman. The observers' task was to indicate the direction of the gap as quickly as possible after the appearance of the pacman. The reaction time was recorded as a function of (i) the depth difference with the (transparent) plane containing the distracting stimulus and (ii) the time-onset difference with the distractor image.

Results show that the reaction time increases with the target–distractor disparity and with temporal delay of the target. This increase reflects the time needed to restore binocular fusion at the target depth. Therefore, it can be applied as an objective measure that is indicative of eye strain.

- **Developing a transformational approach to visual perception**

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A transformational approach to visual perception is presented, in which image structure is encoded in the parameters of those transformations which produce an output that is maximally symmetric with the current input.

This approach is illustrated in two experiments. In the first, the two-dimensional or three-dimensional perception of regular polyhedra is shown to be related to their respective symmetries. In the second, the method of serial reproduction is used to show that memory for shape evolves towards greater symmetry. Results are also presented for a computer program, dubbed SMART (Symmetry Maximising Array using Random Transformations), which simulates perceptual organisation. The program subjects image elements to multiple random transformations. The resulting symmetries are then used to select those transformations that best capture structure in the image.

In addition, these mappings provide a continuously varying measure of relative symmetry. The operation of SMART is illustrated in applications to constrained and random arrays, Glass figures, and the detection of hidden symmetric targets. In the transformational approach, perception is seen as producing hypotheses concerning the way objects develop or have been constructed. This perspective changes the traditional boundary between perception and cognition. It also has implications for the way in which information is remembered.

## COLOUR AND BRIGHTNESS

### ● The perfect retinal mosaic

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What should be the design of the retinal mosaic for the perfect human eye? For direction events of opposite polarity of the two red and one green twin unit of a trion, six fibers are needed in the optic nerve. Another four fibers are required for the red, green, yellow, and white events.

About a million fibers can serve a hundred thousand trions. Seven trions host one blue cone. In a perfect geometrical arrangement, the odd green twins are oriented along circles that are concentric with the fovea. The red twins occupy a clockwise spiral and an anticlockwise spiral that cross these circles at angles of 60° and 120°. The units at 10 deg eccentricity are about 10 min of arc long. Each circle then contains about 316 green units. The rod-free central fovea contains 5000 trions. Beyond 1 deg from the centre there are 95 000 trions accommodated on about 300 circles. The ratio of radii of successive circles is 1.0152. The distance between circles at 10 deg eccentricity is then neatly  $0.0152 \times 600 = 9$  min of arc!

### ● The theoretical analysis of dichromatic vision with an ATD colour model

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In this work we have tried to reproduce a set of curves characterising dichromatic subjects: spectral sensitivity, wavelength and colorimetric purity discrimination thresholds, isochromatic lines, confusion, and neutral points. The curves have been computed with the use of the ATD95 colour-vision model (Guth, 1995 *Proceedings of the SPIE* **2414** 12–26), which at present is the only model which includes, even if not always accurately, the different stages of visual processing (receptor gain control, compression, and two opponent stages).

The model has been modified to simulate dichromatic vision, testing three different hypotheses: first, that cone input corresponding to the missing pigment is zero; second, that L-cones in protanopes contain the M-pigment and the M-cones in deuteranopes contain the L-pigment; and finally, that cone inputs are modified as in the previous hypothesis, but also one of the opponent channels, T in protanopes and D in deuteranopes, is suppressed. We have compared the resulting curves with experimental data, with unequal success. The third hypothesis seems the more adequate one. Nevertheless, curves for trichromats are quite well reproduced on the assumption that the input of S-cones is zero.

### ● Accommodation control intended to reduce luminance artifacts at isoluminous-colour borders

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Chromatic aberration can create luminance artifacts at isoluminous-colour borders. We tested whether observers, when instructed to equally defocus abutting red and green, could accommodate as to yellow, so that luminance artifacts would be reduced.

Accommodation was measured at a viewing distance of 38 cm with an autorefractometer and a vertically divided red/green isoluminous patch (8 deg) with a centred black fixation cross presented on a colour monitor. Under three instructions, observers ( $n = 13$ ) focused on either red, or green, or the middle, equally defocusing both. Accommodative performance was compared with that with monochrome red, green, and yellow.

With the monochrome stimuli, accommodation differences were: red 0.11 D > yellow 0.14 D > green, confirming that accommodation is contingent on target colour. With the compound stimulus, accommodation differences depended on the instruction given: red focused 0.12 D > red/green equally defocused 0.10 D > green focused (all  $p < 0.02$ ). Under the equal-defocus instruction, absolute accommodation matched that for the monochrome yellow (cf Lee et al, 1998 *Ophthalmic & Physiological Optics* **19** 223–235).

Observers were able to focus the target intentionally. The red/green-equal-defocus instruction resulted in a 'compromise' accommodation comparable to that for yellow. This implies that instructive control of accommodation may serve as a means for reducing luminance artifacts at isoluminous-colour borders.

- **Peak detection and probability summation models for RT to stimuli described in DKL space**  
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Reaction times (RTs) to 72 stimuli modulating a white surround along nine directions in DKL space [Derrington et al, 1984 *Journal of Physiology (London)* **357** 241–265] were fitted by a peak-detection model and a probability-summation model. The first model assumed the existence of an achromatic and two chromatic channels, whose responses were the stimuli DKL components scaled to the non-zero components of the incremental thresholds of each isolated channel. Channel RT was assumed to have a Piéron-type dependence on channel response. With the second model, a global response was computed with Quick's formula (Quick, 1974 *Kybernetik* **16** 65–67) from the responses of the chromatic and achromatic channels, with the use of different summation exponents ( $q = 1$  to 6). RT was computed as a Piéron-type law of the global response.

Both models fitted our data equally well. The RT vs wavelength curves measured with the classical hue substitution and incremental paradigms were also correctly predicted by both models, with only slight differences between summation exponents. Nevertheless, only the peak-detection model was consistent with experimental results for equally visible stimuli (Schwartz, 1995 *Journal of the Optical Society of America A* **12** 2089–2093), predicting shorter RTs in the neighbourhood of 565 nm, detected by the achromatic channel.

- **Studies on stimulus processing in haploscopic colour matching**

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In the haploscopic colour-matching paradigm different configurations consisting of an infield with a background are exposed to both eyes so that the different stimuli fuse into an integrated percept. This percept is composed of two particular infields on one homogeneous background. While the two backgrounds and one of the infields (the test field) were kept fixed, the subjects' task was to adjust the remaining infield to match the test field. Von Kries's receptor-gain-control model predicts that the relation between matching stimuli with fixed pairs of backgrounds can be described by affine mappings. In contrast, the octant model (Mausfeld and Niederee, 1993, *Perception* **22** 427–462) assumes different processing of incremental and decremental stimuli. More specifically, it predicts deviations from linearity at the transition between incremental and decremental stimuli. This would lead to 'kinks' in the lines fitting the data within each channel. Actually those 'kinks' did occur frequently in our data.

A generalised model of the matching behaviour is proposed, which includes the aspect of interocular differences. In the light of the data obtained, it is discussed whether the assumption of 'independent' monocular colour codes holds for the paradigm of haploscopic colour matching.

## EYE MOVEMENTS

- **Visual scanning in recent-onset schizophrenic patients: Relationship between impaired scan patterns and deficits of working memory and visual attention**

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Our purpose was to relate visual scanning patterns to neuropsychological test performance in a group of young, recent-onset schizophrenic patients. Scanning patterns of patients were compared with those of normal controls.

Thirty-four schizophrenic patients (aged 21 years) and nine age-matched healthy controls were tested. The neuropsychological test battery included tests assessing working memory, selective attention, and motor speed. Horizontal and vertical eye movements were recorded by the double-magnetic-induction (DMI) method. In the visual scanning paradigm, the subject was requested to freely scan, for 20 s, a drawing depicting a mother with child. Test parameters included mean fixation duration and percentage of time the subject fixated the mother's face, the child's face, or other aspects of the drawing.

The schizophrenic patients spent more time examining the faces of the mother and child and significantly less time examining the extraneous features of the drawing than normal controls ( $p < 0.02$ ). Within the patient group, better working memory was related to increased visual attention to the remainder of the drawing ( $r = 0.42$ ;  $p = 0.02$ ). The findings suggest that restricted scanning patterns in schizophrenic patients are related to impaired functioning of the prefrontal cortex, ie the primary locus of working memory.

- **Visual – auditory interstimulus contingency effects: Prosaccades versus antisaccades**

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The probability of presenting a visual target stimulus at a certain location was varied depending on the occurrence of an accessory auditory stimulus (interstimulus contingency). The auditory stimulus was presented at the same or opposite horizontal eccentricity (15 deg) as the visual target via a virtual auditory display. In a focused-attention task with visual catch trials, subjects were asked to make an eye movement to the visual target every time the auditory stimulus was present, and to use this accessory stimulus as a possible, but unreliable, cue for the location of the visual target. The same instruction was given in an antisaccade task, where the subjects were asked to make an eye movement opposite to the visual target.

In both tasks, saccadic reaction times (SRTs) were shorter when the subjects responded to a high interstimulus contingency (80%) than to a neutral condition (50%). According to preliminary results in the antisaccade task, the SRTs were longer when the subjects responded to the rare cases (20%) where the auditory stimulus appeared opposite to the visual target. This study indicates that subjects have to actively control their eye movements to be able to utilise the probability relation between the two stimuli.

- **Trade-off between memory size and gaze-shift frequency**

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Studies of ‘change blindness’ revealed that only a small part of the visual information is processed from moment to moment. In everyday situations, we do visual tasks with frequent fixations and gaze shifts. Is the visual system constrained to take this frequent-access strategy by the limited visual memory? Are other strategies available?

We analysed the gaze behaviour of subjects who were checking a pair of pictures in which several differences were embedded. This picture-checking task was done with two settings: (i) adjacent pictures and (ii) horizontally separated pictures. Subjects’ eyes were tracked with a limbus tracker. Their gaze pattern varied completely between the two conditions. The subjects shifted their gaze infrequently between the remote pair, whereas they often compared the adjacent pair. Task performance was comparable for the two settings, contrary to the impression that task is much easier for the adjacent pair. This implies that larger amount of information was acquired by one fixation for remote pictures (large-memory strategy). Larger memory may compensate for infrequent fixations. Our results thus show a trade-off between memory size and access frequency in visual information processing.

## LEARNING, MEMORY, AND DEVELOPMENT

- **A natural bias can determine basic-level preference in recognition**

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It is well established that people can recognise the same objects at different levels of abstraction. Of these, the basic level has a privileged status in measures of recognition performance. The origin of this preference remains to be firmly established. We tested the prediction that the basic-level preference can arise from an uneven distribution of basic and subordinate scale cues in the 2-D retinal projections of distal 3-D objects. When an object is moved away from the observer, its retinal projection shrinks in size.

In the first experiment, participants saw pairs of 3-D rendered, Gouraud-shaded animals for an unlimited time. We found that reducing the size of the two stimuli in a pair impaired subordinate judgments more than basic judgments. In experiment 2, subjects saw one animal at a time on the screen for an unlimited time. We again found that subordinate categorisations were less resilient to reductions in stimulus size.

Together, the results suggest: (i) that scale-dependent cues subtend subordinate categorisations, (ii) that basic categorisations are more resilient to scale changes, and (iii) that a basic-level bias could simply arise from the interaction of scale-specific task requirements and available object information.

- **Effects of previous and succeeding target presentations on the displacement of memory for target lightness**

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Two experiments were performed to examine memory for target lightness. In both experiments, a series of three stimuli simulated a gray target that lightened, darkened, or maintained the same luminance, and stimuli were presented against a black or white background.

In experiment 1, observers judged whether the perceived lightness of a probe was the same as the remembered lightness of the third stimulus. Memory was displaced in the direction of previous target luminance when targets lightened on a black background, or darkened on a white background. This pattern occurred regardless of whether the third stimulus in the series was light gray or dark gray. In experiment 2, observers compared the perceived lightness of a probe to the remembered lightness of the first stimulus. Memory was displaced towards darker values regardless of whether the target subsequently lightened or darkened.

Results of experiment 1 are consistent with previous findings (Brehaut and Tipper, 1996 *Journal of Experimental Psychology: Human Perception and Performance* **22** 480–501; Favretto et al, 1999 *Perception* **28** Supplement, 77b), and suggest that displacement is not influenced by the specific luminance of the third stimulus. Results of experiment 2 suggest that memory for initial target lightness is affected by subsequent target luminance regardless of the specific direction of change.

- **Constructing the prototype face**

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I investigated the infants' preference for mother's face and how the prototype face is constructed by infants' early visual experience. My hypothesis is that the prototype face is constructed by the sum of their visual experience, and in natural situation mother's face dominates over this prototype face. If this hypothesis is true, infants prefer the average family face to the mother's face.

In order to test this hypothesis photographic CG images have been made of the average family face, the caricatured mother's face, and the anti-caricatured mother's face. I have tested infants' preference for these faces during a 10-month period. Results showed that there were two different developmental stages in recognising familiar faces, the first stage was at around 3 months of age, and the second stage at around 10 months of age.

## MOTION PERCEPTION AND OPTIC FLOW

- **Heading detection with simulated homonymous hemianopia**

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We examined the influence of a simulated visual-field defect on performance on a heading task. We simulated homonymous hemianopia (HH), the most frequent visual-field defect after post-chiasmatic brain damage. Optic flow patterns simulated forward motion through a cloud of dots, and real-time gaze position was used to simulate gaze-contingent HH. The subjects' task was to direct their gaze at the continuously changing direction of heading. Four subjects performed, separately for each eye, the task with no HH, and with a left and a right HH.

HH was found to affect both speed and accuracy of the simulated heading. For both speed and accuracy, a significant interaction between eye and type of HH was observed, suggesting a naso-temporal half-field difference with subjects performing better using their nasal half-fields. There were no significant advantages in task performance with either eye or side of the HH. We conclude that HH affects the ability to track one's heading.

Previous experiments have revealed a temporal half-field advantage for motion sensitivity, suggesting the presence of a subcortical processing component. In contrast, we found a nasal half-field advantage, indicating that the processing required in our heading-tracking task is not subcortical in nature.

- **Perceptual stability during yaw head movement**

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Normally we perceive the visual world as stable even when head, eye, and body motions induce relative motion that could just as well be interpreted as the world moving. How much mismatch between head motion and the accompanying visual motion can be tolerated and still perceived as head movement in a stable environment?

Subjects wore a head-mounted display coupled to a mechanical head tracker. They moved their heads voluntarily around the yaw axis at an instructed amplitude and frequency whilst viewing a rectangular patch which moved in response to head motion. The motion of the patch relative to the subject was varied between 0 (subject stationary), through -1 (earth stationary), up to -5 that of the head). Ten repetitions of each condition were interleaved. Subjects indicated whether each condition appeared as earth stationary.

Subjects were more likely to accept as earth-stationary visual displays that moved in the appropriate direction but too quickly, rather than displays that moved too slowly. 65% of 'earth-stationary' trials were recognised as such. Only 20% of trials were judged 'earth-stationary' when visual motion was 0.3× that of the head. When visual motion was twice that of the head, 35% of trials were still judged as stable.

- **Relative estimation of time to collision: When  $\tau$  strategy is not used**

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Different studies of the effect of size on the estimation of time to collision (TTC) have yielded conflicting results. In order to address this problem, we carried out an experiment using a 2AFC paradigm in a computer simulation of two simultaneously approaching objects. Specifically, we studied the effect of the optical differences of final size on the accuracy of estimating TTC. Adapting the method described by Regan and Hamstra (1993 *Vision Research* **33** 447–462), we built a matrix of stimuli where TTC and final size were brought into conflict by varying the initial rate of expansion. Discrimination thresholds for TTC and for differences in final size were computed by logit analysis.

Results showed that when mean TTC was 4 s most observer responses were based entirely on TTC information ( $\tau$ ). In contrast, when the mean TTC was 1 s—but only with  $\tau$  opposed to size—observers showed a strong tendency to rely on optical differences in final size. Thus, when the differences in the initial rate of expansion are high, the final size seems to be used to solve the task. However, when the differences in the initial rate of expansion are small, the  $\tau$  strategy is used. Our findings suggest that there may be different processing mechanisms involved with short and long TTCs.

- **Model-based approach to video perception and motion**

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Multimedia systems have become an integral part of today's communication, where a major component of the transmitted data is visual information. In many applications, however, the inherent redundancy in images and video sequences is rather high. Particularly in the case of video teleconferencing, such as head-and-shoulder information with unchanged background, this redundancy is further increased (Porat, 1998 *IEEE – ICECS* **2** 177).

Here, an efficient model-based approach to video perception and motion is introduced, based on spatial characteristics of cells in the visual cortex (Porat and Zeevi, 1984 *Perception* **13** A32b). According to the model, recent localised history of the scene is used to represent the next frames, based on a wavelet-like structure. Partial information is used according to the human sensitivity to spectral information (Porat and Zeevi, 1988 *Perception* **17** A59c).

Based on the proposed model, coding results of video teleconferencing show significant compression rates of more than 100 : 1 for monochromatic sequences, with high-quality reconstruction of the video sequence. Considering these performances, it is suggested that the new approach to video perception be further analysed and integrated in currently available methods for video coding, such as MPEG.



- **Detection thresholds for coherent motion**

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Detection thresholds were measured for a number of dots moving along parallel trajectories on a dynamic noise background of 100 dots within a  $3.6 \text{ deg} \times 3.6 \text{ deg}$  field. The target was three collinear dots moving as a group at right angles to their orientation. Presentation time was 1.14 s. A two-interval forced choice procedure was used. Three highly trained observers participated.

In experiment 1, we found that for dot speeds (target and background) ranging from  $0.26 \text{ deg s}^{-1}$  to  $2 \text{ deg s}^{-1}$ , response accuracy improved from 55% to 85%, reaching an asymptote thereafter (measured as  $3.3 \text{ deg s}^{-1}$ ). In experiment 2, detection thresholds were determined for a constant signal-to-noise ratio of 3% (eg 3 target dots with 100 background dots) with 2–7 target dots and appropriate background dot densities. Performance first increased from 2 to 4 dots (from 67% to 90%) and then again reached a plateau at 90%.

We propose a model where the signals of motion detectors with similar preferred motion directions are integrated over a wide range of receptive field sizes leading to figure–ground segregation according to the Gestalt factor of common fate.

## NATURAL IMAGES, BIOLOGICAL MOTION, AND FACES

- **A factor in feedforward efficiency of visual information processing: natural image categories inferred from ‘edge’ information**

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Some of the fundamental differences between everyday visual scenes that should participate in generating mental sketches of waking visual experience (or in any sensory modality for that matter) have been examined. The aim was to quantify the utility of edge information in primary image analysis.

Observers assigned 3185 high-resolution colour images to broad categories and subgroups according to semantic content, eg architecture, food, people, scenery. The output of computer edge detection (summarising accumulated orientation plus magnitude frequency) was analysed by using Bayesian statistical inference to discover self-similar patterns in the spatial contrast of the originating images.

The most efficient explanation of the data suggested partitioning into several broad categories of images. These categories shared the lowest common denominator that may be cortically plausible (edge-like information). Composite categories were readily interpreted by human observers. Crude information provided by orientation-selective neurons is an effective bootstrap mechanism for image and object classification perhaps as often as 60% of the time, thereby limiting the search space of models necessary for recognition.

- **Hemispheric asymmetries in visual information processing depend on spatial frequency**

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We examined differences in visual processing of spatial frequencies by the left hemisphere (LH) and the right hemisphere (RH) using evoked potentials. In separate experiments, low-pass-filtered images of six facial expressions and food (fruit, vegetable) were used as agents for the transmission of frequency-specific information in a cognitive classification task.

Observers judged whether sequentially presented images were members of the same category of emotion or food (unfiltered image presented centrally, then filtered target presented randomly in left or right visual field for either 50 or 200 ms). Performance accuracy and reaction time improved with increasing spatial frequency; reaction times for left-visual-field–RH stimuli were quicker by 20 ms. P300 potentials (CP3/4, P7/8, T7/8) differentiated between facial and food stimuli; LH responses to spatial frequencies  $\leq 2 \text{ cycles deg}^{-1}$  lagged  $0.5 \text{ cycle deg}^{-1}$  responses by 60 ms–200 ms, while RH waves were insensitive to spatial frequencies. Early N120 and P160 amplitude altered with spatial frequency for all stimuli.

Cerebral asymmetries in cognitive vision could be due to differential representations and access to levels of information for reading and recognition.

● **Can the brain ignore biological motion? Evidence from human MEG**

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How does gamma magnetoencephalographic (MEG) cortical activity in response to biological motion depend on task demands?

Fourteen adults saw a set of 200 displays of two types: a canonical point-light walker and a scrambled figure for which the spatial positions of dots were randomly rearranged. In separate runs, subjects responded to the third identical either canonical or scrambled configuration while ignoring the stimuli of another type. MEG responses were collected with an entire brain system. Neither attended nor ignored scrambled figures evoke any significant increases in the early gamma response.

Both attended and ignored point-light walkers elicit an increase in gamma activity (25 Hz) over the left occipito-parietal areas already at 80 ms–120 ms from stimulus onset. An attended walker yielded further consecutive enhancements over the right parietal and temporal cortices. The latter finding confirms the robustness of our previous data (eg Pavlova et al, 1999 *Perception* 28 Supplement, 52c). For the ignored walker, however, the gamma response was restricted to the left parietal cortex. The findings indicate that early gamma activity over the primary cortex reflects stimulus coherence irrespective of attention paid. The time course and topographic dynamics of later gamma responses undergo top–down influences and may be modulated by attention.

● **Distraction of visual attention reduces integration of audiovisual speech**

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The McGurk effect is an audiovisual illusion where visual information from a talking face alters the auditory speech percept. For example, when an auditory word /epe/ is dubbed onto a face uttering /eke/, the percept is most commonly /ete/. The strength of this effect reflects the strength of audiovisual integration. It has been claimed that audiovisual integration occurs automatically when looking at the face while listening to speech.

To test this proposition, the McGurk effect was measured in two conditions: (i) the subjects attended to the talking face, and (ii) the subjects attended to a visual distractor presented together with the face. For both conditions, video clips of a talker uttering meaningless words /eke/, /epe/, and /ete/ were edited so that each auditory word was paired with each visual word. In condition (ii), the distractor was a leaf flying across the face so that it was next to the mouth when the talker spoke. The clips were presented to subjects who were instructed to write down what the talker uttered. The McGurk effect became weaker when attention was distracted from the talking face. This result suggests that audiovisual integration of speech is not an entirely automatic process.

**SHAPE**

● **Are briefly presented letter-like shapes perceived categorically?**

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In cases of categorical perception (eg speech sounds), discrimination of two stimuli is poor if they both fall in the same perceptual category, and is good if they fall in different categories. An ideal observer's performance, however, depends only on the difference in the stimulus magnitudes.

We tested whether briefly presented lowercase letters are perceived categorically or whether humans act more like ideal observers. A series of stimuli between the letters 'a' and 'd' was constructed from a circle and a line of varying length. If the difference in the line lengths between a standard and comparison letter was small,  $d'$  was constant no matter what the length of the standard. This is the pattern expected from an ideal observer. For larger differences in line length, however,  $d'$  showed a complex dependence on the length of the standard. This pattern is consistent neither with the ideal observer nor with categorical perception.

We conclude that humans act like ideal observers when discriminating letters whose line length differences are near threshold; but they act in a complex (non-ideal and non-categorical) way when presented with suprathreshold differences.

- **Object complexity and visual efficiency**

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We investigated the dependence of efficiency on the intensity of external noise added to images of test objects of different complexity. The efficiency of the human visual system is expressed as the ratio of the threshold contrast energy of exactly known images for an ideal observer to the contrast energy for real human observers under detection or identification of the test objects. We measured and compared correct identification probabilities of test objects in noisy images by a human observer and by our computer model of an ideal observer. We found, that the efficiency depends strongly upon complexity of the test objects with a priori known parameters. We used as a measure of the test object complexity the number of details per object that differentiate the objects forming the alphabet.

We conclude that for simple test objects the efficiency is  $\sim 1$  over a wide range of noise intensities. When the test objects are represented by complex objects, a strong drop in efficiency takes place as the noise increases. The absence of a priori information about the test object rotation resulted in reduced efficiency.

[Supported by the Russian Foundation for Basic Research, grants 98-06-80001, 99-04-49647.]

- **Adaptation and aftereffect of the perception of a surface slanted in the third dimension**

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Bergman and Gibson (1956 *American Journal of Psychology* **72** 354–374) reported that a slanted surface viewed through a small window of a reduction screen seemed gradually to become less slanted with the duration of inspection (adaptation), and a vertical surface newly presented after this observation seemed slightly slanted in the opposite direction (aftereffect).

These results led them to assert that these phenomena cannot be explained purely by the spatial interaction between the inspection figure and the test figure postulated by Köhler and Wallach (1944 *Proceedings of the American Philosophical Society* **88** 269–357), but are mainly due to the adaptation effect. However, as the author has already pointed out, Bergman et al measured only the aftereffect and not the adaptation itself, so their opposition to Köhler and Wallach is not convincing.

In this report, a re-examination of Bergman et al, especially the measurement of their adaptation, was carried out by presenting a stereogram and with 3-D moving patterns, with the use of computer graphics. As a result, the existence of adaptation has been confirmed quantitatively and it is concluded that the figural aftereffects must be explicated by the temporal adaptation and spatial interaction effect.

## SPATIAL FREQUENCY AND CONTRAST

- **The Oppel – Kundt illusion affects the orthogonality judgment**

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Judgments of the 90° angle are combined with perceived distortions in length. The stimuli were constructed of a number (2–50) of bright spots (3 min of arc in diameter) arranged in a horizontal line, as in the filled part of the Oppel–Kundt figure. A single spot of the same size was situated at some distance on the side. The subjects were requested to move the side spot to the left or to the right with the panel keys and place it in a position at which two imaginary lines drawn through the end spots of the filled interval and the side spot would intersect perpendicularly.

The results show that the error varies in accordance with the number of spots in the filled interval. The error is about 0 if only two spots are present, but increases with their number, reaching a maximum at 8–12 spots, and slowly decreases afterwards. The function obtained has the same profile as that of the Oppel–Kundt illusion itself. As opposed to this, standard deviation does not change with the number of spots and remains low. Our data demonstrate the additivity of the two visual processes: the orthogonality judgment and perceived distortions in length.

- **Illusion of curvature and brightness contrast**

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A square, an equilateral triangle, a pentagon, or a hexagon makes the arcs of the circumscribed circle appear puffy. In psychophysical experiments, subjects, viewing the stimulus monocularly and manipulating the panel keys, adjusted the curvature of the arcs to reduce the illusion to zero. The corrections made by the subjects were used as the measure of the strength of curvature distortion. The distortion has been measured as the function of: (i) the contrast of the figures, and (ii) the size of the stimulus. The distortion changed monotonically as the contrast of the inscribed figure varied from 0 to 0.54, with that of the circle being fixed. The distortion has about the same strength for squares, pentagons, and hexagons, and their curves overlap, but the curve for the triangle is clearly below those of the other three figures. The distortion of the perceived curvature does not change noticeably if the contrast of the circle varies and that of the inscribed figure is fixed. The illusion strength varies with the size of the stimulus at any contrast of both the inside and the outside figures.

Predictions of the spatial-filtering model have been found to correspond to the experimental data obtained.

- **Expectancy effects on spatial-frequency processing: a psychophysical analogy to task-dependent processing of 'real world' objects and scenes**

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Research suggests attention can be selectively set to different spatial scales, to extract relevant visual cues in 'real world' object and scene categorisation tasks (Schyns and Oliva, 1999 *Cognition* 69 243–265). The question arises of the visual processing implementation of this mechanism.

In psychophysics, evidence consistent with selective, task-dependent processing of information at different spatial scales has also been found. For instance, sinusoidal-grating detection is worse when spatial frequency varies from trial to trial, than when the same gratings are presented as blocks of stimuli with a constant spatial frequency (Davis and Graham, 1981 *Vision Research* 21 705–712). Such uncertainty effects are consistent with selective activation or monitoring of spatial-frequency processing channels (Hubner, 1996 *Vision Research* 36 3429–3439). We investigated a predicted consequence of this: that when observers are cued to expect a grating at one spatial frequency, detection of gratings at an unexpected spatial frequency is impaired. We found a decrement in grating detection when observers were misled, supporting the occurrence of an 'expectancy' effect. Our results suggest that an implementation of the categorisation-dependent extraction of visual cues could depend on context modulating attentional control of spatial-scale processing.

## VISUAL IMPAIRMENT

- **Reversed localisation in a patient with blindsight**

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Spatial localisation is commonly used as a screening test for 'blindsight' in hemianopes with damage to striate cortex. We tested a 46-year-old patient, DC, who had undergone a left occipital lobotomy for the treatment of epilepsy seven years previously.

Targets were flashed on briefly at four locations along the horizontal meridian of the patient's blind (right) visual field. Following the target and a tone, the patient was instructed to saccade and point to one of four marked locations where the target had appeared. DC consistently selected the mirror-symmetric location; for example, when the most eccentric target was flashed, she indicated the location closest to the fovea and vice versa. Control experiments suggested that her performance did not arise from extraocular light scatter. DC reported highest confidence for the most eccentric targets; however, this was true whether or not the blind field was occluded, suggesting that subjective experience was unrelated to her performance.

These results suggest that DC has reliable access to a spatial map within her blind visual field, albeit a misrepresented one. Further behavioural and neuroimaging tests will address the nature of the misrepresentation.

## ORAL PRESENTATIONS

### SPATIAL ASPECTS OF MOTION PERCEPTION

#### ◆ **Spatial scale determines visibility of image motion**

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Visual image motions usually involve multiple moving features. How are local motion-sensitive mechanisms globally connected? We compared detection thresholds of local motions of individual features and relative motions of multiple features. Effects of the spatial size and separation of multiple moving features were of particular interest. Six Gaussian blobs ( $s = 5 - 30$  min of arc) were arranged in randomly oriented hexagonal patterns around a central blob, with spatial separations varied between 30 and 480 min of arc. In motion-detection tasks, a single peripheral blob oscillated sinusoidally while the others were stationary; and in phase discrimination tasks, one blob oscillated with  $60^\circ$  phase difference from the others.

Thresholds for motion detection were slightly but consistently lower than phase-discrimination thresholds. At spatial separations of 60–120 min of arc, thresholds for both tasks were comparable; however, differences increased for larger spatial separations. Motions of larger features were much more visible than those of smaller features. Motion thresholds for smaller features increased sharply with spatial separation, but thresholds for larger features were almost independent of spatial separation. Additionally, motion thresholds expressed as the contrast change remained constant as the total blob luminance was varied. In general, visual motion mechanisms are globally coherent and dependent on spatial scale.

#### ◆ **Differential effects of the observation aperture on the detection of speed increments and decrements**

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Subjects observed a random-dot pattern that moved horizontally within a rectangular,  $40 \text{ deg} \times 4 \text{ deg}$ , invisible aperture. The long side of this aperture was either parallel or perpendicular to the motion direction. A temporal 2AFC was employed for measuring the thresholds for detection of 100 ms speed increments and decrements superimposed on uniform motion of 1.1 s duration and base speeds of 8, 16, 24, and  $32 \text{ deg s}^{-1}$ .

The 'aperture' factor, parallel versus perpendicular, almost did not affect the detection of decrements. For the lowest speed, the increment thresholds for both the parallel and perpendicular apertures were nearly equal to each other and to the decrement thresholds. However, with increasing base speed, the thresholds for increments within the perpendicular aperture strongly increased, up to 3 times for  $32 \text{ deg s}^{-1}$ , as compared to those for increments within the parallel aperture and for decrements. It is assumed that sequential recruitment of motion detectors along the trajectory of each dot is involved in the detection process. It is shown that, with motion at high speed within the perpendicular aperture, increment detection can severely deteriorate owing to the short lifetime and small visible path of the dots, whereas decrement detection may be almost unaffected.

#### ◆ **Misjudging the speed of random dots moving in apertures**

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In the context of visual motion processing, speed information is crucial in various behavioural tasks. Estimating speed from simple motion detectors, however, is not trivial, because their response is influenced by various stimulus properties, such as the contrast or spatial layout of a moving pattern. We illustrate such ambiguities with computer simulations of a biologically motivated motion-detector model, and suggest a mechanism to overcome some of these problems by combining the outputs from a set of simple spatiotemporal filters.

These theoretical considerations are compared with the ability of human observers to estimate speed in random-dot kinematograms with randomly distributed dots moving behind apertures of different sizes and shapes. We confirmed results from earlier studies that perceived speed increases with decreasing diameter of a circular aperture, and found that the aperture size along the motion path is the critical stimulus variable. Furthermore, preliminary results indicate that under certain conditions dot contrast has comparatively little influence on perceived speed. Some of these results, such as relative contrast independence, can be explained by the filter-combination model. Additional mechanisms for estimating relative speed are needed to account for other aspects, such as the dependence on aperture size.

### ◆ Interaction of local and global processes in motion and stereopsis

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A concentric form of Glass pattern can be obtained by superimposing a random-dot frame and its slightly rotated version. With this type of stimulus, if the rotated version of the two random-dot frames is displaced vertically, the Glass pattern globally defined by virtual concentric lines can appear to move horizontally rather than the dots of the frame being perceived in real vertical motion.

To understand how the local and global motion processes interact in this newly observed phenomenon, we systematically changed the distance of vertical displacement and the interframe interval. When the two display parameters satisfied the condition of long-range motion, the induced horizontal global motion overrode the real vertical local motion. On the other hand, when they fit to that of short-range motion, the induced horizontal motion was completely suppressed and only real vertical motion was observed. When they were in the intermediate range, however, both the global and local motions were simultaneously perceived, with a tendency for either of them to be more dominant depending upon the affinity of display condition to long-range or short-range motion.

We also found a result suggesting that the perception of motion-in-depth based on global matching process is possible even without corresponding local micro structures.

## ADAPTATION IN SPATIAL VISION

### ◆ Orthogonal adaptation improves orientation discrimination

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We investigated the effect of adaptation on orientation discrimination using two experienced observers, then replicated the main effects using a total of fifty naïve subjects.

Adapting and test gratings had spatial frequencies of 1.5 or 6.0 cycles deg<sup>-1</sup>, and were presented at 80% contrast in two 6.5 deg diameter circular apertures at a mean eccentricity of 5.4 deg to the left and right of a central fixation spot. Adapting gratings appeared for 1 min before the first trial, and for 5 s before every subsequent trial, counterphasing at 0.83 Hz. Test stimuli appeared for 100 ms, preceded for 50 ms by a uniform field. Subjects judged which of two spatially separated test gratings oriented at  $\pm x^\circ$  to the vertical appeared to be tilted more clockwise. Orientation discrimination around vertical improved after adaptation to either horizontal or vertical gratings, but was impaired by adaptation at 7.5° or 15° from vertical. Improvement was greatest when adaptor and test were orthogonal.

We found analogous improvements in the motion domain using random-dot kinematograms: direction-of-motion discrimination improved around the adapting direction, but greater improvement was found after adaptation in the opposite direction. The results can be understood in terms of a functional model of adaptation in cortical vision.

### ◆ No pain, no gain? Luminance adaptation in perceptual filling-in

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A grey target peripherally presented within dynamic random noise perceptually fades from view (or 'fills-in') after a period of steady viewing. We investigated whether luminance adaptation occurs in the presence of perceptual filling-in.

Observers fixated the centre of a computer screen filled with dynamic random noise. They were required to detect the presence of a small, bright test probe presented at the centre of the target (eccentricity = 10 deg). Luminance increment thresholds (the amount of extra brightness needed to detect the probe) were obtained for three conditions: (i) no adaptation—test intervals were presented after trial initiation; (ii) adaptation—observers viewed the stimulus until they reported target disappearance, and then viewed the test intervals; (iii) control location—as (ii) but the target was relocated for test intervals.

Surprisingly, luminance increment thresholds were lower with adaptation [condition (ii)] than when observers simply viewed the test [condition (i)] or viewed the test at a different location [condition (iii)]. Thus, stimulus adaptation facilitates the detection of the brief probe. That this facilitation was limited to the target location suggests the process was a target-specific one. This effect could be related to transient detection and may not be related to perceptual filling-in per se.

### ◆ **Depth adaptation and stereoscopic channel structure**

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Stereoscopic channel structure was assessed by the measurement of depth-adaptation effect with adjustment method. Adaptation, test, and comparison stimuli, were all low-pass-filtered random-dot stereograms, which encoded a bulge  $z = d \exp(-r^5)$ , where  $r$  is the radius and  $d$  is the disparity magnitude. The adaptation effect was measured for combinations of adaptation and test stimuli within the disparity range of  $-12$  to  $12$  min of arc.

The major effect was that adaptation to either protruding or intruding bulges had little or no effect at the adaptation disparity but increased the perceived magnitudes of both larger and smaller disparities. Fitting the data with a simple model with several stereoscopic channels showed that a three-channel model provided an accurate fit and that adding new channels improved the fit insignificantly.

The channels derived for the three-channel model are similar to the near, flat, and far channels proposed by Richards (1971 *Journal of the Optical Society of America* **61** 410–414).

### ◆ **Adaptation to oscillating disparity**

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Erkelens and Berends (ARVO 1999) demonstrated the existence of a slant aftereffect from viewing an unslanted planar surface. The unslanted adaptation stimulus contained a specific amount of vertical scale and a subject-dependent amount of horizontal scale. Thus, adaptation to the percept was impossible. The goal of the present study was to investigate whether the aftereffect also occurs when the disparity oscillates around a non-zero value.

An adaptation stimulus contained an oscillating amount of horizontal and vertical scale, so that the stimulus was perceived as frontoparallel at all times. After an adaptation period of 5 min, subjects judged the slant of a thin, horizontally scaled strip, which provided negligible information about the vertical disparity field. A staircase method (MUEST) was used to determine the amount of scale that was required to see an unslanted test strip.

The amount of scale needed to perceive an unslanted test strip was significantly different from zero. Adaptation has been assumed to be caused by a signal which is constant over a longer period. However, the present result demonstrates that adaptation to disparity also occurs if disparity oscillates.

## MOTION AND TIMING

### ◆ **Perceptual delay for rapid direction alternations: A new account in terms of the dichotomy of first-order and second-order temporal changes**

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A large perceived delay for motion was found in experiments when subjects judged the temporal phase of rapid oscillations of direction of motion relative to colour oscillations (Moutoussis and Zeki, 1997 *Proceedings of the Royal Society of London, Section B* **264** 393–399), or when they pressed a button in synchrony with the phase of a given direction of motion [Nishida and Johnston, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) S190].

We found, however, that this perceptual delay disappeared (a) when subjects judged the temporal order of a particular direction transition in a repetitive alternation and an isolated direction/colour transition, and (b) when they copied the stimulus oscillation by synchronously waving a hand-held computer mouse.

We conjecture that the temporal location of first-order change (a colour transition, a motion fragment, a button press, a mouse movement) can be registered even when change occurs frequently, but that there is not a clear representation of the time of occurrence of higher-order changes (eg direction reversal) in this case. The apparent delay for motion perception results from inappropriate matching between first-order temporal signals when correct performance demands rapid cross-order matches. The delay disappears when the task (a) engenders an appropriate use of the second-order events in temporal matching or (b) just requires matching between first-order events.

◆ **Apparent movement and intensity-dependent visual latency: eye and ear method**

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We demonstrated earlier that the relative-intensity-dependent visual latency decreases when stimuli form a clear movement impression (Allik and Kreegipuu, 1998 *Psychological Science* 9 135–138).

In our previous studies, one visual event was always compared with another visual event as a reference. In order to avoid possible interference between two visual events, in this study we used an acoustical signal as the reference against which the beginning of an apparent movement produced by subsequent equiluminous stroboscopic flashes was judged. The observer's task was to decide which, the acoustical signal or the onset of motion, started earlier. The test stimuli had either low or high luminance ( $4 \text{ cd m}^{-2}$  or  $256 \text{ cd m}^{-2}$ , respectively).

Results demonstrated that the relative estimated latency was considerably smaller when flashes produced a strong movement impression than when they did not. Thus, we have provided a converging evidence that the system analysing the movement has a capacity to surpass the differences in visual latency caused by unequal stimulus intensity.

◆ **The colour of the 'perceived void' in the flash-lag phenomenon**

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Observers viewing a white moving ring (background gray) perceive a black disk flashed in the centre of the ring to lag (flash-lag effect) and not 'fill' the moving ring. Intriguingly, the unfilled space inside the ring (perceived void) appears gray (background colour). We asked whether the perceived void (PV) colour was due to the physical background colour before or after the flash.

Observers reported PV colour for a display in which the background was changed from green to red. SOA between flash onset and background colour change was manipulated (range 0 ms to 291 ms; 8 steps). For SOA = 0 ms, PV appeared red, the background colour after the flash. For SOA = 291 ms, PV appeared green, the background colour before the flash. Intriguingly, the transition between PV colour of red to green was not abrupt: for SOAs 50 ms–150 ms some mixture of the two backgrounds was seen.

Consistent with previous findings [Khurana and Nijhawan, 1995 *Nature (London)* 378 565], events after the flash play a crucial role in the flash-lag phenomenon.

◆ **Do motion aftereffects depend on test-pattern temporal frequency?**

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A motion aftereffect (MAE) occurs on static visual noise (SVN) after adaptation to lower speeds, and on dynamic visual noise (DVN) with high refresh rates ( $>20 \text{ Hz}$ ) after adaptation to higher speeds. A DVN pattern is broad-band in the temporal as well as the spatial domain, and many lower temporal frequencies are present as well. To examine the dependence of the MAE on temporal frequency we used a temporally more narrow-band test pattern.

In this 'polarity reversing noise' (PRN) pattern, each bright pixel of a random-pixel array is replaced by a dark pixel and vice versa every  $n$ th frame (frame rate 90 Hz). With a reversal rate of, for instance, 30 Hz, PRN contains only relatively high temporal frequencies. We measured the MAE duration on this PRN test pattern for a range of adaptation speeds ( $0.35\text{--}79.0 \text{ deg s}^{-1}$ ) and compared it to the MAE durations on SVN and DVN (refresh rate: 30 Hz).

Surprisingly, the PRN pattern resulted in a MAE after adaptation to lower speeds as well as to higher speeds. However, they appeared perceptually different. The results show that high temporal frequencies in the test pattern are responsible for the aftereffect of high-speed motion. The aftereffect of low-speed motion, however, seems to depend on other stimulus features, not temporal frequency per se.

## MODELING SPATIAL VISION

◆ **A model for the asymmetric adaptation after increments and decrements of flicker contrast**

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The dynamics of contrast adaptation shows a marked asymmetry: adaptation after a step increment in the contrast of a flickering background is much faster than adaptation after a step



decrement in the contrast [Poot et al, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) S46]. Here we report that a simple model can explain this asymmetry.

Contrast adaptation in the model is governed by a contrast gain signal that consists of a temporal low-pass filtering of the dynamic contrast of the flickering background. The crucial feature of the model that explains the observed asymmetry is the assumption that this low-pass filtering is sandwiched between two instantaneous nonlinearities of the contrast signal  $C(t)$ : an accelerating nonlinearity  $F(C)$  before the low-pass filtering, and a compressive nonlinearity (the inverse of the function  $F$ ) after the low-pass filtering. This structure of the model can explain the observed psychophysics.

DeWeese and Zador (1998 *Neural Computation* **10** 1179–1202) developed expressions for the initial rates of adaptation of a statistically optimal observer after contrast steps in the input. We show that for a specific choice of the nonlinearity  $F$  (a power law), our model leads to results that are fully consistent with these theoretical predictions.

◆ **Processing of real and induced sine gratings by simple cells and filling-in mechanisms**

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Induced sine gratings become visible in a homogeneous grey test-stripe interrupting an inducing sine grating. The strength of this brightness illusion increases with decreasing frequency of the inducing grating and seems to be a special case of simultaneous brightness contrast (Blakeslee and McCourt, 1997 *Vision Research* **37** 2849–2869).

A model is presented in which simple cells in V1 are coding the contrast at the edge of the test-stripe. The activity of these edge detectors determines the intensity of a following filling-in process interpolating local contrast between the edges of the test-stripe. The model predicts, that the strength of the illusion is defined as the positive part of a Gaussian distribution depending on inducing frequency. It is shown that the same filling-in process enhances the sensitivity for low-frequency real gratings, which are implemented in a low test-field: Accordingly, for a test-field height of 0.75 deg, edge contrast determines sensitivity for real gratings of frequencies up to 0.5 cycle deg<sup>-1</sup>. Only for higher spatial frequencies contrast thresholds can be predicted by the activity of spatial-frequency channels.

It is concluded that induced gratings are the visible counterpart of contrast processing mechanisms leading to enhanced sensitivity for real sine gratings in the low-frequency range.

◆ **Modeling the Modelfest data**

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Two years ago a group of vision researchers got together to collect a common set of data to be used for comparing vision models. It was felt that careful comparison of models was too rare in our field. For the year 1999 data set, a battery of 43 fixed detection stimuli were agreed upon, including Gabor functions with a wide range of sizes, aspect ratios, and spatial frequencies, a set of multipoles (edge, line, dipole), Gaussians, random noise, Bessel function, natural scene.

Data have been collected on ten observers in eight laboratories. Two types of modeling of these data are discussed. One approach is a detailed spatial-filter model with parameters for the contrast-sensitivity function, length and width filter bandwidths, separate probability summation exponents for summation over space and over mechanisms.

Our results show that the standard set of parameters developed over the past 10 years does an excellent job of fitting the very wide range of stimuli. The interesting individual differences and significant deviations are discussed. The second approach looks at subsets of the data where several surprises were found in the filter tuning as a function of spatial frequency and in the precise CSF shape.

◆ **Cell assemblies, attentional focusing, and the detection and identification of visual patterns**

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Perceptual learning may be conceived in terms of mechanisms described by Hebb's rule, generalised in a suitable way to avoid infinite growth of synaptic weights (Mortensen and Nachtigall, 2000 *Biological Cybernetics* in press). The approach implies that learning should result in the

formation of sets of neurons (cell assemblies—CAs) that allow for an optimal detection of the stimulus patterns employed in the experiment (CA-model).

We present data from (superposition-) experiments designed to further explore the CA-model, in particular with respect to the effects of attentional focusing on certain parts (features) of a stimulus pattern. For various types of one-dimensional and two-dimensional patterns, the CA-model turns out to be compatible with the data. Focusing on a part of a pattern, however, is not compatible with the hypothesis that now detection (or identification) is mediated by a sub-CA which is specific to the focused feature. The results are discussed in terms of interactions among the neurons of the CA for the complete pattern and with respect to models of attentional focusing, eg the spotlight model.

## POSTER SESSION 2

### (ELECTRO)PHYSIOLOGY AND NEUROTRANSMITTERS

- **Microscopic eye movements synchronise retinal-ganglion-cell activity**

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Under normal conditions, small movements of the visual image relative to the retina are necessary for visual perception. We studied the effect of microscopic eye movements on population activity of retinal ganglion cells. Eye movements of the slider turtle (*Pseudemys scripta*) were measured by video oculo-graphy. They showed microscopic movements of about 5 Hz and 0.05 deg visual angle. This corresponds to approximately 5  $\mu$ m on the retina, which is about one photoreceptor diameter. Spiking activity of large ganglion-cell populations was recorded extracellularly in the isolated turtle retina with the Utah multi-electrode array. Contrast gratings were projected onto the retina via a computer-controlled  $x - y$  mirror system. Moving the mirrors appropriately then simulated natural microscopic eye movement.

We found that the activity of ganglion-cells subpopulation was synchronised with this stimulus movement. Although single cells spiked only on about 5% of movement occurrence, more than 90% of these spikes were preceded by the stimulus. Ganglion cell pairs of this subpopulation showed significant correlation among their spikes. The ensemble of the whole subpopulation reliably coded movement. As a consequence, microscopic eye movements can be detected by correlated activity in retinal-ganglion-cell populations.

- **Visual perception as an epilepsy-prediction factor**

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Human brain system is responsible for many functions: hearing, sensitivity, and others. Visual perception is a very important one. The temporal-occipital brain lobe is responsible for the human visual system. When this lobe is damaged, visual functions are also impaired. Many damages can injure the visual system. Epilepsy can be one of such injuries.

Our task was to investigate the visual perception of epileptics. We created a special computerised system (1998 *Perception* 27 Supplement 164b), which was used for testing visual functions. It contained three parts: size-form discrimination, colour perception, and object-faces recognition testing procedures.

We have tested altogether 300 persons. Test answers were stored in a special database and processed by special mathematical methods. People were investigated by EEG, fMRI, and CT methods before the visual testing procedure. Special regularities were established and were used for diagnosis. We performed such an experiment on 16 epileptics. All the tests mentioned above were used. Epilepsy was recognised correctly for 11 persons. The testing of visual perception functions could be useful in epilepsy prediction. We are planning to continue our experiments. New tests will be created, as well as new processing methods.

### ATTENTION, TEXTURE, AND VISUAL SEARCH

- **Spatial selective attention operates in environment-centred and retinotopic coordinate frameworks.**

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Covert shifts of attention to locations in the visual field have been shown to improve detection and discrimination thresholds for visual stimuli. The spatial coordinate framework in which this selection occurs remains to be fully specified. Previous studies of location priming have suggested that selective attention operates in an 'environment-centred' or relative spatial framework (eg

Maljkovic and Nakayama, 1996 *Perception & Psychophysics* **58** 977–991), although more recently it has been suggested that absolute or ‘retinotopic’ frameworks may also be important (eg Tootell et al, 1998 *Neuron* **21** 1409–1422).

To distinguish between these possibilities, prime and target stimuli were presented in four conditions designed to systematically vary the validity of the prime (in a relative or absolute framework) in a location priming task. The prime was either: (i) nonvalid, (ii) valid relative, (iii) valid absolute, and (iv) relative–absolute valid. Six participants responded to a three-item array in which targets were either absent or present. A reduction in mean RT for valid absolute and relative primes was found ( $p < 0.05$ ) which suggests that covert shifts of attention can be directed equally well in both environment-centred and retinotopic spatial-coordinate frameworks.

- **Hierarchies and reverse hierarchies in the visual system**

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Cortical areas of the visual system are arranged in hierarchical fashion. High cortical areas show spatial invariance while lower areas represent information in a more specific and detailed manner. We recently demonstrated that perceptual learning is initiated in high areas and follows a reverse, feedback hierarchy, proceeding gradually to lower and lower areas. We now suggest that conscious perception itself also follows this reverse hierarchy path. Of course, initial information processing proceeds from lower to higher areas. But the aspects of perception that are available to consciousness or motor action proceed from high to low cortical areas.

We suggest, therefore, that early vision with spread attention is effected by the large receptive fields of high-cortical areas, while lower-area receptive fields are the basis of later stages of visual perception with focused attention. Included in early vision are both crude object identification and feature search (‘pop-out’). Later, visual awareness may access lower cortical areas to obtain image details available there, including precise localisation, retinal size, orientation, and component motion. Reverse hierarchy theory may explain quite naturally a variety of perceptual phenomena including global precedence and word superiority (‘forest before the trees’) and the influence of complex image effects in early vision.

- **Attention and the processing of obfuscated graphical data**

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The tinting of information displays is a design convention intended to engage the reader where an image is placed behind an object positioned in the foreground. A page of text containing a simple line graph was created to investigate the effects of tinting on attention and recall. It was hypothesised that whilst tinting would draw attention towards the graph there would be a detrimental effect on recall.

Three stimulus conditions were created. In condition 1 the graph was unaltered. In condition 2 the graph was highlighted with a grey box, while in condition 3 the graph was tinted with an image of a forest. Four participants were assigned to each condition with the instruction that they would be questioned on completion. Viewing time lasted for 30 s with attention being measured by the SMI remote eye-tracking device. The percentage of total viewing time for attending to the graph showed that participants were mainly drawn to condition 2 while no eye-movement data were recorded for condition 1. Content analysis of responses indicated that peripheral viewing of condition 1 enabled accurate recall of graph details. This suggests that, while attention is drawn to high-interest regions, a plain presentation style facilitates the conveyance of information.

- **Attentional effects on depth and direction aftereffects**

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The perceptions of depth from binocular disparity and motion parallax are typically considered to be low-level pre-attentive processes. In the motion domain, however, such a view was rejected by Chaudhuri [1990 *Nature (London)* **344** 60–62] who showed that the motion aftereffect could be modulated by a secondary attentional task.

Here we investigate (i) whether the duration of depth aftereffects (Blakemore and Julesz, 1971 *Science* **171** 286–288) is also affected by attention, (ii) the relative effects of a secondary task on disparity and motion aftereffects, and (iii) whether attention can modulate the outcome of a disparity-motion-contingent aftereffect (Anstis and Harris, 1974 *Perception* **3** 153–168). Subjects adapted to stationary and/or moving random-dot patterns forming one or more

depth planes while attention was manipulated with a secondary task (character processing at parametrically varied rates).

We found that the depth aftereffect could be affected by attentional manipulations, and both its duration and that of the motion aftereffect varied monotonically with the difficulty of the secondary task. Pre-cueing attention to one aspect of the disparity-motion stimulus (a direction or depth) affected the nature of the aftereffect obtained despite the fact that the visual stimulation remained the same.

- **Influences on scan paths in a feature and conjunction search task**

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In our study we aimed to initiate saccadic visual search and quantify factors that describe the underlying search strategies. Ten subjects participated in a sequence of 100 single-feature and conjunction search tasks (features: colour and form) with 0, 1, 4, or 8 targets among 40, 60, or 80 items.

Data analysis shows that a longer fixation duration in combination with a decreased number of saccades and a much shorter search duration occur in the colour search task, which differs significantly from the conjunction or form search task. Subjects showed one or more general search strategies, eg with a circular, back-and-forth, 8-shaped scan path. In the parallel search task (colour), search strategies were interrupted by the pop-out effect of colour that induces reflex-like targeting. In the conjunction search task, subjects directed their saccades primarily to items carrying the target colour feature, less frequently to items carrying different features. Structured search strategies were more frequently used in the serial search task (form).

Performance data reflect the impact of the search task on the attentional focus. The scan path performed by each subject is a result of an actual global search strategy and a modification by local features.

## **BINOCULAR AND SPATIAL VISION**

- **On the neuroanatomical basis for stereopsis and the integration of two visual hemifields in the cat cortex**

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Partial decussation of retinal fibers in optic chiasma leads to the separation of visual pathways in such a way that each brain hemisphere receives the information on only the one half of the visual field, though from both eyes. The architecture of cortical neuronal connections providing for integration of information from the two eyes and from two visual hemifields is not yet fully understood.

On the basis of our own and other data, a new functional scheme of neuronal connections in the cat cortex is suggested. The scheme includes the callosal connections (as an extension of intrinsic long-range connections), linking in both hemispheres cells driven by the same eye and representing the same locus in the visual field. These connections are supposed to underlie the binding of two half-field representations into one. The scheme also includes an additional set of connections between cells driven by the left eye and cells driven by the right eye ('binocular connections') which provide for formation of disparity-sensitive neurons and mediate stereo perception and depth discrimination.

Peculiarities of neuronal connections in animals with the full decussation of fibers in chiasma and in humans are discussed.

[Supported by RFBR grant 00-04-49289.]

- **Systematic deviations from veridical in a visual collinearity task**

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In previous studies it has been shown that many geometric aspects are perceived distorted. For example, when a subject is asked to set two bars in a horizontal plane parallel to each other, deviations up to 40° occur. These deviations depend on the separation angle between the bars but not on the distance of the bars from the subject. This indicates that either the distance is ignored or that the visual space is intrinsically flat.

In the present study subjects were asked to set two bars collinear. The bars were placed in a horizontal plane at eye height. Distance to the subject and the separation angle were varied. The results show systematic deviations from veridical up to 20°. The deviations decrease as the

distance increases. In conclusion, we find that distance is ignored in the parallelity but not in the collinearity task. Consequently, collinear bars do not appear parallel. This indicates that properties of 'visual space' are operationally defined and may differ between different tasks.

- **Spatiotemporal influence of pre-perceived surfaces on the perception of bistably perceptible surfaces with binocular viewing**

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Previously we reported the phenomena of multistable surface perception where various surface shapes can be perceived from a single stereogram (Idesawa, 1990 *Proceedings of IJCNN-90* pages 17–20; Shi and Idesawa, 1997 *Journal of Robotics and Mechatronics* 9-2 98–103).

Here we investigated the effects of pre-perceived (real or illusory) surfaces on the perception of these stereograms. Perceptually bistable stereograms which can be perceived as convex or concave surfaces, and are given as real or illusory surfaces, were used as probe stimuli. In the experiment, conditioning stimuli, consisting of partial surfaces laid on one of the stably perceptible surfaces, were shown for 1000 ms; probe stimuli were presented for 700 ms after intervals of 100 to 1900 ms; subjects then reported their perceptions (convex, concave, or ambiguous).

Stably perceived surfaces almost coincided with pre-perceived surfaces in the interval from 300 ms to 1900 ms for illusory conditioning stimuli, and in the interval from 700 ms to 1600 ms for real conditioning stimuli. These perceptions were nearly the same for both real and illusory probe stimuli. Remarkable differences in the spatiotemporal influence of pre-perceived surfaces were observed between real and illusory conditioning stimuli, which probably reflect the temporal difference in visual processing stages.

- **Perceived size and distance of virtual targets in convex mirrors**

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We investigated size and distance perception of virtual targets in convex mirrors (650R and 1000R) and a plane mirror. Thirty-six observers matched the distance of a target in a real scene to the distance (10 or 20 m) of a virtual target in mirrors. They also matched the length of a tape to the size of the virtual target (15, 30, 45, 60, or 72 cm) placed at each of the two distances.

The perceived distance for the convex mirrors was found to be much larger than that for the plane mirror and the perceived size for the convex mirrors was not necessarily larger than that for the plane mirror. Multiple regression analyses showed that the perceived size was mainly determined by the virtual size, and the perceived distance was mainly determined by the virtual distance, virtual angle, and virtual size. These results suggest that (i) perceived size is not affected by perceived distance, as is suggested by the size–distance invariance hypothesis, and (ii) both perceived size and perceived distance are directly affected by physical and optical variables.

- **Use of a flexible endoscope in minimally invasive surgery improves surgeon's depth perception**

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During minimally invasive surgery (MIS) an endoscope is used for visual feedback. Depth perception is severely impaired during MIS since the endoscope is a monocular system, and motion parallax is very limited. At the Delft University of Technology a flexible endoscope has been developed which improves motion parallax. Our aim was to investigate the relation between the degree of rotation around a fixation point (FP) and the improvement in relative depth perception.

An endoscope rotated around a FP. At the FP an artery was modelled and an instrument was lined up horizontally next to it. Both maximum endoscope rotation and relative depth between instrument tip and artery were varied. Just noticeable differences (JNDs) were calculated.

Relative depth perception significantly improved with an increase in the degree of endoscope rotation when the instrument was behind the artery (JND = 5 mm for 0° rotation and JND = 1 mm for 10°–50° rotation). When the instrument was in front of the artery, relative depth perception did not improve (JND = 3 mm for 0°–50° rotation). This implies that freedom of movement of a flexible endoscope can be limited to a 10° rotation around a FP to optimise relative depth perception.

## COLOUR AND BRIGHTNESS

### ● Cone-equivalent surrounds demonstrate that more chromatic variability can reduce colour constancy

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The influence of chromatic variability on perceived colour is often evaluated by comparing the appearance of a surface within a structured environment with its appearance within an equivalent surround: a uniform field with the same space-averaged luminance and chromaticity. This approach equates the average physical properties of the stimuli that are being compared.

Considering that nonlinearities within the cones could lead to different average responses at the cone output, we decided to take the notion of equivalent surrounds one step further, and create 'cone-equivalent surrounds'. We took the average light we wanted for the background and determined the extent to which it stimulates each of the three cone types. We then constructed backgrounds in which each of 400 squares stimulated each cone by a random amount between about 8% less and 8% more than this average value. For each square we either used the same random value for all three cones (luminance modulation) or a different random value for each cone (chromatic modulation). Note that for each cone type on its own the two conditions are identical.

We found considerably less chromatic induction for the colourful background, which implies that colour constancy does not necessarily benefit from chromatic complexity.

### ● Bichromatic flickering Ganzfeld as a brightness-matching method for the rod system

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Flickering Ganzfeld was investigated at photopic intensity level. A specially constructed device made it possible to present binocularly Ganzfeld stimuli illuminated by two narrow-band lights with different wavelengths ranging from 400 nm to 660 nm and flickering in counterphase. The intensity ratio was adjusted by subjects.

When the flicker was absent, the subjects watched standard Ganzfeld behaviour. During flicker with only one wavelength used, pictures of disorderly pulsing lines and patches dependent on wavelengths and frequencies of flicker were perceived. When the intensity of the second wavelength was increased, the pulsation at the periphery decreased and at a certain ratio disappeared altogether, whereas the pulsation at the centre continued. It is suggested that this ratio defines equiluminance of two colours for the rod system. Measurements were made for several pairs of colours in the indicated range at frequencies up to 25 Hz.

Some differences from the results of 'classic' methods (flicker photometry, minimal distinct border), can be explained by a different degree of participation of the rod system in brightness-matching procedures.

### ● Cone excitation ratios fail to explain colour appearance when adaptation is prevented

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Cone excitation ratios between a test sample and a background are said to determine colour appearance when illumination changes slowly, allowing adaptation.

We devised three experiments demonstrating a gradual failure of this explanation. Munsell samples (value 7, chroma 4) and a neutral background (N7), which was isoluminous with the samples under illuminant C, were simulated on a Barco Calibrator. Eight variable illuminants were used; each illuminated a sample on the background for 1 s. Subjects had to memorise the colour of a sample and matched its appearance by adjusting hue, saturation, and luminance of the reference sample on the background, under standard illuminant C; the matching time was not restricted (asymmetric sequential colour matching).

Real test samples on a neutral background are not isoluminous when illuminated by a variable non-neutral illuminant; in experiment 1, samples were also surrounded by an annulus (looking like real Munsell chips); no annulus was present in experiment 2. Colour matches poorly correlated with cone excitation ratios. In experiment 3, all samples and backgrounds were made isoluminous; subjects could still match colours, but the correlation with cone excitation ratios was poorest. We conclude that only the first stage of colour constancy may rely on cone excitation ratios.

- **A neuromimetic model of the McCollough effect: Temporal resistance and reverse effect**  
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McCollough effects (MEs) are a set of visual contingent aftereffects that involve colour and contour. These effects have been the subject of a large body of literature concerning their properties and theoretical accounts, but the mechanisms underlying the ME have never been fully clarified.

We make the assumption that the ME is a signature of a more general adaptive neural process tending to generate independent dimensions in visual perception (Hérault and Ans, 1984 *Compte-Rendus de l'Académie des Sciences, Life Sciences* 299 525–528). The architecture of the proposed neural network is composed of colour and orientation units mutually interconnected, with weights being modified according to an adaptative nonlinear anti-Hebbian rule. Despite its minimal complexity, the model not only accounts for the ME but also reproduces various detailed experimental results (such as the reverse-tilt effect contingent on colour) and, above all, the distinctive long temporal persistence of the aftereffect.

It is shown that this latter property cannot be obtained from an adaptive neural process tending to produce only decorrelated (instead of independent) visual dimensions [Barlow and Foldiack, 1989, in *The Computing Neuron* Eds R Durbin, C Miall, G Mitchison (New York: Addison-Wesley) pp 54–72].

- **The crispening effect in luminance and colour**  
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There is large and diverse literature showing that luminance and colour discrimination is best for stimuli that are at or near the adaptation light and that the discrimination worsens for stimuli that differ substantially from the adapting conditions.

In this study, we measured temporal contrast sensitivity for various combinations of test and surround levels for LD, RG, and YV colour directions. Temporal contrast sensitivity in uniform tests embedded in uniform surrounds was compared to that in variegated surrounds of equal mean luminance or chromaticity. The relevance to the phenomenon known as the crispening effect in luminance domain is discussed.

We show that the crispening effect is similar for colour and brightness, and also that the causes are similar, despite the known differences in spatiotemporal sensitivity to colour versus brightness. Habituation to a pedestal edge in static and temporally modulated configurations is the cause for a decrease in test sensitivity for both colour and brightness. When the pedestal is present during the adaptation interval, test sensitivity is not determined by adaptation to the surround or to the test, but rather by habituation to the edge.

## EYE MOVEMENTS

- **Spatial characteristics of intra-saccadic perception**  
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A vertical grating moving at a very high speed (above its fusion frequency) becomes highly visible when a horizontal saccade is made in its direction with appropriate saccadic peak velocity (Castet and Masson, 2000 *Nature Neuroscience* 3 177–183). This paradigm optimises the intra-saccadic visual stimulation. As a result, the intra-saccadic percept is sufficiently clear to allow observers to judge some of its spatial characteristics such as its shape, extent, and/or location.

To study how visual signals from disparate regions in the visual field are integrated to build up shape perception, the horizontal width of the intra-saccadic percept was assessed in two steps. First, the apparent location of the left side of the grating was estimated by presenting a vertical line whose horizontal location was varied by a staircase procedure. In a different block, the apparent location of the right side was similarly measured. Apparent width, in conjunction with eye movements, was measured for different saccade amplitudes and for saccades sweeping over various parts of the screen.

We show that apparent width can be as much as 40% smaller than physical width. This is explained by taking into account responses of adjacent receptive fields which individually receive various spatiotemporal stimulations.

- **Effect of size uncertainty on the speed of visual search and the behaviour of eye movements**

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The task of the observer was to search for, and identify, an uppercase letter from a rectangular array (10 × 10) of characters in which the other items were numerals.

Two different kinds of stimuli were used. In the first kind, all characters were of equal size, and in the second, the size of characters varied at random by a factor of three. The threshold duration of stimulus presentation required for search was determined by using a multiple-alternative staircase method. Eye movements were recorded simultaneously with a video eye tracker. The threshold time for search was higher by a factor of 1.5–2 when the size of the characters were randomised. The average number of fixations per one search was also higher for random-size stimuli. This was associated with a slight increase in fixation duration. Saccade amplitudes were nearly constant.

Since fixations take most of the time needed for visual search, the increase in the number of fixations results in increased search times when character sizes are randomised.

- **Task-evoked eye movements and pupil responses**

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Eye movements and pupil size respond to visual or audio stimuli that require information processing. It is well known that pupil size increases with task difficulty (Beatty, 1982 *Psychological Bulletin* 91–92 276–292). We investigated whether both changes are correlated and can be indicators of mental work-load.

In the first experiment, audio instruction was presented while the subject followed a marked point which moved periodically in the centre (for 1000 ms) and a point on a concentric circle (1000 ms); visual angles were 3 deg, 5 deg, and 10 deg. For the audio portion of the experiment, subjects were asked to perform an oral calculation. In the second experiment, subjects took part in a driving-simulation game with the same tasks. Pupil size and eye movements were observed in both experiments. In the first experiment, the average pupil size and saccadic responses significantly increased with the visual angle and with audio instruction. There are significant interactions between visual angle and audio instructions. This suggests that both changes depend on the visual angle.

In the second experiment, pupil sizes and saccadic responses also significantly increased while the game was in progress. This result provides evidence that both pupil and eye-movement responses can be indicators of mental work-load.

## LEARNING, MEMORY, AND DEVELOPMENT

- **Contrast sensitivity in dyslexia**

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Recent findings suggest that at least some individuals with developmental dyslexia have a deficit in the magnocellular pathway. Such a deficit predicts impaired contrast sensitivity (CS) for low spatial and high temporal frequencies. Previous tests of this prediction yielded mixed results, which were attributed to an inter-study subject variability.

In this study, we addressed the variability problem by characterising the CS of the same (Israeli) adult dyslexics under several paradigms. In a temporal 2AFC task, a drifting or flickering grating appeared in one of two successive intervals. In a spatial 2AFC task, a static or transient grating appeared in either the upper or lower visual field. In the temporal task dyslexics were significantly less sensitive in the low spatial and high temporal frequency range, consistent with a magnocellular deficiency. Moreover, non-word reading accuracy and rate were highly correlated with the sensitivity in this frequency range. Surprisingly, in the spatial task there was no significant difference between groups.

Our findings show that dyslexics' impaired CS is contingent upon a temporal comparison across brief intervals. This suggests that the measurement paradigm (temporal versus spatial) may account for the inconsistencies between previous studies.



- **Neural plasticity as the basis for learning a Vernier discrimination task?**

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Physiological studies provide evidence for neural plasticity in V1 neurons [Kirkwood et al, 1996 *Nature (London)* **381** 526–528]. But there is still no unambiguous evidence that perceptual learning is accompanied by changes of the tuning characteristics of early sensory mechanisms. Saarinen and Levi (1995 *Vision Research* **35** 519–527) used a simultaneous-masking paradigm to show that Vernier discrimination may cause narrowing of orientation tuning of cells maximally activated by Vernier stimuli. But narrowing in simultaneous-masking tuning functions is no unambiguous evidence for changes in early coding mechanisms and may be explained alternatively.

Here we further investigated the hypothesis of neural plasticity in perceptual learning. Using a pretest-learning–posttest-design we assessed orientation-tuning functions, orientation-discrimination thresholds, and summation curves for superimposed Gabor patches before and after extensive training in Vernier discrimination. All subjects showed monotonous reduction of discrimination thresholds due to learning the Vernier discrimination task. Orientation-tuning function showed lowered discrimination thresholds for all mask orientations in the posttest. Learning transfer could be observed for orientation discrimination at 12° oriented Gabor patches. All summation curves showed more summation between superimposed Gabor patches after learning.

We argue for changes within the population of orientation-selective mechanisms caused by perceptual learning.

## MOTION PERCEPTION AND OPTIC FLOW

- **The slalom effect**

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Cesaro and Agostini (1998 *Perception & Psychophysics* **60** 518–523) observed a dynamic illusion of direction and shape that has been named 'slalom effect'. When a dot moving along a straight horizontal trajectory intersects a static pattern of tilted lines, its trajectory is perceived as sinusoidal.

The present work offers additional information on the factors involved in the genesis of the illusion. Three experiments were performed. In two experiments, we manipulated the distance between the inducing lines and the perceived depth displacement between the dot and the tilted lines. In the third experiment, the tilted lines were presented one at a time. In all the experiments, the size of the illusion was measured by the method of adjustment. The strength of the illusion is inversely proportional to the distance between the lines. Depth displacement and temporal presentation of the tilted lines do not cancel out the illusion.

These results are consistent with an interpretation of the effect in terms of an integration of local distortions occurring at the intersections. Some variants of the illusion are presented and discussed.

- **A comparison of pursuit eye movement and perceptual performance in speed discrimination**

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A central goal of sensation and perception is to direct our interactions with the environment. During most voluntary motor actions that are driven by sensory input we consciously experience an internal representation of the visual world. This leads to the question how faithful this internal representation is, and how precise our actions are compared to this reference. To answer that question, we studied the relationship between the perceived speed, which is the experiential representation of the stimulus, and the speed of smooth-pursuit eye movements, the motor action.

We determined psychophysical thresholds for detecting small perturbations in the speed of Gabor patterns (1 cycle deg<sup>-1</sup>) moving at a base speed of 4 deg s<sup>-1</sup>. At the same time we recorded eye-movement traces and used an ideal-observer analysis to compute analogous 'oculometric' thresholds. Our results show a remarkable agreement between perceptual judgments for speed discrimination and the fine gradations in eye-movement speed, with psychophysical and oculometric functions exhibiting the same slope. However, there was no correlation between perceptual errors and eye-movement errors on a trial-by-trial basis. We conclude that the motor system and perception share the same constraints in their analysis of motion signals, but they act independently and have different sources of noise.

- **The time course of perceptual momentum**

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When observers are asked to localise the final position of a moving target, the judged position is usually displaced from the actual position in the direction of motion.

In the present series of experiments, the short-term time course of the displacement was investigated to test different theories that attribute mislocalisation to eye movements or memory distortion. Observers watched a target moving linearly at  $18 \text{ deg s}^{-1}$ . After target offset, a probe stimulus appeared to the left or right of the final target position. Observers' left-right judgments were used to calculate the subjective vanishing point (SVP). It was found that very briefly after target offset (11 ms), the SVP is already shifted in the direction of motion. However, when pursuit eye movements were suppressed, there was no shift of SVP in the direction of motion. Further, the visual persistence of the target was estimated to be about 60 ms.

It is argued that the mislocalisation results at least partially from eye movements after target offset that shift the persisting retinal image of the target in the direction of motion. Observers report the target position at the offset of its retinal image which is displaced in the direction of motion when the target is pursued.

- **Dissociation of rate of expansion and time to contact: A reaction time study**

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Although many authors have assumed that the visual system extracts time to contact (TTC) directly from  $\tau$  and independently of object size and rate of expansion (ROE), few studies have shown evidence for a psychophysical channel sensitive to TTC independent of size and ROE (Regan and Hamstra, 1993 *Vision Research* 33 447–462).

Here we report more evidence for TTC processing independent of ROE by comparing choice reaction times (CRTs) for relative estimation of TTC and ROE. In two experiments, we decorrelated trial-to-trial variation of TTC with trial-to-trial variations of initial ROE. In experiment 1, the task was to signal the object that expanded faster. CRT decreased as a hyperbolic function of trial-to-trial variations of ROE, following Piéron's law (Pins and Bonnet, 1996 *Perception & Psychophysics* 58 390–500), while the CRT curve was flat when plotted versus trial-to-trial variations of TTC. In experiment 2, the task was to signal the object that arrived first. The behaviour of CRT curves was reversed. Furthermore, CRT plotted versus trial-to-trial variations of TTC was significantly lower than CRT plotted versus trial-to-trial variations of ROE in experiment 1. The more ecological relevance of the inverse of relative ROE could explain this finding.

- **Invariant processing of spatiotemporal curves**

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The representation and processing of spatiotemporal information has been studied in a series of experiments. In a temporal forced-choice design we measured the discrimination performance for simple courses of motion which consisted of a black dot moving on a white background along an (invisible) curved path. Each trial consisted of two pairs of motion paths, and the subject's task was to indicate whether the difference in curvature occurred in the first or second pair. We used three conditions with different amounts of curvature and varied presentation time in 15 temporal conditions (100–1500 ms).

The result was a widely invariant performance regardless of curvature and motion time. Neither very fast movements nor long durations had an influence on the sensitivity. On the other hand, discrimination performance was significantly different when we used corresponding static versions of the dynamic stimuli. The observed invariance can therefore neither be explained by motion-selective mechanisms nor by the assumption of a static internal representation in the form of a spatial trajectory of the spatiotemporal stimuli. We discuss the basic representational constraints for the processing of spatiotemporal patterns and present a neural-network model which provides a hierarchical order of spatiotemporal processing on separate self-organising maps.

- **Efficiency of motion transparency for same-direction stimuli**

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Motion transparency occurs when two (or more) motions are perceived in the same spatial location. This phenomenon can be experienced for all combinations of motion directions. We focus here on the efficiency of motion transparency when the signals move in the same direction but at different speeds.

We measured speed discrimination thresholds in two tasks. For the coherence task, two random-dot kinematograms of translatory motions were presented in successive temporal intervals. In the transparency task, single translatory motions were compared with stimuli containing two superimposed translatory motions. In both tasks, the motion signals were in the same direction but with different speeds, and speed noise was added. Subjects were required to indicate which interval contained the fastest component motion. Thresholds were compared to that of an ideal observer to compute subject efficiencies for both tasks.

We found that, while the thresholds were consistently higher for the transparency task, the computed efficiencies were equal in both tasks. This suggests a common mechanism in both tasks. Furthermore, efficiencies rose quickly with the speed ratio between the two component motions. These results are discussed in terms of biologically plausible models of motion perception.

## NATURAL IMAGES, BIOLOGICAL MOTION, AND FACES

- **Categorical and attributional perception of facial expressions—comparing upright and inverted faces**

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It has been reported that facial expressions of emotion cease to be perceived categorically when inverted (De Gelder et al, 1997 *Cognition & Emotion* **11** 1–23), implying that their configural (Gestalt) properties are important for recognition of emotions. We examined whether the configural and componential (feature) aspects of facial-emotion perception are dissociable.

Stimuli were photographs of seven FACS-instructed emotion prototypes, and blended expressions produced by interpolating (morphing) between them. Configural properties of the stimuli were quantified with the use of the FACEM system (Pilowsky and Katsikitis, 1994 *Journal of Affective Disorders* **30** 61–71).

Stimuli were presented upright and inverted, and perceived dissimilarities between them were obtained by a triadic procedure. Processing with multidimensional scaling analysed dissimilarities into contributions from affective dimensions and categories. For both conditions, four-dimensional solutions were obtained, and the relative strengths of these contributions compared. In addition, coordinates of the stimuli were correlated with their configural properties by bivariate and multiple regression.

It was found that, in the inverted condition, correlations of affective attributions with configural measures were lower and categorical perception was reduced. The findings suggest that emotional judgments of inverted faces, though retained, are guided by facial components rather than by configuration.

- **N170 wave and differential processing of faces and objects**

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The potentials evoked by faces are characterised by a N170 wave specific in amplitude and latency for these stimuli but also present for other objects. We investigated whether the differences between objects and faces for this component could be due either to differences in their spatial configuration or reflect specific visual processing (holistic for faces versus feature-based for objects). For this purpose, we used different stimuli: among them an Arcimboldo painting which elicits in the upright position the perception of vegetables in a cup (object condition) and in the inverted position the perception of a human face (face condition). Evoked potentials recorded with 32 electrodes in eleven subjects show a greater amplitude of the N170 for face condition than for object condition, mainly in temporo-occipital regions.

The spectrum of spatial frequencies being the same whatever the orientation of the visual stimuli, this difference suggests that faces and objects engage specific patterns of processing: holistic for faces and feature-based for objects.

- **Efficient adaptive estimation of sensory scales**

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Measurement of sensory scales is a classical problem in psychophysics. In the method of pair comparison, each trial consists of a pair of samples and the observer selects the one perceived to be greater on the relevant scale. This may be regarded as an extension of the method of forced choice: from measurement of threshold (one JND), to measurement of the larger sensory scale (multiple JNDs). While simple for the observer, pair comparison is inefficient, because if all samples are compared, many comparisons will be uninformative. In general, samples separated by about 1 JND are most informative. We have developed an efficient method for adaptive selection of sample pairs. As with the QUEST adaptive threshold procedure, the method is based on Bayesian estimation of the sensory scale after each trial. We call the method 'efficient adaptive scale estimation' or EASE ('to make less painful').

This method has been applied to estimation of subjective quality of digital video. Observers viewed pairs of short sequences of video with various amounts of artifact, and selected the sequence with the greater quality. The resulting quality scales can be compared to those obtained by other methods, such as magnitude estimation.

## SHAPE

- **Perceiving pictorial slopes by hand and by foot**

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The accuracy of judgments of surface inclination has been studied by a range of methods. However, controversy regarding veridicality of judgments continues (see Huber and Davies, 1999 *Perception* **28** Supplement, 106c). In an experiment ( $n = 37$ ), the veridicality of action-based responses and the availability of visual information during the adjustment process was further tested through a comparison of adjustments by hand and by foot. Experimental procedure and stimuli (pictures of slopes ranging from 5° to 45°; different textures and sizes) were the same as used previously. Subjects carried out a total of 120 adjustments in four blocks (paddle visible or not, adjustment by hand or by foot).

The results show an overestimation for small angles (of about 100%) and an underestimation for steeper slopes (of about 50%). When the paddle was visible, the adjustments were steeper. However, no differences were found between the manual and the foot response, except that adjustments by hand increased more rapidly with stimulus slope (slope of regression = 0.47) than adjustments by foot (0.33). The problem of the response mode in slope-perception tasks is discussed.

- **Effects of object-based versus viewer-based transformations on imagined object views**

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Given a specific object image, participants were asked whether a second image could be of the same object. They were given the instruction that there are two ways to reach the correct answer. The participants either had to mentally rotate the object or they had to imagine themselves looking at the object from another position (ie the object-based condition and the viewer-based condition, respectively). In this way, an object-based  $y$ -axis rotation (180°) would result in the same image as a view of the object at the rear side. Similarly, a  $z$ -axis rotation (180°) or an  $x$ -axis rotation (180°) of the object would equal an upside-down view or a rear-upside-down view, respectively.

In the experiment, the objects had various types of symmetries and were oriented in different ways. Overall, the performance was better in the object-based condition than in the viewer-based condition. Furthermore, it appeared that objects with vertical symmetry generally revealed the best results. Finally, there was a remarkable increase in left-right confusions in the viewer-based condition as compared to the object-based condition. These results are discussed in terms of internal and external frames of reference.

- **The role of mirror symmetry in the perception of chromatically homogeneous figures**

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A chromatically homogeneous surface is not always perceived as a single figure. It can sometimes be perceived as the result of superimposing two or more figures; in such a case illusory contours

are seen bounding the figure in the foreground (Petter, 1956 *Rivista di Psicologia* **50** 213–227). Local factors, such as relatability, have been proposed in order to explain perception of two or more figures (Kellman and Shipley, 1991 *Cognitive Psychology* **23** 141–221). However, even when these factors are at work, there are conditions favouring the perception of a single figure which have not been explored so far. Here we propose that one such condition is the mirror symmetry of the surface.

We have run three experiments in order to study several aspects of the problem. The main results show that: (a) mirror symmetry enhances perception of a single figure; (b) effectiveness of symmetry increases with the number of axes of symmetry; (c) vertical and horizontal axes are more effective than a 45°-oriented axis.

We conclude that the global factor of mirror symmetry plays an important role in the perception of chromatically homogeneous surfaces, along with local factors, such as relatability and, more generally, good continuation.

## SPATIAL FREQUENCY AND CONTRAST

### ● A computational contrast-vision model for the analysis of anomalous contrast-sensitivity measurement

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We analysed cortical pathologies (Lado et al, 1999 *Perception* **28** Supplement, 72d) that produce a characteristic loss of contrast vision at high frequencies. However, the chosen model did not allow us to reproduce retinal pathologies, owing to the fact that it did not take into consideration the independence of the frequency channels.

This paper seeks to introduce modifications into the first levels of the model in order to allow for this analysis, and a subsequent differentiation between cortical and retinal pathologies. To do this, it introduces four different inhibition scales into the distribution layer of the inputs. Once the threshold level of the network is fixed, the outputs from that layer are integrated, thus generating the classic contrast-sensitivity curve for a normal observer.

If the pathologies are retinal, involving losses at both high and low frequencies, eg in glaucoma, the sensitivity of the lower levels is modified in order to reproduce an adequate response. If, on the other hand, the pathologies are cortical, involving a 50% decrease in the width of the kernels in the boundary cells, a simulation of the corresponding results is achieved. This decrease shams the abnormal long-range spatial integration of the signals which are observed in amblyopia and in other cortical pathologies.

### ● Contextual modulation of lateral interactions in contrast gain control

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Spatial interactions among gain control processes at early cortical levels of visual processing putatively mediate centre-surround contrast phenomena. The interactions have been assumed to be reciprocal with respect to centre and surround.

We measured both apparent contrast of the centre disk embedded in a surround and apparent contrast of the annulus surrounding the centre. Centres and surrounds were both sinusoidal gratings or plaid patterns (spatial frequency = 6 cycles deg<sup>-1</sup>). Two centre-surround contrast ratios were used (0.08/0.18 and 0.38/0.18). The diameter of the centre disc was 1 deg and the width of the annulus 0.17, 0.33, or 0.67 deg. Subjects compared the apparent contrast of the test centre (or surround) to an identically modulated disc with no surround (or annulus with no centre). A 2AFC method of constant stimuli was used to determine subjectively equal contrasts for test and comparison stimuli.

The apparent contrast of the centre decreased in all conditions as a function of surround contrast and width, replicating earlier results. However, centre contrast had a negligible effect on apparent contrast of the annulus, regardless of centre-surround contrast and size ratios. One interpretation of these results is that spatial interactions presumed to occur at early processing levels are influenced by higher-level information about scene organisation.

- **Transparent image presentation: The role of attention under discordant focus distances**

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See-through head-mounted displays (HMDs) presenting fixed-focus images are used to create augmented reality. We have investigated the role of attention in relation to five virtual-focus distances between 33 cm and infinity. We used a monocular head-mounted display (HOPROS<sup>™</sup>, Delft Instruments) to present transparent virtual images overlaying background images. Background images were presented on a 17-inch monitor at 1 m distance. The two images were perceived as one.

An effective stimulus comprised one Landolt-C within a circular configuration of seven hoops. A checkerboard was used as an affective stimulus. Stimuli were Gaussian blurred. A trial consisted of a fixation cross, the combined stimuli, and random noise subsequently. Correlating fixation either to effective or affective stimulus disband attention and task. Stimulus and presentation characteristics were randomised. Subjects score correct on Landolt-C orientation was obtained by means of a 2AFC paradigm.

Results showed attention to have effect, when virtual distance remained between observer and background image. For decreasing distance to the background, score correct increased when attention was tied to the effective stimulus. Subsequently, the scores decreased for attention tied to the affective stimulus. It suggests visual information retrieval to depend on attention, as focus difference influences distracting image characteristics.

- **A comparison of nonparametric adaptive psychophysical procedures**

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Nonparametric adaptive psychophysical procedures are those where the stimulus that is presented on a given trial depends upon the subject's response on previous trials, and the form of the psychophysical function is assumed only to be a monotonic function of the intensity of the stimulus. [See Treutwein (1995 *Vision Research* **35** 2503–2522) for an overview of these procedures.] Four procedures were compared on yes/no trials and six on 2AFC trials with a variety of psychometric functions, guess and lapse rates, etc. For each procedure studied, initial threshold estimates and step sizes were varied and relatively optimal combinations were chosen in order to compare the procedures.

All of the procedures were essentially unbiased. The worst procedure (parameter estimation by sequential testing with the minimum overshoot and undershoot sequential estimation) exhibited less than one-third the efficiency of the best procedure (stochastic approximation). Further, 2AFC trials require more than twice the number of presentations than yes/no trials in order to reach the same variability in threshold estimates, regardless of the procedures used. The best nonparametric procedures are easy to implement, relatively robust, and extremely efficient.

## VISUAL IMPAIRMENT

- **Processing of a visual illusion of length: a neuropsychological study**

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The neural basis of a visual illusion of length (the Brentano version of the Müller-Lyer illusion) was investigated by a neuropsychological approach.

The line-bisection performance of two groups of right-hemisphere-damaged patients, (a) with and (b) without left visual half-field deficits (assessed by perimetry and visual event-related potentials), associated with left spatial unilateral neglect, was assessed. Two conditions of manual bisection were given: setting the midpoint of (a) a horizontal line, and (b) of the shaft of the Brentano illusion, with either a left-sided ( $>-<=>$ ) or a right-sided ( $<=>-<$ ) expansion.

Both groups of patients set the subjective midpoint to the right of the objective centre of the line, consistent with the presence of left neglect. Patients with left hemianopia showed no illusory effects; these, in turn, were observed in patients without hemianopia, in both illusory conditions, in which they were additive to the rightward bisection bias.

Anatomical clinical correlations revealed an association of damage to the occipital regions with the lack of illusory effects. By contrast, more anterior damage sparing these regions (eg posterior parietal) did not affect illusory processing. The results are discussed in terms of a dissociation between visual and spatial processing of extension.

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**TUESDAY**
**PHARMACIA UPJOHN LECTURE**
**☛ The eye's optics, the trichromatic cone mosaic, and human vision**

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Human vision is limited by aberrations in the eye's optics and also by the photoreceptor mosaic, which has a dual role of providing both spatial and colour vision. The use of adaptive optics to correct the aberrations has provided new ways to measure these limitations, both by improving images of the retina and by improving vision. Adaptive optics made possible spatially resolved retinal densitometry, which was used to identify the individual S-, M-, and L-cones within large patches of foveal retina in two humans.

There were marked differences in the proportions of these cones between individuals and the cone types were distributed randomly. However, in spite of a three-fold difference in the ratio of L:M cones between the two humans, their wavelength choices for unique yellow were very close, indicating the important role of neural factors in stabilising unique yellow against such L:M cone variation. Adaptive optics were also used to present stimuli to the retina that were free from monochromatic aberrations, which resulted in improvements in visual acuity, even in white light. This argues against the notion that the resolution of the eye's aberrated optics and foveal cone spacing are optimally matched.

**ORAL PRESENTATIONS****COLOUR CONSTANCY**
**◆ Contrast and shift of perceived background colour in experiments on colour constancy**

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Under slow-changing illuminations, colour constancy is determined by the differences between the cone responses to light reflected from the background and from objects. We show that, under restricted adaptation, colour appearance is not solely determined by cone contrast. We evaluated colour appearance of a test chip on a neutral background (N5) under variable illumination (restricted time), using asymmetric colour matching: the test chip was matched by a reference chip on the same neutral background under a standard illuminant C (unrestricted time). Matching involved 41 Munsell chips (value 7, chroma 4 and grey N7) for 5–8 variable illuminants distributed around C point. Real chips and colour patches reproduced on a Barco Calibrator were used.

The ellipse representing chips matched in colour was centred around the point of grey-chip appearance, which was located on the line connecting coordinates of C and of a given illuminant on the  $u', v'$  chromaticity plane. This point did not coincide with the point representing colour appearance of the uniform background. The colour appearances of chips having similar cone contrasts (under variable versus standard illumination) differed.

Two hypothetical mechanisms may explain these results, one related to the cone contrast, and the second determined by the background colour to which observers are not fully adapted.

**◆ Colour constancy under conditions varying in spatial configuration**

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Colour constancy was studied for different spatial configurations of the stimulus pattern. A colour CRT was used to simulate the CIE  $x, y, Y$  values of Munsell chips as rendered under two extreme phases of daylight (yellow and blue, 4000 and 25000 K). The pattern consisted of a  $5 \times 7$  matrix of square patches on a neutral background that was either lighter or darker than the samples. The mutual separation between the samples was varied. The stimulus was presented successively to the left and the right eye, simulating two alternating illuminant conditions. Two observers matched the colour of 11 test samples under yellow illumination to the colour of corresponding samples as seen under the blue illuminant.

The observer responses, analysed in terms of cone-specific inputs to the visual system, were compared with predictions of Land's most recent Retinex algorithm (1986 *Proceedings of the National Academy of Sciences of the USA* **83** 3078–3080), and with a response function derived by the authors. Both models perform reasonably well for decremental stimuli, but less well for increments. Retinex predictions were about two times less accurate than predictions of the

response function. Since the latter takes local contrast as input, the results suggest that colour constancy is predominantly determined by the processing of local spatial information.

◆ **Relational colour constancy under rapid changes of illuminant on natural scenes**

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Temporal cues can aid colour constancy judgments with artificial Mondrian-like stimuli [Foster et al, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) S987]. Can such cues be exploited with stimuli that are more naturalistic?

A multi-spectral imaging technique was used to obtain images of natural scenes [Nascimento et al, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) S748]. For each scene, 33 images each 820 × 820 pixels × 10 bits × 10 nm were captured by a high-resolution digital camera with a fast-tuneable liquid-crystal filter. The reflectance function associated with each pixel was derived from a white reference in the scene. Captured scenes were then simulated on a high-resolution colour-graphics display.

Observers saw two alternating images: in image 1 the scene was illuminated by a daylight of 25 000 K; in image 2 it was illuminated by a daylight of 6700 K and the surface reflectance function of one particular object was simultaneously changed, by an amount which varied from trial to trial. Observers were able to detect these changes reliably, suggesting that temporal cues can be used in judging colour constancy with natural scenes.

◆ **Are horizontal cells crucial in colour contrast and colour constancy?**

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Colour constancy is one of the most fundamental physiological mechanisms, which involves peripheral and central parts of the visual system. We have detailed the processes of primary (peripheral) stages of the colour-constancy mechanism and developed an operating model. It includes the well known triad: receptor–system of horizontal cells–bipolar cell. We have assumed three types of horizontal cells, each of which is connected with a particular type of cones (L, M, S). These horizontal cells of each type are organised in three different systems of connected horizontal cells. According to this assumption, the illuminance distribution on the retina transforms into excitations of bipolar cells proportional to the contrast distribution for L-, M-, and S-channels independently, by means of regulation of horizontal cell systems. These processes underlie local adaptation in the achromatic system.

This simplified working model permits us to describe quantitatively colour constancy and thresholds for wavelength discrimination. The model is in good agreement with the fluctuation law and the Weber–Fechner law. The results of calculations performed on the basis of our model are in good agreement with experimental data.

[Supported by the Russian Foundation for Basic Research, grants 98-06-80001, 99-04-49647.]

## READING

◆ **Preferred retinal character size during the reading of text with varying print size by visually impaired and by sighted people**

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Visually impaired persons (VIPs) suffering macular degeneration have a narrow bandwidth in the sensitivity for spatial frequencies and thus are assumed to have, in contrast to sighted persons (SPs), a more-or-less fixed preferred retinal character size (PRCS) during reading.

To study explorative activities in adapting the PRCS during reading text of varying print size, eight VIPs (aged 37–81 years) and four SPs (aged 25–48 years) read text of six different print sizes (VIPs: 80 to 254 points; SPs: 5 to 160 points). Subjects were invited to walk forward to or walk backward from the display (space scaling behaviour) to select an optimal viewing distance for comfortable reading.



The data supported the hypothesis that VIPs use space scaling behaviour to attain a fixed value for the PRCS for reading large printed text. However, the concept of PRCS applied only to the situation in which the participant walked toward rather than backward away from the display. When walking backward the subjects stopped earlier than would have been expected on the basis of a fixed PRCS. In contrast to what was expected, this behaviour was also observed to the same extent in the SPs, pointing to a fundamental process in scaling behaviour during reading and object recognition.

◆ **Letter case and text legibility**

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Common wisdom and numerous sources within the literature on typography assert that mixed uppercase and lowercase text is more legible than all uppercase (all caps). If this is true, then lowercase text alone should be more legible than all caps, since uppercase letters are relatively infrequent. Some studies that have shown an effect of word shape on word recognition have indeed suggested that the shapes of lowercase words are more distinctive than their uppercase counterparts. Are mixed-case and lowercase words more readable than all-caps styles?

Using TrueType Arial and all caps, all lowercase, and mixed-case conditions, we assessed (a) size thresholds for random letter strings and (b) reading speeds for ordinary text (using serial visual presentation) in both normal and visually impaired participants. Size thresholds (with point size characterising letter size) for lowercase were 25% higher than for all caps; thresholds were intermediate for mixed case. No significant effect of case on reading speed was found.

These results suggest that, in contrast to widespread belief, all caps may in fact be more legible (and more economical) to print than mixed or lowercase styles, because lower point sizes can be used than with the other case styles.

◆ **Recognition of low-contrast characters by subjects with cerebral visual-field defects**

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Cerebral visual-field defects following brain injuries are as a rule diagnosed by automatic perimetry, where low-contrast-stimulus detection is the criterion of visibility.

To extend perimetric testing, we compared, in patients and normals, contrast thresholds for the recognition of characters (digits, size 2.4 deg) to those for detection of Gabor patterns (1 cycle deg<sup>-1</sup>,  $\sigma = 1.5^\circ$ ) in the intact and defective visual field at 32 visual field positions. Foveal testing was done for three stimulus sizes (1, 2, and 4 deg). Subjects were ten homonymous hemianopic patients and ten healthy volunteers. The results were compared with the visual field obtained on a Tübingen Automatic Perimeter and with qualitative high-resolution perimetry. Foveally we revealed a significant loss of recognition sensitivity, but not of detection sensitivity, in the patient group. In the zone of transition from the intact to the defective field there was a gradual sensitivity decrease in both recognition and Gabor detection. Most interestingly, recognition sensitivity in some patients was impaired within the intact visual field itself.

The results indicate that visual-field defects following cortex lesions lead to decreased performance in recognition tasks not only along the border of the field defect but also in the intact parts of the visual field.

◆ **The changes in reading rate that result from letter spacing are attributable to the detection of word boundaries, and not the visibility of letters**

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When reading rate decreases with the increase or decrease of letter spacing, does this occur because the changes in letter spacing affect the visibility of individual letters, or because they affect people's ability to detect the boundaries of a word? We found that when letter spacing increased (centre-to-centre spacing >2M), subjects' reading rates fell, unless the spaces between words also increased (5M spaces between words). This was true for 0.5, 1.0, and 2.0 deg letters. Letter size did not affect reading rates. When there were no spaces between words, letter size did affect reading rate.

These experiments support the proposition that increases in letter spacing lead to decreases in reading rate because of a decrease in the ability to detect the boundaries of words; the visibility of letters affects reading only when word recognition can be accomplished through letter-by-letter reading.

## SHADOWS AND EDGES

### ◆ **Extra lightness information at cast illuminance edges**

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Intrinsic-image models of lightness parse the retinal image into overlapping layers of illumination and reflectance. Anchoring theory parses the image very differently—into frameworks, or perceptual groups. These approaches seem incompatible, even though both capture important aspects of lightness experience.

Recent experiments on a lightness paradox point towards a possible resolution. When an illuminance boundary falls across an object, observers give different Munsell matches for its lighted and shadowed parts, but paradoxically report the object to have a single reflectance. Lightness matches given for the whole object are more veridical than those given for its lighted and shadowed parts. And lightness matches for an object lying under a cast illuminance boundary are higher than for objects that fall entirely within a field of illumination.

Exactly the opposite results have been reported for objects at an occlusion edge that forms the boundary of a region of illumination. These findings suggest that cast illuminance edges (i) provide an information bonus for objects they cross, and (ii) play a crucial role in our experience of layers. This in turn implies a role for both edge classification and a visual experience of layers within an anchoring model of lightness.

### ◆ **Shadows are fuzzy and straight; paint is sharp and crooked**

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Brightness illusions typically involve cues for lightness constancy. Evidently, the process of discounting illumination can cause identical grey patches to appear different. The visual system can utilise various cues to distinguish illumination variation (shadows) from reflectance variation (paint). For example, fuzzy edges are likely to be shadow, and fuzzy transitions can support strong illusions. Similarly, White's illusion depends on T-junctions, and the Ts arguably provide evidence for an illumination edge.

We now report a new cue. Contour straightness can strongly affect illusion strength; we propose that crookedness vs straightness is a cue for paint vs shadow. We do not claim that shadows in nature are usually straight; rather, we claim that the visual system 'believes' that they are.

We have modified White's illusion to retain the Ts but not the straight contours; the illusion is decreased. We have put straight and crooked contours in direct competition by crossing them to form plaids; the straight components dominate the illusions, indicating stronger discounting. We have studied the role of straightness in the snake and anti-snake illusions. Finally we have combined cues to produce remarkably strong brightness illusions.

### ◆ **'Coloured shadows': why are they so vivid?**

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The 'coloured shadows' first described in detail by Goethe in 1792 are held to be a special case of simultaneous colour contrast. The effect is much stronger than in the 'normal' case in which a test field is presented within a highly saturated surround. This is surprising because the surrounds of coloured shadows appear highly unsaturated, and induction depends on purity (Valberg, 1974 *Journal of the Optical Society of America* **64** 1531–1540).

In order to understand this discrepancy we investigated the phenomenon by matching the perceived colour by means of a computer monitor. All coloured areas were radiometrically analysed, and the CIE chromaticity coordinates  $x$  and  $y$  and the luminance  $Y$  determined. In the case of red, yellow, and green, we found that the purity of the induced colour was about half the purity of the inducing surround. The effect was much weaker for the blue surround. By matching the inducing surround, we found a decrease in purity in about the same direction and range as the increase in purity of the coloured shadow. The specific effect of the coloured shadows is due to the high luminance of the surround which always exceeded (except for blue) the luminance of the shadow.

### ◆ Separation of filling-in and boundary-detection mechanisms

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It is often assumed that boundary formation initiates filling-in, independently at different spatial scales; this implies that edge-detection and filling-in mechanisms receive input from filters tuned to the same spatial-frequency band. This assumption was studied with critical-band-masking applied to the Chevreul illusion.

Isotropic noise was added to the Chevreul-staircase stimulus. The centre spatial frequency of the noise was varied in 15 steps (0.5–12 cycles deg<sup>-1</sup>, 1 octave) and the bar width of the Chevreul-staircase in 13 steps (0.24–4.2 deg, constant luminance step). The task was to evaluate whether the characteristic brightness pattern, the scallopy appearance of the bars, was visible. Each stimulus was presented 15 times and the frequency-of-seeing was measured by the method of constant stimuli.

Noise of any spatial frequency below a critical spatial frequency was found to mask the brightness pattern. The critical frequency appears to be 1–2 octaves above the spatial frequency of the lowest 1 octave bandpass filter responding to the edges. When masking occurs, the edges seem to ‘float’ on the noise. Surprisingly, the steps are not visible—instead, the noise ‘owns’ a smooth luminance gradient. These findings suggest that, although edge detection may operate independently at different spatial scales, filling-in requires pooling over low spatial frequencies.

## DYSLEXIA

### ◆ Accuracy of visual and auditory representations in dyslexia

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Poor readers often suffer from a variety of basic visual and auditory deficits. Yet, the relations between these deficits have been hardly studied. We characterised the performance of adult dyslexics in two homologous tasks: visual-spatial frequency discrimination between sinusoidal gratings and auditory pure-tone frequency discrimination. Both tasks were measured with temporal 2AFC paradigms.

More than half of the poor readers had severe difficulties with the visual task, while subjects from the control group did not have similar difficulties. Visual deficits were found in about 40% of the poor readers with high scores in other cognitive tasks (eg Raven matrices), and in 70% of the poor readers whose cognitive scores were intermediate or lower. In this group, which also consists of the least accurate speech discriminators, auditory performance was impaired as well.

Proficient reading requires the blending and segmenting of visual and auditory stimuli that are serially sampled in a rapid manner. We propose that the inability of the majority of poor readers to rapidly establish an accurate perceptual (visual and auditory) trace and retain it impedes the acquisition of reading by these individuals.

### ◆ Motion coherence and transparency in dyslexia

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Developmental dyslexics have displayed motion perception deficits in several recent studies. Are these deficits equally important in elementary and more complex motion processings?

Adult developmental dyslexics and controls were tested in two motion tasks. In the motion-coherence task, observers looked at a plane moving in one direction (left or right) and then in the opposite direction. Their task was to report which plane moved faster. In the motion-transparency task, observers looked at the superposition of two planes moving in opposite directions. Their task was again to report which plane moved faster. Discrimination thresholds were recorded and compared across tasks and population of observers.

Transparency thresholds were found to be higher than coherence thresholds for both dyslexics and control observers. There was a trend for higher thresholds for dyslexics in both tasks but this trend did not reach significance. Thus, no significant difference was found between dyslexics and control observers in our motion-coherence and motion-transparency tasks. These results question the validity of a general magnocellular pathway deficit in developmental dyslexia.

◆ **Effects of visual training on antisaccade control in dyslexia**

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Dyslexic children may exhibit deficits in generating saccades and/or in maintaining fixation. We report here the effects of daily practice of three visual tasks on the saccadic performance of 85 dyslexic children in the age range of 8 to 15 years. The children were selected from among other dyslexics because they showed deficits in their voluntary saccade control. Their eye movements were measured in an overlap prosaccade and a gap antisaccade task before and after the training. This training included three conditions: a fixation, a saccade, and a distractor condition. In each condition, the subjects had to detect the last orientation of a small stimulus which quickly changed its orientation before it disappeared. The subjects had to press one of four keys corresponding to the last orientation. The visual pattern was presented on an LCD-display of an instrument given to the children for use at home.

The results indicate that daily practice improved not only the perceptual capacity, but also the voluntary component of saccade control within 3 to 8 weeks. After the training, the group of dyslexics was no longer statistically different from the control group with respect to their voluntary saccade generation.

◆ **Fixation, saccade control, and dynamic vision in dyslexia**

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Dyslexics may have deficits in their magnocellular system, which projects from the visual cortex dorsally to the parietal and frontal areas. It is therefore suggested that dyslexics exhibit deficits in both dynamic vision and saccade control.

We studied the capacity of 140 control and 366 dyslexic children (aged 7–16 years) to detect the last orientation of a rapidly changing small pattern. In one task, stationary fixation was required. In the saccade condition, the pattern was displaced suddenly to one or the other side. In a third condition, a distractor was presented on one side before the oriented pattern appeared on the opposite side.

The performance improved with age in both groups. In all three conditions, the dyslexics performed significantly below the level of the controls. The differences between the test group and the control group were largest in the distractor condition. When compared with eye-movement performance in a gap antisaccade task, a parallel development was observed in both groups. The dyslexics exhibited significant deficits. The study shows that a certain percentage of dyslexic children has difficulties in visual perception in the time domain as well as in generating voluntary saccades, both tasks presumably challenging the magnocellular system.

## POSTER SESSION 3

### ANATOMY AND IMAGING

● **Contrast dependence of visually induced cortical oxygen changes**

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We used functional magnetic resonance imaging (fMRI) to indirectly measure contrast dependence in the response of cortical cell ensembles by visualising changes in cortical blood oxygen levels (BOLD response). Four stimuli were presented in sequence: a dark square, a bright square, a black-and-white checkerboard, and a white-and-black checkerboard.

The correlation was calculated between the signal strength of each voxel of the fMRI response and the corresponding stimulus condition. Seven different contrast values between the bright and dark elements of the checkerboard were used: 1%, 2%, 4%, 8%, 16%, 33%, and 96%. The cortical activation caused by presentation of the checkerboards was relatively independent of stimulus contrast in four observers down to a contrast around 3%, but declined sharply for lower contrasts. Predominantly occipital areas were activated, and the distribution of activation of areas was also rather constant down to contrasts around 2%–4%.

We conclude that an fMRI response specific for figure–ground segregation is clearly present as early as the level of the primary visual cortex V1. This segmentation-specific activation is relatively independent of stimulus contrast down to contrast levels around 4%, but its distribution over cortical areas may vary among observers.

- **The human homologue of macaque area VIP**

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The macaque ventral intraparietal area (VIP) is located in the fundus of the intraparietal sulcus and may play an important role in the encoding of movements and navigation of the head in peripersonal space. A prominent feature of VIP neurons is the sensitivity for the direction of stimulus motion across different modalities and the encoding of polymodal sensory information in a common frame of reference. Interestingly, hemispatial neglect, a polymodal disturbance of the egocentric frame of reference in humans, is often found after damage to inferior parietal cortex.

We were accordingly interested in the question whether a homologue of macaque area VIP exists in humans. Eight healthy subjects participated in an fMRI study in which visual, tactile, and auditory stimuli were applied in order to test for multimodal responses. By employing a conjunction analysis, we show the existence of four cerebral regions activated by all three stimulus types. For one of these areas, the local maximum of neural activity is located in the fundus of the sulcus. On the basis of its functional and anatomical characteristics we consider this inferior parietal region to be the human homologue of macaque area VIP.

[Supported by DFG (FB: SFB 509/B7) and (GRF: SFB 194/A16).]

## ATTENTION, TEXTURE, AND VISUAL SEARCH

- **Orthographic structure mediates peripheral letter-string identification**

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There is a general assumption that visual word recognition is automatic and occurs whenever a letter string is perceived (Stroop, 1935 *Journal of Experimental Psychology* **18** 643–662). We tested this assumption by manipulating target letter strings across three experiments.

Target strings were words, orthographically legal non-words, or orthographically illegal non-words. The experiments were designed to test the effect of retinal eccentricity of a target string and visual similarity of a distractor string on response latencies. Main effects of visual similarity and eccentricity were found for all experiments. An interaction was found between eccentricity and visual similarity for words and orthographically legal non-words. No interaction was found for orthographically illegal non-words. The results suggest that identification of letter strings is mediated by orthographic structure.

In a further experiment, we examined the influence of orthographic factors on eye-movement latencies. Previous work on eye movements has shown that there is a characteristic pattern of increased saccade latencies (20–40 ms) when subjects are presented with simultaneous bilateral targets in different hemifields. This is known as the ‘remote distractor effect’. Using this paradigm, we found orthographic effects on saccade onset latencies.

- **Bisection of tilted lines in monocular viewing conditions**

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Errors in bisecting a line visually are generally explained as a result of perceptual, attentional, and motor factors. Many studies had focused on bisection of horizontal lines in the binocular condition.

To explore other variables, we investigated bisection of tilted lines in monocular conditions. Observers tried to place a cursor at the middle point of lines with orientations that varied counterclockwise from 0° (horizontal line) to 165° on a computer screen. The line lengths varied from 2.86 deg to 14.04 deg. Errors were generally less than 3% and not affected by line length. They tended to be unaffected by line orientation in monocular viewing by the right eye, but they varied systematically as a function of line orientation in monocular viewing by the left eye. The cursor tended to be placed to the right of the line centre. The error peaked at 120° orientation, and the null errors were found with lines tilted about 45°.

We suggest that the difference between the right eye and the left eye in bisecting lines may be related to subcortical mechanisms of attention.

- **Template effects in search for linearly separable and non-separable targets.**

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Recent research (Bauer et al, 1998 *Perception & Psychophysics* **60** 1083–1093) has shown that visual search for a target amongst distractors is 'serial' or difficult if the target is nonlinearly separable from the distractors in a particular feature space (eg colour or size). In contrast, if the target is linearly separable from the distractors, search is easy/parallel. Interpretations of this result have stressed the role of bottom-up factors rather than how stimulus processing might be modulated by expected information about targets.

We investigated this issue in two visual-search experiments, using small, medium, and large circles as possible targets. In the first experiment participants could use knowledge of the target to guide search, whilst in the second experiment the target was unknown on each trial. We found that search for a medium (nonlinearly separable) target amongst small or large distractors benefited least from knowledge of the target as compared to search for a small or large target. Search for linearly separable targets is efficient in part because of the more accurate specification of memory templates for these items.

- **Interactions between orientation and contrast in the processing of texture cues**

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The similarity of models for texture segmentation based on modulations of orientation and second-order processing (in particular the processing of modulations of local contrast) suggests that the two types of cue might be processed within the same early mechanism. If this were so, we might expect facilitatory interactions between these cues. Thresholds for detecting sinusoidal (vertical,  $0.2 \text{ cycle deg}^{-1}$ ) contrast modulations of an oriented-bandpass-filtered noise carrier (centre frequency =  $8 \text{ cycles deg}^{-1}$ ) were measured in the presence of similar modulations of the carrier orientation. The dominant carrier was either vertical or horizontal. Six levels of orientation modulation were used (0, 1, 2, 4, 8, and 16 times detection threshold).

No facilitatory interactions were observed, suggesting that the two cues are not processed in a single channel. However, thresholds for detecting contrast modulations rose with increased orientation modulation, suggesting that the cues interact in a later gain-control-type mechanism. The masking effect is slightly stronger when the dominant orientation of the carrier is vertical rather than horizontal. Given the striking difference in appearance between orientation modulations of carriers with the two dominant orientations, this suggests that interactions may depend, to a degree, on the overall percept created by the image.

## **BINOCULAR AND SPATIAL VISION**

- **Testing predictions from a Bayesian analysis of optimal and robust use of stereo information**

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Differences between the two eyes' views of the world carry information about 3-D scene structure and eye positions. The contemporary Bayesian approach to perception implies that human performance based on this source of eye-position information can be analysed most usefully by comparison with the performance of a statistically optimal observer.

Porrill et al [1999 *Nature (London)* **397** 63–66] argued that the comparison observer should also be statistically robust which leads to qualitatively new behaviours. When stereoscopic stimuli containing inconsistent vertical-disparity information about eccentricity of gaze were presented, estimates recorded from one robust ideal observer (RIO) bifurcated at a critical value of stimulus inconsistency. Porrill et al reported that human observers show the predicted bifurcation phenomenon and that this critical value can be used to estimate the vertical-disparity acuity of an observer.

Here we show how the RIO model predicts a different location of bifurcation point when the inconsistent vertical-disparity information is about fixation distance, achieved with different scalings, and that the bifurcation point is dependent on stimulus size. We provide data from human observers displaying similar behaviour, giving further strength to the proposal that the human visual system's use of vertical-disparity information is optimal and robust.

● **Foveal crowding effect: masking interactions or nature of the highest spatial-frequency mechanism?**

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We have suggested (Bondarko and Danilova, 1995 *Perception* **24** Supplement, 124b) that both foveal crowding effects and lateral masking may be explained by spatial-frequency interactions at the resolution limit in the human visual system.

Following this assumption, we ran a set of psychophysical experiments where a test Landolt C was surrounded by several types of distractors, including rectangular gratings having different spatial frequencies. In this experiment, we attempted to test spatial-frequency tuning of the crowding effect, because this tuning is a characteristic feature of lateral masking (Polat and Sagi, 1993 *Vision Research* **33** 993–999). All the distractors ‘crowded’ the target Landolt C in a similar way showing absence of frequency tuning. This made us reject the hypothesis about masking-frequency interactions underlying foveal crowding phenomenon. Instead, we consider the highest-spatial-frequency mechanism whose properties constrain performance in this visual task. We calculated the spatial-sensitivity profiles of the spatial elements corresponding to this mechanism using space constants provided by Wilson and Gelb (1984 *Journal of the Optical Society of America A* **1** 124–131). The corresponding even functions have on-zones and off-zones whose extent matches the peaks and troughs of masking functions when a test Landolt C is surrounded by distracting bars (cf Flom et al, 1963 *Journal of the Optical Society of America* **53** 1026–1032).

[Supported by RFBI 98-04-48558.]

● **Rigidity in kinetic depth effect**

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The aim of this study was to evaluate predictions of two models of amodal 3-D percepts (model of 3-D rigid structure and model of 3-D elastic structure). Perception of an amodal object was based on two dots moving along parallel horizontal trajectories. Indicator of rigidity was specified in terms of the difference between lengths estimated at the central and peripheral loci of estimation. An additional aim of this study was to establish whether the distance between the dots could influence rigidity of the perceived object.

In the first experiment, three factors were varied: (a) length of trajectory, (b) distance between dot trajectories, and (c) locus of estimation. Subjects were asked to estimate the distance between the dots in depth. The results suggest that both models are valid, although their prediction depends on the length of trajectory. The model of 3-D rigid structure is valid in the case of short trajectories, whilst the model of 3-D elastic structure is valid in the case of long trajectories. In the second experiment the influence of dot velocity on the rigidity of the percept was investigated. The results indicate that dot velocity does not influence rigidity of the perceived 3-D object.

● **Varignon in visual space**

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In an earlier experiment, Koenderink et al (1999 *Perception* **28** Supplement, 13c) investigated the intrinsic projective structure of the visual ground plane, and showed that observers’ collinearity judgments satisfy a theorem by Pappus (340 AD).

In the present study, we investigated the intrinsic affine structure of the visual ground plane using a more recent theorem by Varignon (1700). The theorem states that the midpoints of opposite sides of a quadrilateral define two line segments that exactly bisect each other. Observers saw a ground plane in virtual reality with two fixed marker stakes and one moveable probe stake. They had to place the probe on the midpoint between the markers. In the first phase of the experiment, observers repeatedly bisected edges of quadrilaterals while only seeing one edge at a time. They were unaware of the transition to the second phase, in which the position of the markers was the average of their earlier bisections.

We tested the theorem by checking whether the midpoints in the second phase were coincident. In the majority of cases the settings were statistically different from the physical midpoints, but the bisections in the second phase were statistically indistinguishable, which confirms Varignon’s theorem.

- **The mechanisms of second-order stereopsis are not unitary**

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The nature of the neural mechanisms underlying second-order stereopsis is still uncertain. Various methods of (for example) contrast envelope extraction from monocular images, followed by binocular correlation, seem plausible candidates. We have suggested previously that there are at least two mechanisms: one sensitive and one insensitive to interocular orientation differences [Wells and Simmons, 1997 *Investigative Ophthalmology & Visual Science* **38**(4) S906].

In a fully crossed experimental design we measured contrast thresholds for stereoscopic depth identification (front/back) using Gabor stimuli. Stimulus carrier spatial frequency, envelope size (ie spatial frequency and orientation bandwidth), and disparity were systematically varied. The carrier orientations were either the same (horizontal) in each eye or mutually orthogonal (horizontal/vertical) in order to test only second-order stereopsis. Contrast thresholds for stereopsis were normalised to those for simultaneous monocular detection of the same patterns.

The complex pattern of threshold dependences found, and associated computer modelling of the results, suggest that second-order stereopsis must be subserved by a variety of mechanisms with varying sensitivities to carrier spatial frequency, disparity, and envelope size, rather than a single class of envelope-extracting processes (see also Wells and Simmons, 1999 *Perception* **28** Supplement, 133a; Hess et al 1999 *Journal of the Optical Society of America A* **16** 987–994). [Supported by a Royal Society Research Grant to DS.]

- **2-D tilt and 3-D slant illusions in perception and action tasks**

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There is now a well established dissociation between perception and action based primarily on neuropsychological evidence [Milner and Goodale, 1995 *The Visual Brain in Action* (Oxford: Oxford University Press)]. Although equivocal, an important source of evidence from normals is that 'perceptual illusions' may affect the systems differently (see Franz et al, 2000 *Psychological Science* **11** 20–25).

Here we investigate the relative effects of 2-D tilt and 3-D slant illusions in the two domains, using similar 'posting' tasks to those employed originally by Milner and Goodale. Subjects were required to either 'post' a card through, or set a paddle to match the orientation of, a vertical plane which was presented in two conditions: surrounded by a striped surface tilted between  $\pm 90^\circ$  (2-D tilt contrast), or surrounded by a disparity-defined surface slanted or inclined in depth between  $\pm 60^\circ$  (3-D depth contrast). For 2-D tilt, action and perception were equally affected by the illusion, whereas in the 3-D condition they were not. Here, the illusion appeared greater in the posting than in the perceptual task. This difference was greater for slant than inclination. We conclude that, although no qualitative differences exist, there were quantitative differences between perception and action tasks in the binocular condition.

## COLOUR AND BRIGHTNESS

- **Simple brightness models with low-pass and Gabor filters**

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A syntactical brightness model based on a multiscale line and edge representation obtained by a set of anisotropic Gabor filters is quite complex (du Buf and Fischer, 1995 *Optical Engineering* **34** 1900–1911). Although only tested in 1-D, it was shown to yield correct brightness effects for many patterns. It has also been shown that isotropic low-pass filters in combination with bandpass ones can account for a specific version of the White effect in which different lengths of the flanking bars can lead to simultaneous brightness contrast as well as assimilation (du Buf, 1992 *Perception* **21** Supplement, 80c). Although not considered in most existing models, low-pass filters are required for creating a brightness background.

Recent experiments have shown that very simple 2-D models, in which the responses of low-pass and Gabor filters are directly mixed, can predict Mach bands, grating induction, simultaneous brightness contrast, and assimilation for many patterns, including the specific version of the White effect. Because such models cannot predict the illusory brightness in the Kanizsa triangle and the Ehrenstein circle, we conclude that the 1-D syntactical model must and can be extended to 2-D, because the multiscale line and edge amplitudes are obtained from the Gabor responses.



- **Colour categories in children and adults**

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Paper T-shirts equally spaced along achromatic (black to white) or chromatic (constant lightness and saturation, variable hue) continua were used to study classification and X-AB discrimination in children (average age 4.5 years) and adults (average age 28 years). Individual categorical boundaries along each continuum were estimated by asking observers to sort coloured T-shirts into two teams according to the perceptual similarity with either end-point of the continuum. The experimenter never used colour names. Boundaries were more variable in children than in adults.

However, the two groups did not differ in the X-AB task: irrespective of age, observers discriminated straddling-the-boundary pairs better than within-category pairs. The analysis of AB pairs that included the boundary for some children but not for others indicated that the very same two chips were better discriminated by children who assigned them to different categories than by children who assigned them to the same category.

The development of colour categories entails an increase of inter-observer agreement, but the sensitivity to colour differences and the amount of the categorical boundary effect do not change. Minor differences between achromatic and chromatic continua are discussed. [Supported by MURST.]

- **Mensurating the colour circle: Ostwald's 'principle of internal symmetry'**

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There exist two types of 'colour atlases' that are different in kind: those based upon eye measure and those based upon colorimetric principles. The best known example of the former is Munsell's atlas, of the latter that of Wilhelm Ostwald. Both date from the early 19th century.

Eye measure is intrinsically subjective, whereas colorimetry is a fully objective discipline, involving only judgments of indistinguishability. When the aim is a subdivision of the colour circle in 'equal parts', eye measure simply leaves it up to the observer to do something (anything is—in principle—equally valid). The colorimetric method stands in need of some means to establish 'equal spacing' and Ostwald's 'principle of internal symmetry' provides exactly that. We show that the original principle is flawed and how it can be mended. We calculate an equally tempered colour circle based upon the principle and compare it to the Munsell (eye measure) result.

We find that the differences are small (1 to 2 steps on a 24-hue scale) and of the same order as differences between various published eye-measure results. This implies that eye measure veridically reflects the spectral differences, filtered through the fundamentals.

- **Interactions within chromatic mechanisms underlying visual search for a colour target**

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Our aim in this study was to explore the interactions between achromatic and chromatic mechanisms and within two chromatic mechanisms in visual search for colour.

Target colours were chosen to lie along the L–M or S axes. We measured reaction times (RTs) to search the colour target under conditions: (a) distractors were all identical to each other and lay along the same axis as the target, but less saturated than the target; (b) distractors were heterogeneous and nine distractors were varied along the chromatic cardinal axis which was orthogonal to the target axis; and (c) distractors were varied along the achromatic axis.

RTs were measured also for achromatic targets lying along the achromatic axis under conditions: (d) that distractors were all identical and lay along the achromatic axis; (e) and (f) distractor colours were varied along chromatic axes.

For chromatic targets, RTs in condition (b) increased above those in (a), but RTs in condition (c) were similar to those in condition (a); whereas, for achromatic targets, RTs were similar in all conditions (d), (e), and (f). This implies independence of chromatic and achromatic mechanisms, and interactions between the two chromatic mechanisms or the existence of non-cardinal axes tuned to intermediate hues.

- **Quantitative measurement of colour contrast**

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Apparent colour is known to change where the nearby background colour is somewhat different. That is due to colour contrast. But the mechanism of this phenomenon is not completely understood (Shepherd, 1999 *Vision Research* **39** 1329–1345).

We designed an experiment to investigate colour contrast. A computer-generated stimulus pattern consisted of test stimuli 0.8 deg in diameter surrounded by a red (5R) or blue (5B) annulus (background) 5 deg in diameter. The brightness of the test stimuli and the background was the same (6 cd m<sup>-2</sup>), but colour saturation of the annulus was varied. The colour of the test stimuli was randomly varied between achromatic and background colour. The observers judged when the test stimuli appeared achromatic. The perceived grey depends both on the colour of the background and the size of the black ring interposed between the test stimuli and the annulus. Changes in the perceived colour of the test disc first increase and then decrease as the saturation of the background increases. The black ring between the test stimuli and the background always reduces the change in the colour of the test stimuli.

A vectorial model of interaction between the stimuli and the background is presented and the influence of these phenomena on colour constancy is discussed.

## EYE MOVEMENTS

- **Semantic effects on the detection of intrasaccadic changes of object orientation and position**

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Verfaillie et al (1994 *Journal of Experimental Psychology: Learning, Memory and Cognition* **20** 649–670) found that whereas intrasaccadic changes in in-depth-orientation of a point-light walker were easily detected, intrasaccadic changes in image-plane position were not. This is because transsaccadic integration subserves object identification, and object orientation, unlike object position, is an integral part of the viewpoint-dependent object representations that are matched to achieve identification. Boucart and Humphreys (1997 *Perception* **26** 1197–1209) found that object semantics interfered with object matching whenever matching required a global shape judgment. This is because shape is an integral part of the representations in the object lexicon which interfaces object identity and semantics.

Combining these findings, we hypothesised that object semantics should interfere with the detection of intrasaccadic changes in object orientation, but not in object position. To test this, viewers performed saccades from one object to another and had to detect intrasaccadic changes in the position or orientation of one of the objects. The objects were categorically related or unrelated. As predicted, semantics interfered with the detection of a change in orientation, but not of a change in position. Moreover, interference was strongest for related foveal and extrafoveal objects in similar orientations. We conclude that transsaccadic object perception is mediated by an object lexicon containing orientation-dependent but position-independent representations.

- **Unintended saccades can be executed without presaccadic attention shift**

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In an antisaccade task, subjects produce 19% erroneous prosaccades to the stimulus. When subjects were asked to indicate such erroneous prosaccades, they did not recognise 62% of them (Mokler and Fischer, 1999 *Experimental Brain Research* **125** 511–516). We hypothesised that these involuntary reflexive prosaccades planned simultaneously with voluntary antisaccades are programmed without presaccadic attention shifts.

In a dual-task paradigm, subjects performed antisaccades to a stimulus that appeared right or left of a central fixation. Also they discriminated between letters (E and mirror-E) which were presented for short durations before the eye movement either at the stimulus position or on the opposite side (instructed saccade goal). Additionally, they pressed a button when they thought that they had made an erroneous prosaccade.

For the correct antisaccades (as for prosaccades in a prosaccade-control task) the data confirmed classical results: discrimination was selectively enhanced at the saccade goal (Deubel and Schneider, 1996 *Vision Research* **36** 1827–1837). For unperceived erroneous prosaccades, however, discrimination was far better where the subject wanted to look than where the subject actually

looked. We conclude that visual attention is focused in accordance with the voluntarily planned saccade, and decoupled from the simultaneously executed unintended prosaccade into opposite direction.

- **The influence of an auditory accessory stimulus on target choice and reaction time with two visual stimuli**

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Subjects were instructed to look at any one of two visual stimuli presented at eccentricities of 8 deg or 24 deg to the right or left of fixation. The intensity of the visual stimulus at 8 deg was matched to that of the visual stimulus at 24 deg for equal choice probability. An auditory stimulus (white noise) was presented, via a virtual acoustic environment at the same eccentricity as either visual stimulus and with a stimulus onset asynchrony (SOA) of -50 ms, 0 ms, or 50 ms.

Although subjects were instructed to ignore the presence of the white noise, subjects gazed more often at auditorily accompanied stimuli than at unaccompanied ones for all visual stimulus pairs. This was more pronounced for stimuli at 24 deg than those at 8 deg and for SOAs of -50 ms and 0 ms than those of 50 ms. Furthermore, for both visual stimuli, reaction times for auditorily accompanied stimuli at either eccentricity were always shorter than for unaccompanied stimuli. The results provide evidence that audiovisual interaction increases with eccentricity of the stimuli.

## LEARNING, MEMORY, AND DEVELOPMENT

- **Spatial integration of local orientation on the perpendicular bias in children's drawing**

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Orientation coding develops early in infancy and by the age of 5 years children can copy and draw horizontal, vertical, and oblique lines with almost adult-like performance. Yet this competence can easily break down—when an oblique baseline is attached to the vertical line to be copied, children reliably perpendicularise the orientation of the test-line relative to the baseline. This 'perpendicular bias' is one of the most robust spatial phenomena in development (Bremner, 1984 *Perception* 13 117–128).

In order to study the spatial constraints on this bias we varied the separation between the test-line and the baseline. Spatial separations tested were 0 cm, 1 cm, 2 cm, 4 cm, and infinity (no baseline present), presented in random order. Forty-eight children (aged between 5 years and 1 month and 6 years and 6 months) were asked to copy the test-line (4 cm), onto a pre-drawn baseline (8 cm). The results show that, as spatial separation increases, the bias gradually and significantly decreases (from 19° to 1°). We suggest that the bias results when angular coding occurs via the integration of two local orientations and is therefore reduced when baseline and test-line are spatially separated.

This finding has important implications for theoretical accounts of the perpendicular bias and the development of spatial coding in general.

- **Influence of the illuminant in the comparative study of simultaneous and successive colour matching**

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Following up the line of work developed by our group in the field of colour memory under different observation conditions (Perez-Carpinell et al, 1998 *Color Research and Application* 23 234–237, 416–427), we have studied how changes in observation illuminant influence the perceptual descriptors and the total colour difference between pairs of matched samples, both by simultaneous matching and memory matching.

Two experiments were carried out (symmetric and asymmetric matching), each consisting of two parts: simultaneous matching and successive matching (or memory matching). In the symmetric matching, samples were always seen under D65 illuminant. In the asymmetric matching, the observers matched first the samples haploscopically, but each eye was adapted to a different illuminant (D65 and A) and, at a second stage, samples were memorised under D65 and recognised under A. The results were analysed with the SVF space (Seim et al, 1986 *Color Research and Application* 11 11–24), which is specifically adapted to the Munsell Colour Atlas and presents a high degree of uniformity.

We conclude that the best-matched colours, both by simultaneous matching and by memory, lie along the red–green axis, whereas the worst-matched colours lie along the blue–yellow axis.

## MOTION PERCEPTION AND OPTIC FLOW

### ● Optimal spatial frequency in the Ouchi illusion

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The illusory sliding motion in the Ouchi pattern can be used as a clue to uncover the way we integrate local motion signals into a 2-D or a 3-D structure (Fermuller et al, 2000 *Vision Research* 40 77–96). Hine et al (1995 *Vision Research* 35 3093–3102), using simplified patterns that consisted of 1-D gratings, reported that the optimal spatial frequency was around 10 cycles  $\text{deg}^{-1}$ , which is surprisingly high for a motion-related phenomenon. Fermuller et al explained this result by the receptive-field size, which lead us to conjecture that the optimal spatial frequency may depend on the stimulus size.

The present study basically supports this conjecture. Both for the checkerboard and the grating patterns, the optimal spatial frequency was shifted downwards as the inset size was increased. The inverse was not exactly the case: the optimal spatial frequency was only halved when the inset was four times as large. The results are in line with the idea that the Ouchi illusion reflects two distinct processes, possibly local integration and global grouping/segmentation. The optimal spatial frequency might depend on both processes, while the optimal inset size might depend primarily on the latter process.

[Supported by MESSC Grant-in-Aid, Japan.]

### ● Cyclopean motion perception at different orientations

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Periodic patterns moving in opposite directions in the two eyes can generate a static percept. Presumably, this phenomenon results from the binocular integration of motion signals in visual cortical areas where cells respond to both motion and disparity [eg Bradley et al, 1995 *Nature (London)* 373 609–611].

We reasoned that moving binocular patterns would be integrated more easily when competing less with disparity, ie when they are oriented vertically rather than horizontally. We therefore studied the integration of the binocular motion signals at different orientations. The stimuli were pairs of Gabor patches moving perpendicularly to their orientation and in opposite directions relative to the fixation cross. The Gabors moved inward in one eye and outward in the other. Observers had to indicate whether the stimulus was moving in or out. We used six global orientations, equally spaced between  $0^\circ$  (horizontal) and  $150^\circ$ . We looked for points of subjective equality for stimuli moving at  $0.2 \text{ deg s}^{-1}$ , and used the slopes of the psychometric functions as measures of sensitivity of the binocular motion integration.

We found that the average sensitivity at  $90^\circ$  was almost twice that at  $0^\circ$ . We describe a model based on elements of Bayesian decision theory.

### ● Movement production and movement prediction

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Accurate interaction with the environment requires prediction of movement, whether movement be actively produced or passively observed. In fact, visually perceived movement is the principal cue in motor guidance. Of interest is the potential role of motor action, especially nonvisual cues, in the prediction of visual movement.

We investigated the influence of motor action on internal movement representation using a trajectory extrapolation paradigm, in which subjects predicted future positions of a temporarily occluded visual target. Subjects experienced the same visual stimulation in two main conditions, active and passive; in the active condition, the target was displaced by subject's motor action.

In the first series of experiments, we studied manual action. The main result was that subjects' predictions of actively caused motion were more anticipatory than for passive observation of the same movement, whether or not the visual movement was congruent with the motor action. Concurrent eye movements were found to interact with the predictive process.

In the second series of experiments, we are studying the prediction of viewpoint changes due to head movements. Preliminary results indicate that actively produced head movements lead

to predictions that are anticipatory compared to those resulting from passive optic flow, thus playing a role in spatial constancy.

- **The role of object orientation in affine structure-from-motion judgments**

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Human visual system is sensitive up to a stretching transformation to the line of sight; therefore we cannot discriminate two structurally identical objects that differ just in their  $Z$  values. How does a deviation from this extreme orientation influence the accuracy of perception? As the deviation from the  $Z$  direction increases, the accuracy can change gradually or can improve abruptly, after reaching a specific value of orientation.

Stimuli were two half-ellipsoids, the first of which was of constant width/depth ratio of 1.0; the second one was stretched in depth, with this ratio ranging from 1.05 to 1.2. The half-ellipsoids were oriented at a  $0^\circ$ ,  $4^\circ$ ,  $8^\circ$ ,  $12^\circ$ , and  $16^\circ$  angle relative to the line of sight, convex with respect to the observer. Both stimuli were rotating about a vertical axis; the extent of rotation was fixed at  $8^\circ$ . Subjects were asked to compare the depth of the two half-ellipsoids.

Observers' judgments were influenced by both variables. Subjects detected even a 5% stretching of structure, when the orientation was  $16^\circ$ . Discrimination threshold for the  $12^\circ$  condition was found to be 15% stretching. Discrimination threshold further increased at smaller deviations. It is concluded that, for optimal performance in affine structure-from-motion tasks, deviation of  $16^\circ$  from the  $Z$  direction is sufficient.

- **Self-generated motion parallax counts more**

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3-D structure is perceived from both actively generated and passively observed motion. In passive viewing, motion must be computed simultaneously with structure. In active vision, on the other hand, extra-retinal information about motion is available, and in principle could be used to help compute structure. To what extent does depth perception incorporate this extra-retinal information in the active viewer?

We addressed this problem using a cue-conflict paradigm, in which static perspective cues sometimes conflicted with motion parallax. In the active condition, subjects wearing a head-tracker generated motion by lateral head movements around a virtual surface inclined in depth. In the passive condition, subjects experienced identical optic flow, but without self-motion. The subjects' task was to report the surface tilt.

We found that self-motion had a selective effect on depth perception. In the absence of cue conflict, subjects were equally precise in the active and passive conditions, in agreement with previous findings. With static and dynamic cues in conflict, however, subjects showed a significantly greater preference for dynamic cues in the active than in the passive condition. Our results support the ecologically valid notion that, in extracting 3-D structure, observers rely more on the rigidity hypothesis in active vision than in passive motion parallax.

## NATURAL IMAGES, BIOLOGICAL MOTION, AND FACES

- **Investigating categorical perception of gender with 3-D morphs of familiar faces**

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We could find no evidence for categorical perception of face gender using unfamiliar human faces (I Bühlhoff et al, 1998 *Perception* 27 Supplement, 127a). Therefore we have investigated whether familiarising participants with the stimuli prior to testing might favour categorical perception.

We created artificial gender continua using 3-D morphs between laser-scanned heads. The observers had to classify all faces according to their gender in a classification task. If perception of face gender is categorical, we would expect participants to classify the morphs into two distinct gender categories. Furthermore, they should differentiate pairs of morphs that straddle the gender boundary more accurately than other pairs in a discrimination task. The participants were familiarised before testing with half of the faces used for creating the morphs. They could categorise most familiar and unfamiliar faces into distinctive gender categories. Thus, they could extract the gender information and use it to classify the images. On the other hand, we found no evidence of increased discriminability for the morph pairs that straddle the gender boundary. Apparently, observers did not perceive the gender of a face categorically, even when these faces were familiar to them.

- **What aspects of facial motion are important for the recognition of familiar faces?**

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Recent experiments suggest that seeing a familiar face move adds dynamic information for the viewer, useful in the recognition of identity (Knight and Johnston, 1997 *Visual Cognition* 4 265–273; Lander et al, 1999 *Memory & Cognition* 27 974–985). This finding is consistent with the idea that familiar movement patterns, either generally, or of specific faces, aid recognition. It is unclear whether this advantage is due to movement of particular face features, or whether movement of the whole face configuration is important.

Here, we report a number of experiments in which this issue has been investigated. First, recognition of moving and static familiar faces is compared, when viewing just the top or bottom of the face. Motion aids recognition, but the advantage is more pronounced when viewing the bottom half of the face.

Next, we use the Thatcher illusion (Thompson, 1980 *Perception* 9 483–484) to explore the role of face configuration. The eyes and mouth of the face are inverted, with the rest of the image unchanged. The resulting face looks grotesque, but less so when inverted. We describe an experiment that compares the recognition of moving and static thatcherised famous faces, presented both upright and inverted. Motion also aids the recognition of these images.

- **Discrimination thresholds for morphed objects in peripheral vision**

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In previous work (Párraga et al, 2000 *Current Biology* 10 35–38) we demonstrated that the human visual system is optimised to encode the second-order statistics of the visual environment. This was done psychophysically by measuring human discrimination thresholds for small spatial changes in stimuli with natural and unnatural Fourier statistics, by using a ‘morphing’ technique and assuming that the subject can direct his/her gaze at the region of interest so as to project this into the fovea.

However, we know that peripheral vision differs from foveal vision in the representation of spatial information (eg there is a marked change in the shape of the peripheral contrast sensitivity function compared to the foveal one) but we do not know how this would affect the ability to perform real tasks such as the one considered in our experiment.

Here, we extend our study to peripheral viewing. Three observers were presented monocularly with morphed objects and we measured their discrimination thresholds foveally and at 3 deg eccentricity. Our results show less evidence for optimisation to natural scenes in peripheral vision than in foveal vision. We conclude that there is a qualitative difference in discrimination strategy between the periphery and the fovea.

[Supported by BBSRC.]

## SHAPE

- **Hierarchy of shape cues in recognition of bent pins**

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In discriminating articulated objects, observers may use cues such as number of components, length of components, angle between components, and curvature of components. When each potential cue is normalised in terms of its fractional change, are they equally salient?

Computer-generated images of two bent pins, viewed from different directions, were displayed for 100 ms and 2000 ms. Each bent pin comprised 2–4 abutting arms, each of which varied in length, angle, and curvature. Each arm was no more than 35.0 mm long and 3.5 mm wide when viewed at 2 m. Images were realistically rendered with no perspective cues. In half of the trials, images were of the same bent pin viewed from two directions; in the other half, images were of different bent pins viewed from two directions, the difference being in the number of arms, or length of one arm, or angle between two arms, or curvature of one arm. Discrimination was best for a difference in arm number, next best for a difference in arm length, followed by a difference in angle, and worst for a difference in curvature. Observers may use a hierarchy of cues in the recognition of simple, rotated, articulated objects.

- **Aspects of the first milliseconds of human information processing**

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Last year, we presented two new illusions: feature inheritance and shine through (Herzog et al, 1999 *Perception* **28** Supplement, 35b). In both cases a stimulus, like a Vernier, precedes a grating for a very short time. If the number of bars of the grating is small, the foregoing element might remain invisible but bequeathes its features, eg the whole grating looks offset in the direction of the Vernier. For a larger number of grating bars the preceding element shines through the grating yielding far lower Vernier discrimination thresholds.

Using the Vernier paradigm, we show that if elements of the grating are delayed by only 10 ms relative to each other, shine-through can be strongly diminished. Therefore, differences of temporal onsets, in the range of only two or three neuronal spikes, can switch perception and change performance dramatically. We also show that information available only during the first milliseconds can prevail over features displayed later. We presented two Verniers successively at the same position for a short time, eg 30 ms each, followed by a grating. Offset direction of the two Verniers was always in opposite direction. In feature inheritance as well as shine-through it is always the first Vernier that determines performance and perception.

- **Stereomorphing: Shape transformation of an illusory form moving in depth**

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A new 3-D illusion was produced with the use of the newly reported methodology (Minev and Likova, 1999 *Perception* **28** Supplement, 135b) for investigating stereoscopic vision, based on computer-generated dynamic autostereograms. Each dynamic autostereogram was generated as a succession of static autostereograms with separate elements whose disparity was modified to produce a percept of motion in depth.

Here, conflicts between corresponding elements of two sequential autostereogram frames were introduced: experiment 1 involved a 'changing-form' conflict (for instance, circles were matched with respective squares); both forms were specified by their uniformly coloured surfaces; experiment 2 involved an additional 'surface/contour' conflict: one of the two forms was specified only by its contour.

It was found that (i) the lack of form correspondence between the alternating forms creates an illusory object moving in depth and simultaneously transforming its shape in time. The resulting spatiotemporal phenomenon may be termed 'stereomorphing'; (ii) adding the 'surface/contour' conflict disrupts the stereomorphing process. During the stereomorphing, directional anisotropy of speed perception (which I have previously shown with only disparity variations) was observed. A possible underlying mechanism, subsuming the temporal correspondence-matching problem and the stereo-motion interactions, is discussed.

- **New visual illusory distortions originated by orientation polarities through luminance**

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We present new visual illusions through patterns made up of simple elements that define an orientation polarity. An 'element' can be defined as any clump of lines that is rendered through luminance contrast such as the diagonal organisation of the light and dark sides in square elements. With such elements it is possible to introduce new illusions, and a comprehensive model of all the effects.

The illusions proposed here concern orientation, shape, apparent movement, and parallelism distortions of perceptual grouping. A model is suggested which is based on local and global dynamic interactions in which: (i) a local polarity distortion occurs at each single-square element and in the field around each of its elements, and (ii) an interaction of global grouping processes acts on the pattern of elements.

The properties of this model might be coded by orientation-sensitive cells found in area V1 of the primary visual cortex. The model is in part different from Grossberg's and introduces a double competitive process: a local on-off competition between like and perpendicularly spatially tuned oriented cells produces local orientation distortions in the field around, which is the input of a global opposite competitive process, producing global orientation distortions.

## SPATIAL FREQUENCY AND CONTRAST

### ● Dynamics of spatial frequency tuning in macaque V1

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We studied the dynamics of spatial-frequency tuning of macaque V1 neurons by recording the responses of individual cells to a rapid sequence of sinusoidal gratings at a fixed orientation (optimal for the cell) but varying spatial frequencies and spatial phases. Blank images of uniform luminance were interleaved in the sequence to provide a measure of baseline response. We measured the probability that a spike followed a given spatial frequency (or blank) after a time delay of  $T$  ms, and observed how the probability distribution evolved as a function of  $T$ .

The data indicate that the preferred spatial frequency of V1 cells shifts towards higher spatial frequencies over time, with an average shift of  $0.78 \pm 0.16$  octaves. In 15% of the cases, the magnitude of the shift was higher than 2 octaves. No differences were observed between simple and complex cells. The preferred spatial-frequency shift may be related to a lagged suppression at low spatial frequencies, revealed by response probabilities below baseline.

The results indicate that V1 receptive fields cannot be considered static spatial filters. The shift from low to high spatial frequencies over time may also support the idea that V1 processes images using a coarse-to-fine strategy.

### ● S-cone spatial contrast sensitivity as derived from high-spatial-frequency tritanopia data

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The colour of patterns is determined by both their spectral and spatial-frequency content. Grey strips inserted into a yellow–pink square-wave grating change their colour appearance when grating spatial frequency increases. This occurs because grating contrast is attenuated by the receptor colour channels unequally—the S-channel has poorer spatial resolution. This effect was measured for three observers to derive S-channel spatial-contrast sensitivity.

An asymmetric colour-matching technique was used to measure appearance of grey (test) strips presented against a yellow–pink grating on a Barco colour monitor driven by a VSG 2/3 board. The test strip width was 25% of the grating strip width. Observers adjusted the uniform (matching) strip beneath the grating to appear the same as the test strip by using a keypad to control hue, saturation, and luminance of the matching strip. The grating frequency was varied from 0.5 to 10 cycles  $\text{deg}^{-1}$ .

Contrast sensitivity function of the S-channel obtained is reasonably in line with the previous data for frequencies  $> 2$  cycles  $\text{deg}^{-1}$ . However, we found no contrast attenuation in the low-frequency region. In other words, it follows from our data that the spatial-frequency characteristic of the S-colour channel has the shape of a low-pass rather than bandpass filter.

### ● Perception of form and texture through complementary bar and grating cell channels

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A line that is a part of a grating of parallel equidistant lines is more difficult to perceive as a part of a contour of an object than an isolated line. The effect cannot be explained by the function of simple cells which give a stronger response to the former type of stimulus than to the latter one.

Elsewhere we proposed computational models of grating and bar cells which are selective for gratings of bars and isolated bars, respectively. While the behaviour of grating cells has been studied in considerable detail, evidence of the existence of bar cells is only occasional. In this paper we elaborate on the role of grating and bar cells in the visual system. We propose a model in which visual information about lines, as coming from simple cells, is split into two complementary and mutually exclusive channels: the grating-cell channel and the bar-cell channel. The former is responsible for the processing of oriented texture, the latter for (isolated) contours of objects. The results derived from the model are in agreement with the psychophysical observation that the perception of texture and form are complementary processes.



- **Temporal integration and reaction time to grating-onset detection**

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It is usually assumed that the first 10–20 ms of stimulus presentation are important for the reaction time (RT) to stimulus-onset detection. However, does this critical interval depend on stimulus spatial frequency and what are the temporal-integration properties of underlying mechanisms at different spatial frequencies?

To evaluate these properties we studied the stimulus-duration effect on the RT to gratings with different spatial frequencies. At each duration value, the product of the contrast and the duration, ie the contrast ‘energy’, was kept constant. We found that at near-threshold ‘energy’ levels the RT was constant for durations up to 20 ms at lower spatial frequencies and up to 40 ms at higher spatial frequencies. At higher ‘energy’ levels this critical interval was the same (up to 20 ms) for both lower and higher spatial frequencies.

The results might be interpreted as new evidence that RT is determined by two mechanisms at a near-threshold contrast and by one mechanism at higher contrast.

[Supported by the NSF, Bulgaria, Contract L809/98.]

## VISUAL IMPAIRMENT

- **Spatial interactions in strabismic and anisometric amblyopia**

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We measured spatial interactions and determined their relationship to the degree of spatial distortion in strabismic and anisometric amblyopes. Spatial interactions were assessed for each eye of five strabismic and three anisometric amblyopes by comparing the apparent contrast of a single foveally viewed Gabor to that of a Gabor centred in an array of Gabors. To estimate intrinsic spatial distortions, we then introduced Gaussian jitter to a similar array and determined the minimum amount of jitter necessary to detect spatial misalignment.

Apparent contrast was reduced on average by 29% in nonamblyopic eyes, 18% in anisometric eyes, and 5% in strabismic eyes, indicating highly abnormal spatial interactions in strabismic amblyopes. The jitter necessary to detect spatial misalignment in the array averaged 0.06 deg for non-amblyopic eyes, 0.30 deg for anisometric eyes, and 0.95 deg for strabismic eyes, indicating a high degree of intrinsic spatial distortion in strabismic amblyopes. A normal observer viewing an array of Gabors that contained similar amounts of jitter to that found in strabismic amblyopia displayed similar reductions in apparent contrast. The abnormal spatial interactions that we show in the strabismic group can be accounted for on the basis of their known positional deficit.

[Supported by MRC grant MT 108-18.]

- **Visual perceptual assessment of children with ocular visual impairment**

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Detailed visual profiles of children with visual disabilities can provide correlations between visual impairments, disabilities, handicap, and development. Data have been collected in a research group of forty-five children and youngsters aged 6–21 years with only ocular diseases/disorders. Here we describe the first two experiments: assessments of several functions of visual perception—cognition, visuomotor integration, and some reaction-time tests. The results obtained from the research group have been compared with the results for a matched control group with normal vision. The expectation was that children with ocular visual impairment would have lower scores and longer reaction times.

We found no significant difference between the scores for the research group and the control group. The exceptions were significantly lower scores on the facial recognition test and mazes and higher scores on the visual memory test. But the total times to do these tasks were significantly longer. Corresponding with the expectation, children with ocular visual impairment have significantly longer reaction times. With a limited time or under time pressure the scores on

visuomotor functions and on facial recognition are significant lower. We conclude that children with ocular visual impairment need more time compared with normal sighted children, but when they get that time the scores are near average.

- **'Lazy eyes' miss out visual illusions**

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Amblyopia ('lazy eye') is an impairment in visual acuity resulting from abnormal neural development in the visual cortex. We tested the responses of amblyopic and normal observers to illusions of perceived orientation in textures of Gabor patches: the 'Fraser illusion', the 'phase illusion', and the 'tilted chain' illusion.

Amblyopes (viewing with their amblyopic eyes) showed a significant increase in the strength of the 'Fraser illusion', a decrease in the 'phase illusion', and a reversal of the 'tilted chain' illusion (compared with their nonamblyopic eyes). In fact, amblyopes observed the amount of illusory tilt recorded by normals when viewing only a small portion of the image [Popple and Levi, 2000 *Investigative Ophthalmology & Visual Science* **41**(4) S4244].

To account for the illusions, information must be integrated across visual space (Fraser, 1908 *British Journal of Psychology* **2** 307–320). A failure to integrate effectively across visual space could explain the differences in performance between normal and amblyopic eyes, whereas noisy image degradation alone (sparse sampling, topographical jitter) cannot. These results can be modeled by a novel theory which places the neural abnormality in amblyopia at the level of second-stage grouping processes. Additionally, the illusions might be useful in the early diagnosis of amblyopia without the need for prior refractive correction.

## ORAL PRESENTATIONS

### ATTENTION

- ◆ **Gabor contrast sensitivity depends on task relevance of collinear flankers**

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Gabor contrast thresholds are often lower in the context of collinear flankers (Polat and Sagi, 1993 *Vision Research* **33** 993–999). We find that this phenomenon depends on the task relevance of the flankers.

We presented two pairs of flankers displayed in an 'X' configuration around the foveal target, which was collinear with one diagonal and orthogonal to the other. Subjects performed two concurrent 2IFC tasks with 80 ms stimulus duration: target detection, and Vernier alignment of flankers on one pre-specified diagonal. The relevant diagonal was manipulated between blocks, with no other manipulations of stimulus, task, or relevant display area.

For target–flanker separation of 4 wavelengths, collinear flankers produced target facilitation when relevant ( $\sim 0.2$  log units relative to an isolated-target single-task baseline) but little or no facilitation when irrelevant (orthogonal flankers relevant). Surprisingly, this pattern was very similar for displays comprising only one set of (collinear or orthogonal) flankers: in terms of their effect on target threshold, therefore, the additional irrelevant flankers in the 'X' configuration were as good as absent.

Our results suggest that goal-directed attention can affect early visual integration processes, supporting growing evidence that activity of V1 cells is modulated both by lateral interconnections and by top–down input.

- ◆ **Visual marking is affected by the attentional blink**

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We can successfully ignore old, irrelevant visual distractors by inhibiting them before new, relevant information appears. This mechanism has been termed visual marking (Watson and Humphreys, 1997 *Psychological Review* **104** 90–122).

We present an experiment showing that a secondary task creating a so-called attentional blink (Raymond et al, 1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 849–860) severely disrupts visual marking. In further two experiments, we explored how the attentional blink affects visual marking. We found evidence for a reduction in spatial memory, as well as for reduced inhibitory power.

The results support the idea that visual marking is a top-down mechanism, demanding attentional resources. Furthermore, they suggest that the attentional blink disrupts a wide range of processes in the visual system.

◆ **Eccentricity and object-based selection**

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Search efficiency falls off with increasing target eccentricity only when distractors occur closer to fixation than the target (Wolfe et al, 1998 *Perception & Psychophysics* **60** 140–156). This suggests that the effect of eccentricity originates from a bias to attend to central items. We ask whether this spatial selectional bias can be overcome by object-based selection: even when distractors occur closer to fixation than the target, can we ignore them and attend selectively to a ring of items at the target eccentricity?

Three concentric differently coloured rings were centred around fixation. Eight white letters, one target and seven distractors, were then displayed on the surface of these rings, and participants were asked to signal which one of two possible target letters was present. Letters were either arranged on one ring or distributed across rings. The ring on which the target letter appeared was either unpredictable or predicted by brightening. The presence of distractor letters closer to fixation than the target significantly slowed search at larger target eccentricities on uncued, but *not* on cued, trials. We conclude that we can ignore central items and attend to ring-shaped objects with holes in the middle.

◆ **One-step feature-based learning in the deployment of transient attention**

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Previously we have shown that when transient visual attention is summoned by a sudden luminance onset, these deployments can be focused to a part of the suddenly appearing object that has proved behaviourally relevant on previous appearances [Kristjansson et al, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) S80]. This learning of a cue–target relationship was not under voluntary control and developed over the course of a few trials. Here we further investigate this form of learning during deployments of visual attention.

In experiment 1 we show that when there is consistent relationship between the colour of a part of the cue and a target, learning develops rapidly. Such learning was also observed for a similar relationship based on the shape of the cue, whereas a higher-order relationship between the cue and the target, where the colour of the cue predicted where the target would appear, did not result in the same form of learning. Thus we hypothesise that transient attention is capable of one-step inferences, based on particular features. These results are further evidence for the surprising adaptability of transient attention shifts to abrupt luminance onsets, which have often been thought to be stereotypical, stimulus driven, bottom–up reflexes.

**MECHANISMS OF SHAPE PERCEPTION**

◆ **Perception of orientation: an empirical Bayesian model**

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Perception of the orientation of objects is important in our interaction with the environment. So far, research has focused on the orientation of lines and gratings, with the main result that vertical and horizontal orientations are perceived more accurately and precisely than oblique ones (the oblique effect).

We tested the orientation perception of ellipses with different length-to-width (aspect) ratios in various orientations. A circle was included in the test set. Six naïve subjects adjusted a broken line (probe) to match the major-axis orientation of an ellipse that was placed at the centre of the probe.

Results show the oblique effect, especially for the low aspect ratios (close to a circle). For the circle, subjects had a non-uniform distribution of settings. Furthermore, there are large individual differences among the subjects. We can explain these differences by a Bayesian model that takes the distribution of settings to the circle as a prior distribution. Thus the prior is obtained from the settings to a neutral stimulus. Going beyond the domain of perception of orientation, we believe empirical Bayesian modeling to be a powerful paradigm for vision research.

- ◆ **Competitive global and local dynamics in the formation of contours from perceptual grouping**  
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We introduce a neural-dynamic model of boundary perception, different from Grossberg and Mingolla's, and based on two distinct opposite competitive processes without a feedback architecture.

A local on-off competition between like and perpendicularly oriented cells acts as output to a global process. In the local process, the neurons that react to output signals of like-oriented masks compete in an on-centre off-surround organisation. The neurons that react to output signals of perpendicularly oriented masks compete in an off-centre on-surround organisation. In the global process, the neurons that are fed from like-oriented masks compete in an off-centre on-surround organisation. The neurons that are fed from perpendicularly oriented masks compete in an on-centre off-surround organisation. The two processes synthesise two different perceptual boundary contours: modal contours for the local process, and amodal contours for the global one.

We hypothesise that both kinds of contours can be illusorily distorted. The model has been tested with psychophysical data derived from new visual illusions suggested by the model itself. The new illusions concern apparent misalignment, global shape distortions due to internal element organisation, and apparent eccentricity. We find that both local and global distortions can be explained without invoking cognitive top-down processes.

- ◆ **Perceptual strength and time course of illusory contour generation explained by a neural model of recurrent cortico-cortical interaction**  
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Cells in monkey area V2 contribute to the perception of illusory contours. Orientation-sensitive and contrast-sensitive neurons selectively respond to illusory-contour stimuli generated by abutting gratings or aligned contrast fragments (von der Heydt and Peterhans, 1989 *Journal of Neuroscience* 9 1749–1763).

We used a neural network model of recurrent V1–V2 processing (Neumann and Sepp, 1999 *Biological Cybernetics* 81 425–444) to explain physiological as well as perceptual data.

Computer simulations demonstrate that the strength of an illusory contour varies as a function of the ratio of physical to total contour length in a Kanizsa square (Shipley and Kellman, 1990 *Perception & Psychophysics* 48 259–270). Abutting gratings of moderate density generate larger V2-cell response than oriented real contrasts. Correspondingly, the response strengths of illusory contours generated in Varin figures exceed those of a Kanizsa square with continuous inducers (Leshner and Mingolla, 1993 *Vision Research* 33 2253–2270). Model V2-cell responses to illusory contours of abutting gratings develop more gradually than in response to real contours.

The computational model explains a variety of empirical data on illusory-contour perception and predicts underlying mechanisms and their time course. This helps to further unravel early mechanisms involved in the generation of neural representations of visual surface layout.

- ◆ **First-order structure induces the 3-D curvature-contrast effect**  
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Last year we reported a 3-D curvature-contrast effect in motion-defined stimuli (Kappers and te Pas, 1999 *Perception* 28 Supplement, 82d). We set out to investigate whether the structure that induces the 3-D curvature-contrast effect needs to contain second-order (curvature) information, or whether a similar effect can be obtained through inducers containing only first-order (slant and tilt) or zeroth-order (depth) information.

Stimuli consisted of a small central paraboloid (4.6 deg radius) with relatively high curvature surrounded by one of three possibilities: a large paraboloid (11 deg radius) with a lower curvature than the central one, a large cone with the same average slant, or a large plane at the same average depth. The stimuli consisted of random dots and moved with an angular velocity of 30 deg s<sup>-1</sup>. Viewing was monocular. Observers were presented with two stimuli successively and had to decide which of the two central parts had the highest curvature. We varied the curvatures, the slants, and the depths of the outer parts systematically.

We found a distinct curvature-contrast effect that is similar for both the second-order and the first-order surrounds, but only a small effect for zeroth-order surrounds. We conclude that the first-order structure is sufficient to induce a curvature-contrast effect.

## LEARNING

- ◆ **A sparse coding network learns both V1 receptive fields and topography from natural images**  
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The receptive fields of neurons in the primary visual cortex have been characterised as localised, oriented, and bandpass; and neurons with similar position, orientation, and frequency preferences are grouped together, forming a topographic map. Numerous neural-network models have been proposed that learn some of these properties from natural-image data, but to our knowledge no model has been able to learn all these properties.

Olshausen and Field [1996, *Nature (London)* **381** 607–609] showed how the single principle of sparseness of a linear representation leads to realistic simple-cell receptive fields when trained on natural-image data. We extend this model by seeking sparseness of local energies instead of linear outputs. This straightforward extension leads to a topographic representation in many ways similar to that observed in V1, while maintaining realistic receptive fields.

In addition to revealing the topography, the same principle also helps explain the principal properties of complex cells. Most local energies behave in many ways similarly to complex cells: they tend to show phase- and (limited) shift-invariance, in addition to orientation- and frequency-selectivity. This supports the notion that the topography seems to define the pooling into complex cells.

- ◆ **Position-dependent and position-independent statistical learning of shape-conjunctions**  
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How do humans encode the local and global statistics of images that are essential for developing new visual features? Twelve simple shapes were grouped into six two-element base-pairs. Each base-pair had a specific spatial arrangement (horizontal, vertical, oblique). During a 10 min learning phase, subjects viewed display sequences consisting of three randomly selected base-pairs presented simultaneously within a  $3 \times 3$  grid. The joint probability of the two elements in a base-pair was 0.5; all other joint probabilities were below 0.02. During the test phase, subjects viewed two shape-pairs (a base-pair and a pair in novel arrangement) in a temporal 2AFC task and judged which of the two pairs was more familiar from information presented during the learning phase.

Subjects selected the base-pairs significantly more often than the novel shape-pairs (72% correct,  $p < 0.0001$ ) when the local spatial correlations of element-pairs and the element-positions matched the training set. Performance was poorer, but still significant, when only local spatial correlations distinguished between base and novel elements (60% correct,  $p < 0.015$ ). Thus subjects can learn higher-order spatial statistics across multiple images and these learned ‘features’ incorporate available relational, positional, and temporal correlations.

[Supported by NSF SPR-9873477 and JSMF 96-32.]

- ◆ **Does perceptual learning affect early stages of visual processing?**  
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Theoretical concepts of perceptual learning fall into two classes: Early-stage theories conceive perceptual learning to be due to synaptic modifications at early sensory coding stages [Karni and Sagi, 1991 *Proceedings of the National Academy of Sciences of the USA* **88** 4966–4970; Kirkwood et al, 1996 *Nature (London)* **381** 526–528] while higher-stage concepts conceive the gradual improvement of visual discrimination to be the result of task-dependent attentional focusing and information selection refinement (Beard et al, 1995 *Vision Research* **35** 1679–1690).

We report results from various pre-test – discrimination learning – post-test experiments which show that (i) learning spatial-frequency discrimination broadens grating-detection tuning functions; (ii) learning Vernier discrimination broadens orientation-detection tuning functions and lowers discrimination thresholds obtained with simultaneous grating plaid masking for all orientations. Further, we present results which show that spatial-frequency-discrimination learning improves spatial-phase discrimination. The phase-discrimination learning transfer obtained for control learners (spatial-frequency discrimination with spatially jittered gratings) suggests that a wide range of spatial positions must be involved in coding improvement.

We introduce an early-stage multiple-mechanism coding model with bandwidth plasticity and nonlinear pooling which is consistent with our findings.

◆ **Roles of conscious efforts in perceptual learning**

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Our sensory systems are under a constant barrage of superfluous information. We compared the effects of attention to the effects of an internal comparison between response and feedback, in preventing the sensory architecture from erosion by superfluous information. A random-dot cinematogram (RDC) consisting of dots engaged in spatiotemporally local motion was used. When subjects were trained to discriminate either the global flow direction or the brightness of the fixation point in the RDCs without response feedback, the discriminability of presented local motion directions was enhanced irrespective of the global motion direction. This passive learning preceded the learning of the global flow discrimination. When subjects received response feedback during their global motion discrimination training, improvement was found for the global motion but not for the presented local directions.

We conclude that attention alone, generally thought to filter out extraneous information, cannot block the sensory modification resulting from mere exposure to irrelevant stimulus features. In contrast, response feedback enables nearly complete suppression of irrelevant signals while allowing the sensory system to adjust to only the stimulus features relevant to a task.

**BIASES IN SHAPE PERCEPTION**

◆ **Ambiguous figures and reading direction. A case for small-scale hysteresis?**

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A normative study was undertaken in order to establish levels of ambiguity for a set of ambiguous figures. Triplets of figures were presented to the subjects, consisting of an ambiguous figure in the middle flanked by its two possible interpretations (ie more extreme versions). Subjects had to indicate whether the ambiguous figure resembled more the interpretation to the left or the one to the right.

Results show that the interpretation of the ambiguous figure tended to be more influenced by the interpretation presented to the right. This influence increases with the level of ambiguity of the middle figure. It can be hypothesised that this effect results from reading the triplet from left to right, followed by a return to the middle figure. Hence the rightmost figure is the last one seen, and it therefore may exert a more dominant influence on the interpretation of the ambiguous figure. This phenomenon resembles hysteresis—the tendency to interpret an ambiguous figure similar to the last ones seen. In this study, this effect seems to work on a small scale (one preceding figure in contrast to a whole series). This hypothesis is currently under investigation.

◆ **The veridicality of shape representation is not altered by shape categorisation**

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Theoretical and empirical work has shown that humans represent artificial shapes in a faithful way, ie the structure in the artificial shape space is reflected in the perceived similarities between shapes.

We investigated whether prior categorisation of artificial shapes into two discrete classes can harm this original veridicality of shape representation by altering the perceived similarities. Our stimuli were Fourier descriptors in which we manipulated the amplitude of two different frequencies. In line with previous studies (Cortese and Dyre, 1996 *Journal of Experimental Psychology: Human Perception and Performance* 22 133–143), we found that this two-dimensional structure in parameter space is reflected in the perceived similarities.

Prior categorisation for which only one of the two dimensions is relevant made observers more sensitive to differences between the shapes. However, the perceived two-dimensional structure in the shape space was not altered. Moreover, not only differences in the shape dimension that is relevant for categorisation are perceived better, but also differences in the other dimension. This basic result was found even after extensive categorisation training (more than 5 hours). We conclude that the veridicality of shape representation is preserved after shape categorisation.

◆ **A preference for global convexity in local-shape perception**

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A hollow face mask tends to appear convex even if the mask is rotating, viewed binocularly [Gregory, 1970 *The Intelligent Eye* (London: Weidenfeld and Nicolson)], or illuminated from above. The standard explanation for this illusion is that the visual system has a strong preference for familiar shapes (faces) over unfamiliar ones (hollow masks). This illusion confounds two preferences, however: the first is for a familiar shape, the second is for a globally convex shape. Here we demonstrate that the latter preference can be significant, using unfamiliar stochastically corrugated smooth surfaces that are viewed statically and monocularly under perspective projection. Each surface is illuminated by a collimated light source that is either above or below the line of sight, and each surface is either globally convex or globally concave. Nine naïve observers judged the local qualitative shape at 320 isolated points on 64 such surfaces. The percentages of correct scores were 57% vs 38% for globally convex vs concave, and 70% vs 23% for light source from above vs one from below. Both differences are significant ( $p < 0.01$ ). We conclude that a preference for global convexity plays a significant role in local-shape perception, even in the presence of other significant shape cues.

◆ **Positional and symmetry information of concave and convex vertices**

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By using irregular polygons and measuring RT, it was found that comparing the position of convex vertices was significantly faster than comparing the position of concave vertices. This was true for a task of relative-position judgment (which contour has a higher vertex, the left or the right?) and a task of bilateral-symmetry detection (are the contours symmetrical?).

A reversal of the figure-ground interpretation reversed the effect, leading again to an advantage for convex vertices, even when they belonged to separate objects. These data are problematic for any theory that emphasises the role of concavity (Hoffman and Richards, 1984 *Cognition* 18 65–96), in that the location of concave vertices does not seem to emerge and be easily accessible. However, it is possible that concavities are not easily accessible because they serve to segment a shape into parts and as such are not part of the shape itself.

It was also found that in a symmetry detection task the effect can be reversed if the shape has more than just one large vertex. It is suggested that a specialised symmetry mechanism based on virtual quadrangles and bootstrapping (Wagemans et al, 1993 *Vision Research* 33 1067–1088) may explain this difference.

## POSTER SESSION 4

### ANATOMY AND IMAGING

● **Mapping the visual cortex with stereotactic TMS and functional MRI**

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Focal transcranial magnetic stimulation (TMS) is able to elicit phosphenes when applied over the occipital pole. The aim of this study was to test whether the site of the phosphenes in the visual field is linked to the retinotopic map of the visual cortex.

In four subjects we determined the individual retinotopy of the visual field by means of a dynamic mapping technique (eccentricity and polar angle) with functional MRI. Then we used focal TMS to register phosphene sites with different coil positions. These positions were monitored with respect to the head by a custom-made stereotactic measuring device. At each stimulation position, the subject drew the perceived phosphene directly on a touch screen.

Phosphenes were reproducibly elicited not only from positions corresponding to V1 but also from extrastriate areas V2–V4. The general appearance of the phosphenes did not change with the visual area. In all subjects, displacement of the coil from a cortical position which represents the fovea to a position of more peripheral representation displaced the phosphene from the centre of the visual field towards the periphery. Our data demonstrate that stereotactic TMS can be used to create a detailed map of the visual cortex.

- **fMRI of the scintillating-grid illusion**

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We studied activation patterns in the human visual cortex during the presence or absence of the scintillating-grid illusion by functional magnetic resonance imaging (fMRI). The stimulus was a Hermann grid consisting of grey bars and black squares. Bright disks were superimposed upon the intersections (test grid). Dark illusory spots are perceived transiently within the white disks during saccadic eye movements or a brief exposure (Schrauf et al, 1997 *Vision Research* **37** 1033–1038). Shifting the disks horizontally away from the intersections (control grid), abolishes the illusory scintillation (Schrauf and Wist, 1996 *Perception* **25** Supplement, 78a).

Data acquisition and imaging were performed with a 1.5 T Siemens scanner (anatomical resolution:  $1 \times 1 \times 1 \text{ mm}^3$ ; functional resolution: voxel size =  $3 \times 3 \times 3 \text{ mm}^3$ , 16 slices; TR = 3 s, TE = 60 ms, flip-angle =  $90^\circ$ ). The contrast for the test grid vs control grid during brief exposure and steady fixation revealed an enhanced level of activation within the region of MT/MST.

The result suggests that the dynamic luminance-contrast illusion is mediated by the human motion complex. hMT+ activation has been found to correlate with other instances of subjective dynamic perception [Zeki et al, 1993 *Proceedings of the Royal Society of London* **252** 215–222; Tootell et al, 1995 *Nature (London)* **375** 139–141].

## ATTENTION, TEXTURE, AND VISUAL SEARCH

- **Amplitude changes of beta activity in cat's lateral posterior – pulvinar complex during attention-related behaviour**

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It is generally believed that the lateral posterior–pulvinar complex (LP–P) is involved in modulation of visual signals passing between primary and higher visual cortical areas during attention-related behavioural situations.

To reveal the role of different parts of LP–P in visual processing, we recorded local field potentials from several cortical areas and three subdivisions of cat's LP-P: the pulvinar proper, and caudal (LPI-c) and rostral (LPI-r) parts of the lateral zone of this nuclear group. These recordings were done during a behavioural task based on delayed spatial discrimination of visual and auditory stimuli. During a visual but not an auditory attentive situation we observed an elevation of beta band (16–24 Hz) amplitude of fast Fourier transform function calculated from signals recorded from LPI-c as well as from cortical areas 17, 18, and PMLS. This beta activity appeared only on trials that ended with a successful response, proving its relation to the mechanisms of attentive seeing. In contrast, no enhanced beta activity was observed in LPI-r and pulvinar proper. Our observations indicate that LPI-c (which is the only region of LP–P that reciprocally connects with striate cortex) is involved in the cortico-thalamic functional system activated by enhanced beta activity depending on the behavioural needs of the animal.

- **The spread of visual attention in curve tracing**

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In a curve-tracing task, subjects have to judge whether items are located on a single, continuous curve. Here we try to distinguish between an object-based attention model and a moving-spotlight model of curve tracing.

Subjects had to trace a target curve that connected a fixation point to a circle. Another curve served as a distractor. To probe the distribution of attention, colours appeared at different curve segments at various time intervals during the trial. After the curve-tracing task had been completed, one of these segments was cued and subjects had to report the colour of that segment. The percentage of correctly reported colours was used as a measure for the distribution of attention.

We found that the initial segments of the target curve received attention during all time intervals. This is not consistent with a moving-spotlight model, since in such a model attention is not maintained on the initial segments of this curve. Instead, our results support an object-based model in which attention gradually spreads over all segments of the target curve.



- **The benefits of training visual attention in a real-life situation**

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Visual attention could be described as those mental processes that ensure that some visual stimuli are processed while others are not. The aim of the study was to determine the effect of visual attention training on everyday tasks.

Sixteen subjects participated in the study. The experiment consisted of four sessions. In the first session, visual attention was assessed by means of a laboratory task as well as by means of a more realistic task. Subjects were then divided into two groups: the experimental group was given instructions on how to perform maximally on the laboratory task on the basis of their results in prior sessions. Subjects in the control group merely repeated the task. In the fourth session, a parallel version of the realistic task was administered.

Results show that visual attention can be trained successfully. In the laboratory task, repeating the task proved to be as effective as being trained by well-specified instructions. However, in the realistic task, the instructions proved to be necessary: subjects in the experimental group improved significantly more than subjects in the control group. Furthermore, the performance of older subjects saturated after three sessions, whereas younger subjects continued to improve.

- **Legend placement in an active viewing condition**

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Traditionally the placement of figure legends is at the bottom of the graph or image, while a similar convention positions the title above a table. Occasionally design characteristics of a document mean these are displaced from their usual locations. How does this affect how much people attend to such legends?

A bar chart was placed within a body of text and the position of the legend was varied. The four conditions were top, bottom, left, and right. Four participants were assigned to each condition, with each person viewing the stimuli for 30 s. Attention was measured with the SMI remote eye-tracking device. This recorded the percentage of total viewing time spent attending to the legend. Both fixations and simple eye-movements showed that the left side of the figure received most attention, while the top received the least. When viewing embedded figures the optimal location for the legend is to the left.

## **BINOCULAR AND SPATIAL VISION**

- **Interocular distance, enhanced disparity information, and the control of prehension**

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Binocular disparity is considered pre-eminent in the control of reaching behaviour. One reason for this is that, once suitably scaled, it can specify metrical depth relationships within a scene. Such information is necessary to plan the transport-and-grasp phase of a reaching movement (ie absolute distance and size are required). If prehension is controlled via a binocular telepresence system, an opportunity arises to augment disparity information by increasing the intercamera distance (ICD) beyond normal interocular distance, thereby increasing the magnitude (and range) of binocular-disparity information.

Whether an observer can take advantage of enhanced disparities to control reaching movements is unknown. Here we examine the effects of manipulating ICD on reaching movements with ICDs ranging from 6.5 cm to 26 cm. Typically sized, real-world objects (both familiar and unfamiliar) were placed in a scene and reaching performance was assessed. An experimental sequence consisted of three blocks. In the first and last blocks a normal ICD/IOD of 6.5 cm was used, whereas in the middle block the subjects used an increased ICD. Larger than normal ICDs were found to disrupt reaching performance, with slower peak velocities and smaller grip apertures being observed. This was more pronounced for unfamiliar objects. Little evidence for learning was found.

- **Visuomotor adaptation to translated visual space**

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We investigated the ability to adapt goal-directed arm movements to translations of visual space. We expected that the magnitude of adaptation to a changed relationship between vision and kinaesthesia would depend on the direction of the translation, owing to differences in the sensitivity of these senses in different directions.

To study this issue, we asked subjects to align a real cube with a 5 cm side that they could not see, with a visual simulation that they saw via a mirror. Subjects made successive self-paced movements between different target locations. During adaptation phases, subjects received continuous visual feedback about the position and orientation of the real cube. This visual feedback could be veridical or translated up to 5 cm in one of three orthogonal directions. Each adaptation phase was followed by a test phase, during which no feedback was given.

Comparing test movement endpoints after translated feedback with ones after veridical feedback showed that subjects adapted to the distortion they were exposed to. Visuomotor adaptation was slightly more than 40% and cross-talk between orthogonal components was less than 5%. Adaptation was roughly equal for all three directions, despite differences in variability, suggesting that there is no relationship between sensitivity and the ability to recalibrate.

- **Does motion information interact with binocular disparity in object segmentation?**

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Considerable amounts of recent evidence suggest that binocular disparity and motion information are combined during such visual processing as structure-from-motion and computation of depth.

An assumption about the common function of these two types of information is that they serve to segment objects from their background. On the basis of this assumption, we investigated whether motion direction interacts with binocular disparity in the process of object segmentation, using a subthreshold summation method. First, we measured subjects' thresholds to discriminate vertical and horizontal rectangles defined by common direction or common binocular disparity alone in a random-dot display. Then, we measured threshold to discriminate the target in a compounding stimulus defined by both binocular disparity and motion direction.

The result shows that the threshold for the compounding stimulus is lower than that for the stimulus defined by each cue alone. However, such decrease in threshold fell short of allowing us to reject the prediction of the probability summation, suggesting that motion and disparity information may be independently processed, at least at the stage of object segmentation.

- **Effect of binocular vision training on the proximal fixation disparity curve**

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In near vision, the vergence response may lag behind the vergence stimulus; this exo fixation disparity amounts to a few minutes of arc for central fusion stimuli. When the viewing distance is shortened, fixation disparity increases linearly with the vergence stimulus (expressed in metre angle); subjects with a steeper slope of this proximal fixation disparity curve tend to have near-vision strain (Jaschinski, 1998 *Ophthalmic & Physiological Optics* **18** 30–39).

To investigate whether binocular vision training can improve, ie flatten, this curve in subjects with normal binocular vision, we tested fixation disparity (with dichoptic nonius lines at viewing distances of 100 cm to 40 cm) on days 1 and 9, while 25 min of daily visual training was performed on days 2 to 8. We analysed 19 (of all 34) subjects with curves steeper than average (–1.5 min of arc/metre angle) since only in these subjects can large improvements be expected. This subgroup showed a reduction in slope from before to after training (–4.2 and –1.2 min of arc/metre angle, respectively), which was significantly ( $p = 0.016$ ) larger than in a control group.

Thus, these tests revealed vergence training effects, as previously shown for the prism fixation disparity curve (Hung et al, 1986 *Documenta Ophthalmologica* **62** 165–179).

- **Recovery of the 3-D centre from three collinear dots moving in a slanted plane**

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Subjects were shown three collinear dots that were rotating rigidly around a fixed centre in a slanted plane. The task was to decide whether the middle dot was centred in 3-D between the two other dots.

Lappin and Fuqua (1983 *Science* **221** 480–482) showed that subjects are accurate at detecting displacements of 2%, 4%, and 6% away from the 3-D centre. They interpreted the results as evidence for the use of 3-D properties that are projectively invariant. However, Wagemans and Tibau (1999 *Perception* **28** 267–282) found effects of 2-D properties that were not reconcilable with this interpretation.

We suggest that in the present study subjects did the task by means of a heuristic that maps the relative length of the two line segments in the image onto their 3-D relative length. We varied the slant of the plane in which the dots were moving and the focal distance from which they were projected. This way, for every combination of slant and focal distance, the 2-D properties of the stimulus were different. Subjects tended to see the middle dot centred in 3-D in most of the conditions, except when the ratio of the two line segments exceeded some criterion.

- **Volumetric colour filling-up perception with binocular viewing**

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A transparent volumetric illusory object filled with a transparent medium is perceived when inducing objects are arranged in suitable relations and displayed stereoscopically. We named this phenomenon 'mime effect', and the inducing object 'sustaining cues' (Zhang and Idesawa, 1998 *Japanese Journal of Applied Physics* **37** L329–L332).

Volumetric colour filling-up, in which the illusory volumetric object is perceived as filled with coloured medium according to the coloured sustaining cues, is observed in mime effect. When cones act as the sustaining cues, the perceived volumetric filling-up colour and its brightness are subjected to the colour of the cone bases and conical surfaces, as well as the cone direction and composition. When the cones point outward of the illusory object, the filling-up colour is largely determined by the base colour, but is also affected by the colour of conical surfaces, owing to the colour contrast between the base and the conical surface. When the cones point inward, or are composed of two parts in different colours, the volumetric filling-up colour is to a large extent determined by the colour of the parts inside the illusory object, but is also affected by the colour of outside parts.

## COLOUR AND BRIGHTNESS

- **The detection of coloured Glass pattern in the presence of chromatic noise**

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Glass patterns are made by juxtaposing two identical arrays of random dots. The detection of these patterns is mediated by high-level mechanisms important for object perception and recognition. We studied the chromatic properties of these mechanisms. We used a two-interval forced choice task to measure a subject's ability to reliably detect a circular Glass pattern in the presence of a variable number of random noise dots. We measured detection thresholds for various combinations of signal and noise colours.

When signal and noise were in the same direction of colour space, the thresholds remained constant across the colour directions we have tested. When the chromatic content of the signal and noise were varied independently: (i) the noise was most effective when it was in the same direction as the signal; (ii) when the chromatic content of the noise was varied relative to that of the signal, the thresholds increased proportionally to the cosine of the angle between the respective directions of signal and noise in colour space.

Thus, circular Glass patterns are detected by multiple mechanisms whose chromatic properties are determined by a linear combination of their cone inputs.

[Supported by SNSF grant 31-56711.99 to D C Kiper.]

- **Measuring double-increment illusions**

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The specific grey shades in a visual scene can be derived from relative luminance values only when an anchoring rule is given. The anchoring theory of lightness (Gilchrist et al, 1999 *Psychological Review* **106** 795–834) assumes that the highest luminance is perceived as white, and the appearance of all the other regions depends on their relationship to such white. It is thus a crucial prediction of the theory that equal regions representing luminance increments relative to their surrounds shall be perceived as identical.

Our stimuli were incremental targets on two uniform surrounds placed side by side. We used the method of adjustment: observers varied the luminance of the test patch (set on a black surround) to match the achromatic colour of the comparison patch (set on a variable surround). We found that a target on a black surround looks always lighter than the same target on a more luminant surround. Previous failures to observe double-increment illusions may have been due to the fact that the strength of the effect rests on the specific luminances of the target and of the pair of surrounds chosen for the display.

- **Illusory contours as elements of abstract art**

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Following the emergence of abstraction as an art form around 1910, artist techniques gradually drifted from freehand painting to the more formal geometrical patterns requiring ruler and compass. These technical aids sharpened and straightened fuzzy contours and it was the sharpness of contours, combined with high-contrast borders of the geometric figures, that formed the elements of illusory contours embedded in some of the pictures. Although spontaneous emergence of illusory contours must have been a common occurrence in the sketchbooks of the numerous 'abstract' painters in that period, apparently only Frantisek Kupka, who was well versed in natural sciences, elaborated on this perceptual phenomenon.

The elements of illusory contours are already evident in Kupka's monochrome-gouache work executed in the early twenties and reach their zenith by the mid-thirties long before illusory figures drawn by Ehrenstein and Kanizsa appeared in print. Kupka's numerous monochrome and polychrome water-colours and oil paintings from the thirties document the entire range of linear and curvilinear illusory figures, including spatial superposition and occlusions. Finally, Kupka's practical as well as theoretical contributions, compiled in *La Création dans les Arts Plastiques*, provide a historical framework for the origins of amodal completion: seeing or thinking?

- **Chromatic quality of natural scenes represented by low-dimensional approximations to reflectance functions**

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Surface spectral reflectances of many naturally occurring surfaces and of entire natural scenes may be mathematically well represented by low-dimensional linear models. The aim of this work was to investigate the chromatic quality of such approximations with real countryside and urban scenes.

Multispectral images of outdoor scenes were collected with a fast multispectral imaging system. For each scene 33 images were captured by a high-resolution digital camera through a fast tuneable liquid-crystal filter with peak wavelengths in the range 400–720 nm [Nascimento et al, 1999 *Investigative Ophthalmology & Visual Science* **40**(4) S748]. The spectral reflectance for each pixel was estimated against a white reference located in the scene. The principal components and the distributions of reflectances along each principal axis were computed for each scene. Chromatic representations in CIELUV space of each pixel under D65 were determined both from the measured reflectances and from the PCA approximations.

Three principal components provided colour reproduction that was good for natural countryside scenes but rather less so for urban scenes. For all scenes, however, the larger errors occurred with the less common reflectances. Low-dimensional approximations to reflectance functions successfully reproduce natural images of country landscape, but are limited with urban scenes.

- **Lighness determination for an object under two illuminations**

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When a shadow is cast across half of an object, observers can make a separate lighness match for (a) the whole object, (b) the shadowed region, and (c) the nonshadowed region.

We tested three hypotheses concerning whether matches for the whole object agree most closely with: (i) matches for the region in higher illumination, (ii) matches for the region within the larger field of illumination, or (iii) whichever matches show the least error. A row of five adjacent rectangles, ranging from black to white, was suspended in mid-air. A shadow with a blurred edge was cast across this row so that only part of each rectangle was under the shadow. Previously we reported object matches for the black-and-white targets only, and these were closer to veridical values than to the matches obtained for either higher illumination or larger field size. In order to understand how the visual system could minimise the error we tested intermediate shades of gray as well as a truncated range of grays.

The results show object matches to agree with target regions that appear to lie in the prevailing illumination, even if this entails a significant shift away from veridicality.

## EYE MOVEMENTS

- **Transsaccadic representations of saccade-target and flanker objects: Location independence versus dependence**

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To account for the integration of extrafoveal and foveal views across eye movements, two representational systems have been proposed. The first is a permanent lexicon of object detectors, which fire whenever evidence for particular objects is apprehended, regardless of their location in the visual field. The second is a set of temporary, episodic object files, each constructed for a specific object occupying a particular location in space.

Four experiments are reported in which transsaccadic preview benefits have been examined by (i) manipulating the spatiotemporal continuity of a to-be-identified object across a saccade, and (ii) the status of that object, ie saccade-target versus flanker object.

The results show substantial preview benefit (reduced gaze durations) for the saccade-target object, regardless of its spatiotemporal continuity (location independence). For the flanker object, preview benefit was dependent on the object's spatiotemporal continuity (location dependence). Results are interpreted in terms of a revised dual-code theory of transsaccadic object perception (Henderson, 1994 *Journal of Experimental Psychology: General* **123** 410–426).

- **Effect of stimulus contrast on the speed of visual search and the behaviour of eye movements**

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The task of the observer was to search for, and identify, an uppercase letter from a rectangular array of characters in which the other items were numerals.

The threshold duration of stimulus presentation required for search was determined by a multiple-alternative staircase method. Eye movements were recorded simultaneously with a video eye-tracker. At all set sizes, threshold time for search decreased with increasing contrast. The average number of fixations per search decreased with increasing contrast. For the smallest set size (3×3 items), only one fixation was needed except at the lowest contrast. Average fixation duration decreased only slightly with increasing contrast. Also, the saccade amplitudes were nearly constant. The reduction of the number of fixations with increasing contrast suggests that visual span, ie the area from which information can be collected in one fixation, increases with increasing contrast.

Since fixations take most of the time needed for visual search, the reduction of the number of fixations results in reduced search times. Therefore, it seems that most of the improvement of visual-search performance with increasing contrast can be explained by the increase of visual span, which in turn results in a smaller number of fixations per search.

- **Motion illusions and eye movements**

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The initial interpretations of motion illusions are often in terms of eye movements. For example, both Purkinje and Addams related the motion aftereffect to eye movements that continued

following inspection of moving objects. Purkinje also linked visual motion illusions generated by prior body rotation to eye movements. His brief analysis was in a long article on vertigo, published in 1820. However, William Charles Wells (1757–1817) had previously demonstrated the relationship between involuntary eye movements and postrotary visual motion. He compared the motion of a stabilised retinal image, generated before body rotation, with that of real images viewed afterwards. Wells established the characteristics of postrotary nystagmus, its dependence on head position during rotation, its suppression by fixation, and its diminishing amplitude with time. He also demonstrated torsional nystagmus. The origins of eye-movement research, and its links with visual phenomena, are to be found in the eighteenth century.

## LEARNING, MEMORY, AND DEVELOPMENT

- **Visual-working-memory characteristics in monkeys with bilateral prefrontal cortex lesions**  
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We have investigated the characteristics of visual working memory in a delayed-discrimination task on two groups of rhesus monkeys. The prefrontal-cortex sulcus principalis was removed bilaterally in monkeys of one group. The remaining animals served as unoperated controls. The monkeys were trained to discriminate stimuli (16 pairs) with different types of visual information (geometrical figures of various shape, size, colour, orientation, various spatial relationships between components of two-dimensional scenes) during development of a delayed (by 0–8 s) instrumental reflex.

The data obtained demonstrate that the duration of information storage markedly decreases (by a factor of 2–3) in the monkeys after bilateral lesions of sulcus principalis for delayed discrimination of visual stimuli connected with different spatial relationship features, different colour, size, orientation, black-and-white geometrical figures of different shapes. These changes of working-memory characteristics were accompanied by increase of motor reaction time. The results suggest that prefrontal-cortex sulcus principalis is involved in the mechanisms of working memory associated with neural correlates of visual awareness and caused by the synchronisation processes which bind neural networks distributed across the visual object-processing pathway in synchronised assembly activities.

[Supported by the Russian Foundation for Basic Research, grant 99-04-49645.]

## MOTION PERCEPTION AND OPTIC FLOW

- **Interactions between visual and auditory movement perception in a direction discrimination task**

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We investigated interactions between the perception of visual and auditory movement. Five observers viewed random-dot kinematograms while listening to sound movement simulated by interaural amplitude modulation (IAM) of a pure tone over headphones. Each trial began with a 'noise' phase, during which the dots moved at random while the sound remained stationary, followed by a 'coherent' phase, during which a percentage of randomly selected dots moved together leftwards or rightwards, while the sound moved in the same or opposite direction. Observers maintained visual fixation on a central marker throughout. In the visual task, observers ignored the sound and reported the direction of coherent dot movement. In the auditory task, observers reported sound movement direction. The degree of IAM and the percentage coherence were both varied independently in all combinations from subthreshold to suprathreshold levels.

For all five observers, the presence of concurrent visual motion enhanced performance on the auditory task, whereas conflicting visual motion degraded performance. For three observers, sound movement had significant effects on the visual task performance; for two observers, both concurrent and conflicting sound movement degraded performance. The effects cannot be explained by probability summation of two independent mechanisms signalling motion direction.

- **Attentional tunnel vision for motion**

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Distracting an observer's attention away from a target moving in depth can degrade motion processing (Gray, 2000 *Vision Research* **40** in press). Does attention also modulate the amount of motion-in-depth information processed?

After adaptation to an expanding radial-flow pattern, observers detected an expanding target amongst 11 static targets. Fixation was 5 deg from the focus of expansion (FOE) of the flow pattern.

There were two attention conditions during adaptation: (a) attend flow—observers detected odd elements in the flow pattern; (b) attend fixation—observers discriminated characters presented at fixation.

For expanding targets located in the position previously occupied by the FOE, detection times (DT) were significantly elevated. The DT elevation was significantly greater for (a) than for (b). The DT elevation decreased as the separation between the expanding target and the FOE increased. For (a) DT elevations were significant for separations less than 2 deg. For (b) DT elevations were significant for separations less than 0.6 deg. The decrease in lateral extent of the aftereffect could not be entirely explained by the reduction in gain of motion-in-depth detectors. These results suggest that when an observer's attention is distracted away from the FOE, motion-in-depth information is integrated over a narrower spatial extent.

- **Total least squares: a general tool to explain motion and tilt aftereffects**

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To explain motion and tilt aftereffects, a model of visual processing is proposed which assumes that image measurements are prone to errors in both space and time. Response suppression (ie adaptation) caused by automatic gain control stems from processes which affect the transfer functions (feedback gain) at two neural sites in the model: simple or complex cells.

Predictions from these adaptive processes can be used to explain (i) the reduction in the magnitude of aftereffects as a function of increasing image contrast; (ii) the increase in perceived speed when testing with a higher speed in the same direction, or the decrease in perceived speed when testing with motion in the opposite direction; and (iii) tilt aftereffects (both repulsion and attraction) when varying the relative orientation between adapting and test patterns.

Systematic differences between tilt and motion aftereffects, most notably the absence of reduced perceived speed after adaptation to static patterns (Ascher et al, 1996 ARVO) are attributed to differences in prior assumptions when processing spatial and motion signals.

- **Path-length estimation of oscillating lines**

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The influence of some factors relating to an oscillating line on the path-length estimation was investigated.

In the first experiment, lines of five length values (10, 30, 50, 70, and 90 mm) were presented moving along two directions: vertically and horizontally. In the second experiment, velocity effects (30, 60, 90, 120, and 150 mm s<sup>-1</sup>) on path-length estimation during ocular pursuit and during steady fixation were compared. The subjects observed the display from a distance of 500 mm. They had to adjust the amplitude of oscillation. The task was to make the path length of the oscillations equal to the length of the line. In general, results show an underestimation of the path length of an oscillating line. Moreover, the effect increases both when the line length and its velocity are increased. This effect is stronger during ocular pursuit.

The hypotheses that line movement shifts the system of reference and the illusion of apparent size shrinkage for a moving object (Ansbacher, 1944 *Journal of Experimental Psychology* **44** 1–23) are discussed.

- **Motion adaptation shifts the apparent positions of remote objects**

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We show that an aftereffect of motion adaptation causes a shift in the apparent position of a flash even when the flash appears stationary and is located several degrees from the adapted region.

Following 30 s of adaptation to a rotating radial grating, 500 ms test and 8 s adaptation periods were alternated. In the test period the visual display was blanked and a Vernier stimulus composed of two flashed lines was presented. Each flash was horizontally separated from the adapted region by 2–20 deg. A second experiment demonstrated that the flashes appeared stationary at flash durations greater than 300 ms.

When the two flashes were physically aligned and appeared stationary, they nevertheless appeared misaligned as if they had moved in the direction of the motion aftereffect (MAE). The maximum perceived misalignment was ~20 min of arc, and was produced even when the flashes were separated from the adapted region by over 20 deg. The misalignment illusion reveals that the MAE can influence apparent position well beyond regions in which the MAE is traditionally seen.

## NATURAL IMAGES, BIOLOGICAL MOTION, AND FACES

### ● **Translational motion alters the visual perception of articulatory movements of human gait**

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Actions of a living body are usually goal-oriented. For example, the goal of gait is translation. However, there are only few studies on relations between biological motions and their goals. In this research we investigated the effects of translational motion on the visual perception of human gait. Eleven observers discriminated among four types of walker defined by the combination of body orientation (left or right) and the direction of articulatory movements of limbs (forward or backward). A walker was presented in texture-defined animation, in which both a stick-figure walker and a background were made of random-dot textures. A horizontal movement of either a walker or a background produced translational motion. The main result was that discrimination of directions of articulatory movements was heavily disturbed when the direction of translational motion was incompatible with the walking direction. In other words, such incompatibility tended to produce the perception of reverse articulatory movements. This result could be due to a synergic effect of daily perceptual experiences and a smaller contribution of articulatory movements toward conveying the goal of a walker.

### ● **The Batman effect: Selective enhancement of facial features during familiarisation**

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Several experiments were designed to isolate the facial information utilised in the learning of new faces. In these experiments, two groups of subjects were each trained on different groups of faces, with a dynamic video presentation. They were then shown both trained and novel faces in a same-different decision task, where 'different' trials included manipulations of internal and external facial features, and their task was to decide whether two images were identical or had a difference in one or more features. Our experiments show several enhancements, notably that hair change was most easily detected in untrained (unfamiliar) faces. When faces had been trained (familiar), detection of eye changes was selectively enhanced and sensitivity to hair changes was maintained.

While previous studies have suggested that familiar face representations are weighted towards their internal features, our experimental results show that this is due to selective enhancement of the eyes alone, with no reduction in the salience of the hair. Moreover, within the limits of the familiarisation used here, there was no enhancement of the representation of the other internal face features examined. It appears that by concealing both hair and eyes a familiar face identity can be effectively disguised—the Batman effect.

### ● **Local structure facilitates rapid scene perception**

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Local structures, presented briefly in the form of a scrambled image, prime recognition of a target picture (Tjan et al, 2000 ARVO). Does this priming reveal a mechanism intrinsic to rapid scene perception?

Participants had to judge which of two black-and-white cut-outs belong to a natural-scene picture embedded in a presentation sequence. Three types of images could be presented in combinations within the sequence: a coherent colour picture (C), its block-scrambled ( $46 \times 46$  pixels) version (J), or its pixel-scrambled colour-preserving version (F). Prior studies showed that performance for 3J2C (three frames of J followed by two frames of C,  $14 \text{ ms frame}^{-1}$ ) is better than for 2C alone.

In the present study, we found that performance decreased if either the 3J or the 2C component of 3J2C was removed by replacing it with 3F or 2F, respectively. Performance also worsened when observers were shown two presentation sequences, one containing only the 3J and the other only 2C, before making a decision. Taken together, these results show that the level of facilitation by local structures (3J) is beyond a simple combination of two sources of information (3J and 2C). Local structures prime scene recognition by interacting with the normal process for rapid scene perception.



## SHAPE

### ● Getting depth from flat images

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We investigated the relative strength of contour and shading cues in eliciting a 3-D impression from a flat image. 2-D images of a card were computer-simulated and displayed on a CRT. Each image had one of four possible types of shading (spatial gradient in brightness and colour) corresponding to: (i) a flat card uniformly illuminated; (ii) a concave card (corner) with direct and indirect illumination on both sides; (iii) a corner with direct illumination on one side only; and (iv) a convex card (roof) under direct illumination. Each image had one of three types of contour (flat, convex, or concave). Twelve different images (72 distinct pairs) were created, in which all combinations of contour and gradient were used. On each trial, one image pair appeared for 750 ms, followed by a mask which remained until the observer responded which image appeared flatter. Eight observers contributed to a total of 26 comparisons for each pair.

We found that, for any given contour, the addition of a corner or roof gradient makes it appear less flat, whether or not the gradient is appropriate for the shape depicted by the contour. The gradient with the strongest chromatic component (iii) produces the strongest 3-D impression.

### ● Phonetic – iconic congruency: Takete – Maluma phenomenon

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Some pseudowords (ie patterns of phonemes), can be associated with different visual patterns. For instance, Köhler suggested that Takete can be taken as a pseudoname for angular, sharp, rectilinear patterns, and Maluma as a pseudoname for smooth, curvilinear patterns [eg Köhler, 1949 *Gestalt Psychology* (New York: Liveright)].

Our purpose was to evaluate phonetic – iconic congruency. 126 Serbian-speaking undergraduates were asked to give 20 pseudonames for each of 8 abstract achromatic patterns. The patterns were varied by different dimensions (simplicity – complexity, angularity – curvilinearity, whiteness – blackness, dispersion – compactness). The corpus of 2520 pseudonames per stimulus was obtained. The two clusters of visual patterns were extracted, a cluster of Taketes (four patterns) and a cluster of Malumas (four patterns). A  $\chi^2$  analysis showed that each of the Taketes included significantly more phonemes R, Z, K, T, C (tz), etc than the Malumas. On the other hand, Malumas included more phonemes M, A, L, O, N, etc than Taketes.

The results show that the distribution of phonemes in pseudonames of abstract patterns is not arbitrary. It strongly depends on some physical characteristics of visual patterns: All Taketes contain angular contours and darker surfaces, whereas Malumas are brighter and curvilinear.

### ● Visual surfaces: perception of illusory contours and neon colour spreading in squirrel monkey

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The purpose of this study was to compare the perception of subjective contours (SC) to that of neon-colour spreading (NS) in a squirrel monkey. One squirrel monkey was trained on a matching-to-sample task. On each trial a sample stimulus first came in the centre of the monitor.

Four forms were simultaneously presented, equidistant from the sample stimulus when the monkey touched it. The task was to touch the target stimulus that was similar to the sample. Target stimuli were composed of SC or NS and consisted of crosshatched lines of various widths and spacings. The performance was measured in terms of the percentage of correct responses and reaction times. The performance varied with the width and spacing of crosshatched lines. It also varied with the luminance ratio of the inner to outer segments in the NS condition.

The ability of squirrel monkey to perceive SC and NS indicates that the perception of these visual surfaces relies on the early visual system. The longer latencies in the NS condition than in the SC condition support the results with humans suggesting that SC occur in earlier functional stages in the visual system than NS.

### ● Similarity effect in the perception of two simultaneously presented figures

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Strategies used in the analysis of two simultaneously presented figures were investigated in a psychophysical experiment on human subjects. Test stimuli were irregular polygons composed on the basis of a  $4 \times 3$  matrix. Five groups of figure pairs with different degrees of reciprocal similarity were presented for recognition under the backward masking conditions. Masking of

test figures was followed by a special marker that indicated which one of two test figures must be detected in the subsequently presented table that included all 12 test figures.

Two distinct patterns in the performance of individual subjects were revealed. The same recognition accuracy for the pairs of identical and different figures as well as no effect of similarity on the recognition of different figures characterised the results of 33 subjects. 17 subjects recognised identical figures more accurately than different ones, and the recognition of different figures depended directly on their similarity—the more similar the figures were, the more accurately they were recognised. Experimental results are interpreted on the basis of different analysis strategies applied by different subjects.

## **SPATIAL FREQUENCY AND CONTRAST**

### ● **Interaction of two illusions seen through different eyes**

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Errors in length discrimination have been measured on two superposed illusory figures. On the monitor, the paired figures differed in orientation (by 180°), contrast (in one figure it was fixed at -1.0 or 0.54, in the other it varied from -1.0 to 0.54 in 50 steps), but had equal size and shape, and coincided precisely, with their arrow tips matched. The shaft section was absent. Each figure was exposed in different frames and presented to different eyes of the subject. The frame rate was 120 Hz, and the subject saw the figures without flickering.

The subjects reported the figure with inward wings as being shorter than that with outward wings. The subjects, using the panel keys, made the two figures equal in size. The illusion strength was found to be as large as 20% of the figure length. It did not change with contrast variations. If both figures were presented simultaneously in the same frames to one or both eyes, a different effect was obtained: the figures appeared to be equal in length, but the illusion persisted—it varied from 0% to 20% with variations of the contrast of one figure. The data are interpreted in terms of two-dimensional spatial filtering in the retinocortical pathways.

### ● **Reaction times as a behavioural measure of contrast gain; comparison of low and high luminance levels and different eccentricities.**

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It has been shown physiologically that the sensitivity of visual neurons is dependent on their contrast gain (Lee et al, 1990 *Journal of the Optical Society of America A* 7 2223–2236). In the present study we investigated the link between reaction times (RTs) and contrast sensitivity by deriving an index of contrast gain from RT data.

Binocular RTs were measured by using vertical, achromatic gratings presented over a range of contrasts from threshold to 0.5. Spatial frequencies of 0.49, 1.71, and 5.57 cycles deg<sup>-1</sup>; luminances of 0.02 and 20 cd m<sup>-2</sup>; and eccentricities of 0, 5, 10, and 15 deg for both hemifields were tested. Stimuli were generated with a PC. A smart interface 'CED1401' measured response time (1 ms resolution).

The RT-based contrast gain changed with eccentricity and spatial frequency in the same way as does the contrast sensitivity; it was maximal at the fovea and decreased linearly with eccentricity. At low luminance, contrast gain was reduced for all conditions and was independent of eccentricity for the low spatial frequencies. These observations were symmetrical for the two hemifields. We conclude that the RT-based contrast gain matches contrast sensitivity over a range of suprathreshold stimulus conditions.

### ● **Detection thresholds for the Hermann-grid and scintillating-grid illusions and the effect of temporally separating the disks from the grid on the latter**

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The scintillating-grid illusion is a brightness-contrast phenomenon in which small white disks are added to the intersections of a gray-on-black Hermann grid. Dark illusory spots are perceived within the disks as flashing with each flick of the eye (Schrauf et al, 1997 *Vision Research* 37 1033–1038).

In the first experiment, duration thresholds for the Hermann-grid and scintillating-grid illusions were compared. The threshold of the latter is some 30 ms longer than that of the former. In the second experiment, illusion strength was rated for an entire scintillating grid exposed for various durations as well as for one consisting of a Hermann grid onto which the white disks

were briefly projected. Illusion strength was found to increase less rapidly with exposure duration when only the disks, rather than the whole scintillating grid, were briefly exposed. Furthermore, when the grid and disks were presented briefly but successively, no illusion occurred.

The result of the first experiment is consistent with the assumption that a greater spatial integration is involved in the scintillating-grid than in the Hermann-grid illusion, while that of the second underscores the role of the greater temporal integration in the build-up of this illusion over time.

## VISUAL IMPAIRMENT

### ● **Data on dark adaptation and central visual sensitivity in patients with endocrine optic neuropathy**

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The onset of compression of the optic nerve in patients with endocrine ophthalmopathy is frequently insidious and is serious since about 20% of patients with this disease become blind.

The purpose of our work was to evaluate dark adaptation and central visual sensitivity in patients with endocrine optic neuropathy. We investigated dark adaptation with an ARP adaptometer and a Humphrey automated computerised perimeter with a threshold testing programme extending over the central 30 deg visual field. Seventeen patients with endocrine optic neuropathy were examined. Their age ranged from 27 to 59 years (mean 42.3 years). The control group consisted of seventeen healthy persons of similar age. Mean proptosis was  $19.7 \pm 2.1$  mm. In patients with duration of the illness of more than 3 years, dark adaptation was impaired and a reduction of the mean sensitivity of the central visual field was noted ( $24.1 \pm 1.3$  dB,  $p < 0.001$ ). It is suggested from the data that tests on dark adaptation and central visual sensitivity allow earlier detection of retinal disturbances in endocrine optic neuropathy.

### ● **Evidence for individual effects of intermittency of light at 100 Hz on static accommodation**

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We investigated whether visual functions may be affected by temporal modulation of light at a frequency of 100 Hz (ie above flicker fusion), which is present on cathode ray tubes and in room lighting.

In a series of 2-min test intervals, subjects binocularly read printed text back-illuminated by a special fluorescent lamp with either intermittent light of 100 Hz or with steady light as a reference (produced with DC current, luminance  $61 \text{ cd m}^{-2}$ , viewing distance 50 cm). While pupil size and blink rate were unaffected, static accommodation (measured with an autorefractometer) showed the following results: in some of the twelve subjects accommodation at 100 Hz was stronger, in others it was weaker, by up to 0.15 dioptre. These differences were significantly correlated between two sessions made on separate days ( $r = 0.66$ ;  $p = 0.01$ ; for the second half of the sessions when subjects experienced visual fatigue). Further, one subject had an individually significant effect (Bonferroni corrected  $p = 0.01$ ).

Thus, in some individuals accommodation appears to be affected by non-visible intermittency of light, probably mediated by the autonomous nervous system. Such effects could be related to the higher visual fatigue under 100 Hz light that has been reported in some studies.

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## WEDNESDAY

### PROF. MULDER LECTURE

#### ✦ Aging and scotopic dysfunction

C Owsley, G R Jackson (Department of Ophthalmology, School of Medicine, University of Alabama at Birmingham, 700 South 18th Street, Birmingham, AL 35294-0009, USA; fax: +1 205 325 8692; e-mail: [owsley@eyes.uab.edu](mailto:owsley@eyes.uab.edu))

A ubiquitous problem of growing old is difficulty seeing under low illumination. Poor vision under low light levels hinders the performance of daily activities, and has been linked to the occurrence of falls and vehicle collisions.

A programme of research is described that seeks to reveal the neural mechanisms underlying scotopic dysfunction in older adults. By the age of 70 years adults have a half log unit loss in scotopic sensitivity, which cannot be attributed to preretinal factors or retinal disease, implying it represents an aging-related neural change. Cross-sectional data suggest that this impairment does not have a sudden onset in late life, but rather gradually emerges over adulthood. Furthermore, older adults experience delays in adapting to darkness. The time needed for 70-year-olds to reach prebleach light sensitivity is over 10 min longer than for those in their 20s. This slowing in dark adaptation appears to be mediated by a slowing in the visual cycle, specifically a delay in rhodopsin regeneration. The extent of this delay in older adults is not correlated with the extent of scotopic threshold elevation, implying different underlying mechanisms. These rod-mediated deficits are accentuated in early ARM, and in most patients are more severe than cone-mediated deficits.

### ORAL PRESENTATIONS

#### MOTION MECHANISMS

##### ◆ Do humans act as cross-correlators in motion detection and discrimination?

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An ideal observer discriminates two signals by cross-correlating the noisy received waveform with each of the signals. The cross-correlation model has been used successfully in the past to explain grating detection; we now apply the model to the discrimination and detection of motion. Three types of motion task were used: motion detection, speed discrimination, and direction discrimination. The stimuli were moving gratings with superimposed dynamic normal luminance noise; the grating contrast and noise power spectral density were fixed. For each motion task, the observer discriminated grating pairs with several speed differences. In this experiment, an ideal observer's  $d'$  is inversely related to the cross-correlation of the two moving gratings to be discriminated, and this cross-correlation depends only on the speed difference. The obtained psychometric functions ( $d'$  as a function of the cross-correlation between the signals) were well described by the ideal-observer model prediction. The same curve described the data from all motion tasks. Human motion discrimination is therefore consistent with a mechanism that cross-correlates the received spatiotemporal waveform with a stored representation of the signals to be discriminated. This cross-correlation can be computed by a linear spatiotemporal filter (oriented in space–time).

##### ◆ Velocity adaptation is consistent with a ratio model

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Speed adaptation experiments have told us little about how speed is coded in the visual pathway, but most have been contaminated with concomitant contrast adaptation; we have examined the time course of speed adaptation under conditions that minimise contrast effects.

Subjects adapted to moving low-contrast (10%) gratings (2 Hz or 12 Hz) presented to the left of a fixation point for periods of 8, 16, 32, or 64 s. After adaptation, a standard of the same speed (70% contrast) was located in the adaptation-grating position while the test (70% contrast) was presented to the right of the fixation point. Subjects indicated which grating appeared to move faster. Thirty such adaptation runs, governed by a modified PEST routine, were analysed by probit for the 50% point. The mean of four such estimates was taken as the PSE. Two authors were subjects.

The results show: (i) perceived speed declines exponentially with adaptation duration; (ii) the time constants for the 2 Hz and 12 Hz adaptation rates are different (15.88 s and 1.9 s respectively). We show that a model that assumes that speed is based upon the ratio of two underlying mechanisms (with time constants of 2–4 s) can capture much of these data.

◆ **Motion opponency in motion detection**

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Several theoretical models of motion detection incorporate an opponent stage of analysis, in which motion direction is coded by the difference in output between opposite (eg leftward and rightward) detectors. Psychophysical evidence for motion opponency, however, has been weak or disputed.

We used a two-alternative forced-choice staircase procedure to measure contrast thresholds for moving sine-wave gratings (0.5 cycle deg<sup>-1</sup>, 8 Hz or 20 Hz drift rate) superimposed on a counterphase flickering mask of the same spatial and temporal frequency. Low-contrast maskers made movement detection easier (facilitation) while higher-contrast masks made it more difficult (masking), resulting in a characteristic dipper-shaped threshold function. The slope of the masking function was close to 1 (Weber's law). Importantly, sensitivity to motion depended on the difference between opposite motion signals. Sensitivity doubled when the test signal (an increase in rightward energy) also had a decrease in leftward energy (or vice versa).

A motion-energy model that incorporates subtractive motion opponency and a divisive gain control—with only two free parameters—successfully accounts for both unmasked-detection and masked-discrimination performance. In further experiments we investigated the nature of this gain-control mechanism.

◆ **Neural and behavioural correlates of ambiguous local motion measurements in cortical visual area MT**

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Local measurements of velocity along the length of a moving contour are insufficient to specify the global stimulus motion direction. This ambiguity is called the aperture problem, and it applies to cells in the early stages of visual processing, where receptive field diameters are often smaller than the length of a visual contour.

To study this problem at the neuronal level, we recorded from motion-sensitive cells in the middle temporal (MT/V5) visual area of an alert macaque monkey, while patches of oriented bars were swept through the receptive fields. The orientation of the bars was varied across blocks of trials, so that it deviated from the motion direction by 45°, 90°, or 135°. We then measured the time-varying direction selectivity of each neuron. The results indicate that the earliest responses (< 100 ms) of most MT cells primarily encode the component of motion perpendicular to the orientation of the bar, while the later responses encode the actual direction of bar motion, irrespective of orientation.

When a second monkey was trained to pursue the centre of a moving bar, analogous results were obtained, with initial eye movements being displaced in a direction perpendicular to bar orientation.

## IMAGE STATISTICS

◆ **Centre – surround contrast interactions of textures depend on image statistics**

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The perceived contrast of a small random-dot patch is known to depend on the physical contrast of a surrounding random-dot pattern. Unlike random-dot patterns, whose spectra are flat, natural images have characteristic second-order statistics; their amplitude spectra fall off with spatial frequency ( $f$ ) roughly as  $1/f$ . Here, we have synthesised  $1/f$  texture-probes and inserted them into natural images in order to determine how their perceived contrast is affected by the statistics of the surrounding images. Probes (1 deg × 1 deg) were centred on natural images (4 deg × 4 deg) whose statistics we have manipulated systematically. At each image-statistics, the contrast of a surrounding natural image was modulated sinusoidally in time (0–100% contrast, 0.5 Hz). Subjects had to adjust the contrast modulation of the probe in order to cancel the induced changes in its perceived contrast.

We have found that the perceived contrast of a probe is strongly affected by the particular statistics of the surrounding natural image. Suppression is maximal around the characteristic second-order statistics of real-world images. This result supports the suggestion that neurons in our visual system are 'tuned' to the statistical structure of the real world.

[Supported by the Wellcome Trust 047064 and the University of Newcastle upon Tyne.]

◆ **Perceived contrast of natural images is mediated by higher-order image statistics**

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Previous research (Párraga et al, 2000 *Current Biology* **10** 35–38) has indicated that human vision is optimised for processing the information in natural visual images. We defined ‘natural’ as having a normal value of the slope of the Fourier amplitude spectrum (the  $1/f$  slope). The task used was the discrimination of objects subtly varying in shape. The results suggested (a) that object discrimination was optimal for natural values of slope; and (b) that a simple model, based on contrast discrimination mediated by local spatial-frequency detecting units, successfully predicted object discrimination performance.

We now ask how this may relate to the perception of overall image contrast. For a variety of natural images, we varied the spectral slope and found that, in general, maximal contrast (as indicated by a matching task), occurs for natural values of spectral slope. This remains the case even when the natural slope deviates from the common value of around  $-1.2$ . However, this peak in perceived contrast for natural slopes is removed by phase-scrambling the image. Since this destroys higher-order statistics, while leaving the Fourier spectrum unchanged, we conclude that perceived contrast is mediated by higher-order statistics of images.

[Supported by BBSRC.]

◆ **Higher-order statistics and the multivariate probability density function of natural images**

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The statistical structure of natural images is analysed by two complementary approaches: by the measurement of higher-order spectra and by our method of ‘wavelet statistics’, which explores interesting projections of the multivariate probability density function (pdf).

We show that the probability mass is concentrated in low-dimensional subspaces which represent intrinsically one-dimensional image features, and that the multivariate pdf thus resembles a ‘hyper star’. The polyspectra show a corresponding concentration of polyspectral energy for aligned frequency components. This basic statistical structure provides the explanation for the generation of a sparse representation by oriented filters: the kurtosis is maximised if the filter decomposition is adapted to the shape of the tri-spectrum, which is closely related to the fact that only oriented filters can cause the projection of a maximum part of the probability mass to the zero level.

Since the hyper star is not separable in Cartesian axes, linear filters cannot yield independent components of natural images, and there remain substantial statistical dependences across orientation, phase, scale, and position. We show how these dependences are exploited by basic cortical nonlinearities, like the phase-invariance of complex cells, cortical gain control, and end-stopping. The visual cortex thus seems to pursue a higher-order whitening strategy.

◆ **Diagnostic spatial frequency for object recognition in natural images**

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Form perception is primarily based on a spatial-frequency (SF) coding of the visual stimulus. A limited range of spatial frequencies may be more relevant for object recognition. Filtered images of natural scenes were briefly displayed (for 50 or 150 ms) and the subjects had to choose among four objects which one had been displayed. Performance varied according to the SF content ( $0.8$  to  $12.8$  cycles  $\text{deg}^{-1}$ ) of the stimuli. The performance peak (ie the diagnostic SF; Oliva and Schyns, 1997 *Cognitive Psychology* **34** 72–107) shifted toward lower spatial frequencies as larger objects were considered as target.

In a second experiment, the task was more complex—the subjects had to define the orientation of the object in the scene. Neither the diagnostic SF nor the optimal performance changed but the peak effect was enhanced. Splitting the test images in different experimental blocks according to their SF content modified the relative weights of the various bandpass stimuli for object recognition. Performance was improved for most of the filtered stimuli. These data exhibit a

diagnostic SF for recognition depending on the object size. They also show that when visual uncertainty is reduced, the best use of each SF-tuned mechanism is made to optimise performance.

## MOTION MECHANISMS 2

- ◆ **Third-order versus first-order and second-order motion in ambiguous stimuli: Competition reveals temporal tuning functions, monocular/binocular, and the role of attention**  
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Motion stimuli consisting of rows of grating patches have been constructed to produce apparent movement in either of two directions depending on which patches perceptually matched in successive frames (Werkhoven et al, 1993 *Vision Research* **33** 463–485; Ho, 1998 *Proceedings of the National Academy of Sciences of the USA* **95** 400–404). In a first-order direction, patches matched in luminance (light/dark); in a second-order direction, patches matched in texture contrast (high/low); in a third-order direction, patches matched in slant orientation ( $\pm 45^\circ$ ). Perceived movement was measured in first-order versus third-order displays and second-order versus third-order (frequencies 1–30 Hz). Stimuli were presented interocularly (motion perception requires combining signals from both eyes) or monocularly; the slant cue was either present or absent (same slant throughout).

We found that perceiving the third-order direction requires the slant cue; third-order dominates below 5 Hz. Each competition type (1 vs 3, 2 vs 3) yields two independent, consistent estimates of the temporal tuning functions for each competitor. First-order and second-order motions peak around 10 Hz, whereas third-order motion declines monotonically with frequency between 1–5 Hz. First-order and second-order motion are monocular, third-order motion is indifferent to monocular/interocular presentation but requires attending to slant direction. The temporal, monocular/interocular, and attentive properties of the three perceptual motion systems derived from motion competition are consistent with previous findings.

- ◆ **Motion standstill perceived from rapidly moving red–green gratings**  
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A moving red–green grating may appear to be stationary yet is clearly perceived. Motion standstill occurs when the motion systems fail (because the amplitude of modulation is too low) but shape/colour systems have adequate signals. Lu et al (1999 *Proceedings of the National Academy of Sciences of the USA* **96** 15374–15379) showed that motion of an isoluminant chromatic grating is detected only by the third-order motion system, which computes motion from salience modulation. When all the colours in the red–green grating are equally ‘different’ from the background—equally salient—the input to third-order system has no modulation, so motion standstill results.

An experiment was performed in which a sensitive calibration procedure removed residual luminance contamination. At isoluminance, first-order and second-order motion failed. Isosalience was achieved by setting the saturation of red stripes at a large value and varying the saturation of green (Blaser et al, 1999 *Proceedings of the National Academy of Sciences of the USA* **96** 11681–11686). At the presumed isosalience point, different for each observer, motion direction judgments were at chance and rated speed was ‘absolutely motionless’—a clear, stationary grating was perceived. Small deviations from isoluminance or isosalience restored apparent motion. This confirms that isoluminant motion is third-order; shape/colour can be computed from rapidly moving images; and only motion systems yield perceived motion.

- ◆ **Absolute judgments of the trajectory of motion in depth**  
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A body of research has shown that observers can precisely use binocular information to judge the angular difference between different trajectories of motion-in-depth (eg towards or slightly to one side of the nose). However, such relative judgments do not tell us how veridical that perception is. Can observers correctly judge the trajectory angle of an object moving in depth? An absolute trajectory judgment task was used to address this question.

Observers viewed a single point on a computer display, presented via stereo goggles, moving in depth in the dark. A stationary reference pattern at zero disparity was continuously present (distance = 1 m). After viewing the motion, observers indicated the perceived trajectory direction by drawing a straight line on a data collection sheet. They were informed that any angle from  $-90^\circ$  (leftwards), through  $0^\circ$  (towards the nose) to  $+90^\circ$  (rightwards) could appear.

Observers systematically overestimated the angle of the trajectory. For example, for a physical range close to  $4^\circ$ , one observer perceived a range of  $20^\circ$ , and two others of  $40^\circ$ . This is consistent with incorrect scaling for viewing distance by the visual system, resulting in different systematic errors for the lateral ( $x$ ) and depth ( $z$ ) components of motion in depth.

◆ **Short-latency ocular following responses to moving plaids in humans: temporal dynamics and spatiotemporal tuning**

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Control of tracking eye movements requires an unambiguous 2-D velocity vector of object motion. To investigate the underlying motion processing, we recorded by the scleral search coil technique the ocular following responses to moving plaids. Stimuli were presented for 200 ms, within a 22 deg diameter circular window. All conditions were interleaved so that direction of pattern motion was unpredictable. Grating speed was constant ( $25 \text{ deg s}^{-1}$ ).

Grating motion triggered ocular following responses at ultrashort latencies (85 ms). These responses were also elicited at similar latencies in the pattern motion direction of plaids constructed from two sinusoidal gratings ( $0.27 \text{ cycle deg}^{-1}$ ; 10 Hz) moving in orthogonal directions. To disentangle the contribution of grating-related and plaid-related motion signals, we recorded ocular responses to monokinetic plaids, where only one grating moved (orientation difference:  $45^\circ$ ). Tracking was initiated in the direction of grating-related motion signals at short latency but a second component was initiated 20 ms later, towards the direction of plaid-related motion signals. With a fixed spatial frequency of the moving grating, we found an inverted-U-shape relationship between the amplitude of the second component and the spatial frequency of the stationary grating, peaking when both gratings have similar spatial frequencies. These results reveal both temporal dynamics and spatiotemporal properties of linear and nonlinear motion processing.

## VISUAL FIELDS

◆ **Visual perception and performance under conditions simulating prosthetic vision**

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In preparation for retinal and cortical prosthesis prototypes for the blind we are conducting experiments on the properties of pixelised vision. Using a video headset with eye-position feedback, subjects performed reading and face-recognition tasks; in an interactive virtual-reality environment, they will perform mobility, object recognition, and manipulation tasks. Phosphenes are presented as 100 to 1024 uniform dots in a square array; size, separation, contrast, simultaneous gray levels, and random drop-out of dots are varied. The dot array scans the underlying image under control of eye position or mouse movement. Sentence reading speeds of 75 to 100 words  $\text{min}^{-1}$  and close to perfect face recognition (four-alternative forced choice) were possible.

In reading, drop-off occurred for any of the following: grid width  $< 4$  letters,  $< 4 \text{ dot} + \text{gap}$  cycles per letter,  $< 10\%$  contrast, or  $> 50\%$  drop-out; grey levels: no lower limit.

In face recognition, drop-off occurred for any or the following: face width  $> 3 \times \text{grid width}$ ,  $< 8 \text{ dot} + \text{gap}$  cycles per face,  $< 20\%$  contrast,  $< 4$  grey levels,  $> 50\%$  drop-out.

We are adding dynamic noise and will examine the effects of imposed rather than self-initiated image scanning.

◆ **The healthy visual field of recognition**

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The fovea and perifovea are the locus of highest contrast sensitivity for pattern recognition (Strasburger and Rentschler, 1996 *European Journal of Neuroscience* **8** 1787–1791). Outside this small centre, recognition contrast sensitivity declines, and at medium to high eccentricities at a



rate steeper than would be expected from the mere detectability of stimuli. Low-contrast stimuli are therefore detected but not recognised peripherally.

We have now directly and in a finely-spaced raster compared contrast sensitivity for recognition to that for detection in the full central 20-deg radius field for a group of young healthy observers ( $n = 20$ ). Detection stimuli were Gabor patterns (1 cycle  $\text{deg}^{-1}$ ,  $\sigma = 1.5^\circ$ ); recognition stimuli were the digits 0–9 (size 2.4 deg), the contrast thresholds of which were determined at 65 positions in a polar raster. Overall, we acquired close to 100 000 observer responses. Contrast thresholds were obtained by a maximum-likelihood adaptive procedure (R\_Contrast, ML-PEST). All subjects showed stable, inter-individually somewhat different sensitivity surfaces. Contrast thresholds for detection and recognition increased linearly with eccentricity (up to 10 deg eccentricity by 0.03 log unit  $\text{deg}^{-1}$ ). Recognition contrast thresholds were systematically higher than those for detection. We thus show normative data for character-recognition contrast sensitivity in the visual field, for young normal observers.

◆ **Training of visual scanning behaviour and perception in homonymous hemianopia**

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Homonymous visual field losses can cause severe functional as well as social limitations. In this project we study visual scanning behaviour of patients with homonymous hemianopia. Subjects showing scanning behaviour insufficiently adapted to their hemianopia are trained to develop a more efficient scanning pattern. We have investigated whether improved scanning also carries over to more complex and ‘real-world’ visuospatial functioning. Our training procedure consists of three consecutive phases. In the first phase, we teach subjects to make large and fast saccadic eye movements into the blind hemifield. In the second phase, these compensatory eye movements have to be applied in more complex and dynamic situations. In the final phase, the scanning pattern has to be employed while driving a car. Training is preceded and followed by registration and evaluation of scanning behaviour.

Results indicate that large differences in scanning performance can be found within the population with homonymous hemianopia showing that not all subjects automatically develop compensatory strategies. Comparison of performance before and after training indicates that, indeed, a number of aspects of visual scanning behaviour can be adapted in a relatively short period of time. Training can also lead to improvements in visuospatial neuropsychological test performance.

◆ **Compensatory viewing strategies and driving performance in a group of subjects with visual field defects**

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Viewing behaviour and driving performance were assessed in seventy-two subjects with central or peripheral field defects who did not comply with the Dutch vision requirements for driving. Those who failed the driving test were given further training in order to acquire compensatory viewing strategies. Three different training programmes were compared: a function training, making use of computer tasks; a mobility training, instructing the subject while walking and cycling; and a strategy training, consisting of driving lessons.

Many subjects (44%) passed the driving test and showed that they had spontaneously adopted compensatory viewing strategies to overcome their visual field defects. For those subjects who failed the driving test, viewing behaviour in the laboratory was enhanced after training. Scanning speed improved in all training groups, but more so in the function (26%) and mobility (24%) training groups than in the strategy training group (12%). In contrast, viewing behaviour while driving a car improved only in the strategy training group. Subjects in the function and mobility training groups did not show any progress at all. These data suggest that training is task-specific and does not necessarily generalise.

## POSTER SESSION 5

### ATTENTION, TEXTURE, AND VISUAL SEARCH

- **The effect of target luminance on the attentional blink**

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When two targets appear within 200–500 ms of each other in an RSVP sequence, identification of the second is poor. This has been dubbed the attentional blink (AB). The relationship between the extent of the AB and the stimulus energy of the targets has been examined in three new studies. In the first study, five spots of varying luminances appeared before a single target. The results—target identification found to be a function of the luminance of the spots—suggest that the speed of shifting attention to a new target is influenced by the energy of the spots. This interpretation is supported by the results of the second study where two targets were identified: the extent of the AB varied with the luminance of the first target. In the third study, where the luminances of both targets were correlated, AB was attenuated when the luminances of the two targets were enhanced. Critically, the luminance of the second target played a bigger role in this enhancement. It is concluded that, while shifting attention to a new temporal location is constrained by the luminance of the first target, the AB can be weakened by enhancing the energy of the second target.

- **Memory in visual search: an eye-movement study**

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When visual search becomes difficult, a series of attentional movements from item to item in the display occurs. Recent work (Horowitz and Wolfe, 1998 *Nature (London)* **394** 575–577) suggests that these movements are not accompanied by a memory for previously visited locations and so occur randomly.

We recorded eye movements, to investigate memory in search. Three observers made over 30 000 saccades in over 2000 trials. For each trial, we calculated the expected probability of a saccade returning to a previously fixated item on the assumption of sampling with replacement (no memory), and compared this with sampling without replacement (perfect memory). Combined across trials, this leads to a memory index from 0 to 1 for each observer. All three subjects showed some evidence for memory (AH 0.49; MH 0.60; SC 0.12). These estimates are inflated as the model assumes sampling of a single item in each fixation, and includes benefits from inhibition of return. We conclude that memory mechanisms are present in multi-fixation visual search but that these effects are small.

[Supported by EPSRC UK.]

- **Reaction time and spatial accuracy of manual aiming at a visual target manipulated in size, luminance contrast, and location**

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We investigated whether the performance of manual aiming at a visual target on a touch-panel monitor is affected by either the size, luminance contrast, or location of the target. A graphic circular disk was presented as the target. The size of the target was manipulated to be either 4 cm, 2 cm, or 1 cm in diameter. The luminance contrast was either 80%, 40%, or 20%. The location of the visual target was also manipulated to make it appear at one of seven horizontal positions on the monitor. A computer mouse button was used as the response key to measure reaction times (RTs) of the aiming movements.

Subjects were asked to press the mouse button to initiate each trial; then a fixation point appeared at the centre of the monitor. After a while, a visual target appeared at one of the seven loci. Subjects were then asked to touch the centre of the target as rapidly as possible, after releasing the index finger from the mouse. RTs, movement times (MTs), and positions aimed at were measured. Results show that RTs decreases with increasing target size, whereas luminance contrast does not affect either RTs or MTs. Regarding the aiming accuracy, there appears to be a significant interaction between the size and the luminance contrast.

- **Reading rate is affected by word length, distinct from letter spacing and the number of letters in a word**

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Previous studies have found that reading rates fell when word length differed from 6M, regardless of the number of letters in a word, with random presentation of words via RSVP text (Florer et al, 1999 ARVO). This study extends that conclusion to meaningful text, with word breaks. Subjects read uppercase and lowercase Bookman type. Letters subtended 1 deg. We measured reading rate for text composed of sentences that had constant word length, and variable letter spacing. For example, a sentence that would be hard to read, with words longer than 6M, might look as follows,

“I f o u n d t h e c o i n o n t h e b e a c h .”

Average reading rates were 113, 170, and 127 words min<sup>-1</sup> for words 3M, 6M, and 9M spaces long, respectively. These results support the proposition that word length, separate from the number of letters in a word or letter spacing, is an important parameter in models of the visual span.

- **Modelling multiple-target visual search**

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Multiple target search augments standard visual search by including trials in which all elements are ‘targets’. The method distinguishes serial and parallel mimics, and has proven successful at revealing parallelism in the presence of inefficient processing. The goal of the present work was to build a quantitative model incorporating sensory, attentional, and decisional parameters to account for empirical reaction time and accuracy data.

A random-walk model was constructed that assumes parallel processing, and includes a parameter corresponding to capacity limitation that is independent of sensory and decisional parameters. The model generated excellent fits to data from a variety of basic stimulus domains (colour, size, orientation, motion sign, shape, relative position, and letter identity), using a relatively small number of parameters.

Our model captured important trends in the data not predicted by existing models of search, in part by allowing response criteria to scale with set size. In addition, the value of the best-fit attentional parameter differed systematically across tasks, providing ordinal measures of capacity limitation that ranged from low (colour, translation, size), to moderate (letter), to high (relative position, shape, rotation). The ability of the model to fit search data of varying efficiency argues against a simple processing dichotomy.

## **BINOCULAR AND SPATIAL VISION**

- **Tonic accommodation predicts perceptual – motor error under stereogram but not under natural viewing**

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We compared two forms of viewing the child’s game of manipulating a hand-held hoop around a bent wire. The first was natural binocular vision. The second was via a monitor displaying video anaglyphs configured to be as similar as possible to natural vision. This was achieved with two video cameras located to simulate parameters of interpupillary distance, image size, etc, and mirrors that made the hoop/wire displayed with anaglyphs appear in the same place as the real hoop/wire. Thus the motor task was very similar in each case.

Observers were selected to cover a wide range of tonic accommodation (TA), measured some months previously in a different study. The main error measure was total time that the hoop was in contact with the wire. No error/TA correlation was found for natural viewing but a strong and significant relationship was found for stereogram viewing. The details of this effect depended upon whether the observers were emmetropes or myopes, and on the plane of the bent wire (giving more/less depth variation with respect to frontoparallel).

We conclude that TA may contribute to individual differences in perceptual – motor performance guided by stereo displays. This result has potentially wide significance for applied settings such as endoscopy.

- **Decluttering displays: interactions of depth, colour, and shape**

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The effects of colour, shape, and stereoscopic depth on symbol identification have been investigated. The target and distractor stimuli were green or red horizontal or vertical bars, placed in the frontal plane (9 min of arc crossed) or back plane (no disparity) of the display. The target stimulus was surrounded by eight identical distractors. The task of the subjects was to discriminate the colour, orientation, and depth of the target stimulus while fixating a dot placed at one of seven eccentricities (varying in equal steps from 5.7 to 21.7 deg).

The orientation of the target was the most easily discriminated and the depth the poorest. Two pronounced biases were found at the more peripheral eccentricities: the target colour tended to blend with the distractor colour, consistent with colour assimilation, and the target orientation tended to be judged as different, consistent with orientation contrast. Surprisingly, the orientation and depth discriminations were significantly poorer when the target was surrounded by distractors in the frontal plane.

Guidelines for the arrangement of symbols in 3-D displays are derived from these results. For example, the results indicate that stereoscopic depth is of limited use for increasing the peripheral identification of small, isolated symbols.

- **A multi-spatial-frequency channel model for stereopsis**

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Stereopsis is supported by spatial-frequency-selective mechanisms operating both at monocular and at cyclopean stage (Glennister and Parker, 1997 *Vision Research* 37 2143–2152). Coarse-to-fine models of stereo matching take advantage of this selectivity to process binocular disparity iteratively from low to high spatial frequencies in the stereo images (Rohaly and Wilson, 1993 *Journal of the Optical Society of America A* 10 2433–2441).

A cooperative model of stereo matching is proposed as an alternative. It is based on the computation of correlation processed on a vectorial description of the stimulus, the coordinates of each vector describing the spatial-frequency content of the image at that specific point. So, a simultaneous contribution of all the spatial-frequency-tuned components of the stimulus is considered for stereopsis. First, the relative weights of the various spatial frequencies of the stimulus in binocular vision are determined with uncorrelated filtered random-dot stereograms (RDSs). Data exhibit a band-pass mechanism. Second, spatial-frequency interactions associated with the pooling process are considered from mixed filtered RDSs. This multichannel pooling initiating stereo-matching may be a relevant model for human stereopsis.

- **Global spatial layout affects local disparity judgment**

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We measured the precision of depth encoding for disparity-defined illusory contours that are either in front or behind a background. Classical illusory Kanizsa squares were generated for the left-eye and right-eye images on a light background ( $L = 7 \text{ cd m}^{-2}$ ) with the use of dark 'pacmen' ( $L = 1 \text{ cd m}^{-2}$ ). The pacmen were displaced horizontally in each eye's image causing an illusory square to appear stereoscopically either in front of the background, producing modal edges for the square, or behind, producing amodal edges. The screen positions of the illusory squares remained fixed across conditions.

As a control, we duplicated both configurations with a luminance-defined square ( $L = 9 \text{ cd m}^{-2}$ ), also presented stereoscopically. The task of the observers was to decide if a small probe, shown above the top edge of the square, was in front or behind the square. Excluding response bias, sensitivity for this relative-depth judgment was higher for modal edges than for amodal edges. For the real-square conditions, sensitivity was constant but uniformly lower than that in the illusory-square conditions.

Our results show that both modal and amodal contours are encoded in depth; however, the encoding is more precise for contours in the foreground than those in the background. Clearly, global percept of spatial layout affects local sensitivity of stereoscopic depth.

## COLOUR AND BRIGHTNESS

### ● **Detecting violations in colour constancy: distributed versus focal attention**

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Measuring colour constancy by colour matching is difficult, and surface-colour matches may be influenced by hue-saturation-brightness matches. In principle, the former depend on distributing attention over several, possibly all, surfaces in the image, the latter on focusing attention on a particular patch. Attentional effects may, however, be less important when there are strong temporal cues.

To test this hypothesis, observers binocularly viewed CRT computer simulations of an illuminated Mondrian pattern consisting of 49 (7×7) abutting square patches; the pattern was first illuminated for 1 s by a daylight of 25000 K and then illuminated for 1 s by a daylight of 6700 K, but at the same time the reflectance of one of the patches was changed. In one experiment the position of the patch was fixed at the centre; in the other it varied randomly from trial to trial. Mean colour constancy indices from the two experiments were not significantly different, suggesting that temporal cues can override attentional effects in colour-constancy judgments.

### ● **Illusory contours and neon colour spreading reconsidered in the light of Petter's rule**

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A black pattern formed by two overlapping surfaces may segregate into its component patterns separated by an illusory contour. Typically, the surface with the shorter contours appears in front of the larger one (Petter's rule, PR).

We studied PR for illusory contours (ICs) and neon colour spreading (NCS) to test the hypothesis that contour formation determined by PR can affect the presence/absence, the strength, and the appearance in depth of ICs and NCS. In the cases of ICs or NCS induced by lines, PR determines the contour orientation (same or perpendicular) abutting a line end. In the 'same' condition, ICs and NCS should be absent. In the 'perpendicular' condition, both ICs and NCS should be strong. Medium strength would be expected for ambiguous orientations. Eight experiments were carried out to test cognitive theories, and computational theories based on interactions at line-ends. The inducing stimuli were interrupted parallel lines, and we varied the thickness of lines, the spacing between lines, and the magnitude of the gap between line-ends.

Results show that both ICs and NCS follow PR. It is proposed that PR derives from the formation of two different kinds of contours, modal and amodal, linked to the dynamics of filling-in of contour gaps.

### ● **Differential threshold of saturation in two-dimensional and three-dimensional perception**

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We studied discrimination of colour purity in 2-D and 3-D modes of perception. The test figure of a given hue was a double square with or without lines connecting each corner, binocularly observed on a CRT screen. For 2-D vision, one test figure was used; for 3-D vision, two figures with parallax in the inner part were displayed with a separation and were visually fused. The reference purity of the outer part was kept constant and the purity of the inner part was varied by the method of limits. Four females judged whether the double square was of the same colour or not. Eight hues were tested.

The results showed that the differential threshold of saturation depended on the mode of appearance and the configuration of the test figure. In 3-D vision, the threshold was wider and significantly more effective in figures with no lines. The lines increased the threshold in yellowish hues and in purplish blue; however, the effect was not clear when the inner area appeared farther.

These results indicate that the perception of the original figure, namely the figure which is originally solid and the same in colour, works like colour adaptation as a basis of colour constancy.

- **Flicker-based colour illusion in peripheral vision**

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We describe a novel illusion reflecting different temporal processing of colour information in the central and peripheral parts of the visual field. Five subjects with normal colour vision (aged 23 to 52 years) viewed a red–green flicker at eccentricities of 2, 5, 10, 20, and 50 deg. The 35 Hz flicker consisted of alternation of a red and a green Gaussian patch. The standard deviation of the circular luminance profile of both patches was 2 deg. The peak luminance of the red patch was 6.3 cd m<sup>-2</sup> and that of the green patch 9 cd m<sup>-2</sup>. The flicker was presented for 1 s after 1 s adaptation to a red or a green patch.

In the central 5 deg the flicker colour was perceived as yellow independently of the adaptation. In the peripheral vision at eccentricities >20 deg the reported flicker colour was opposite to the adaptation colour—if the adaptation colour had been green, the flicker was perceived as red and vice versa. In addition to the eccentricity dependence, the perceived flicker colour depended on the adaptation. When the adaptation time was shortened from 1 s to 0.5 s, the smallest eccentricity at which the illusion was observed increased from 20 to 50 deg.

- **An assimilative primacy effect in colour-difference judgments**

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We asked whether colour-difference judgments are biased by the order of presentation, especially by stimuli and/or responses, occurring early in a run. Pairs of colour stimuli, each presented twice ( $n = 240$ ), were rated according to their perceived similarity on a 0–9 scale. No feedback was provided. On different blocks of trials, either small or large colour differences, defined by objective CIE 1976 distances and their subjective similarity, occurred on initial trials.

A consistent primacy effect was found, in that initial five judgments sufficed to bias the subsequent judgments, which tended to be larger with initial large differences, and smaller with initial small differences (assimilation). This assimilation effect was accompanied by small and inconsistent counteracting effects of response contrast and repetition and, hence, waned by approximately the second half of the run.

Though in general agreement with the response consistency principle, our finding is at variance with the primacy-contrast effect found for absolute judgments (Haubensak, 1992 *Journal of Experimental Psychology: Human Perception and Performance* **18** 303–309). The present primacy-assimilation effect is assumed to represent a special case of the sequential effect, with assimilation propagation considered a strategy of stimulus-response mapping employed under uncertainty (Ward and Lockhead, 1971 *Perception & Psychophysics* **9** 73–78).

## EYE MOVEMENTS

- **Auditory intensity effects on visual – auditory integration in the control of eye and hand movements**

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The presentation of an accessory auditory stimulus reduces mean reaction time of saccadic eye movements and of hand movements towards a visual target stimulus (eg Hughes et al, 1994 *Journal of Experimental Psychology: Human Perception and Performance* **20** 131–153). For both types of movements, the reduction depends on the spatiotemporal relationship between visual target and auditory nontarget (Arndt and Colonius, 1999 *Proceedings of the 27th Neurobiology Conference, Göttingen* page 194). Moreover, the data suggest a stronger dependence on the auditory stimulus for hand movements than for eye movements.

In this experiment, both the intensity of the accessory auditory stimulus and the spatial stimulus arrangement were varied, allowing an analysis of the processing architecture of visual–auditory interaction. The results provide evidence for a separate processing of stimulus intensity and spatial stimulus configuration and support the model of Colonius and Arndt (submitted) where the effect of stimulus intensity is mediated completely by changes in peripheral processing time.

[Supported by DFG (SFB 517).]

- **Detection of intrasaccadic changes in stationary and moving objects**

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Previous research with stationary objects indicated a low detection rate for intrasaccadic position changes and a high detection rate for intrasaccadic in-depth-orientation changes. However, for translating objects these results may not apply.

The stimulus used in all four experiments shows one object moving horizontally towards another stationary object. The primary aim was to clarify the influence of the object's dynamic status (stationary or moving) and the object's saccadic status (target or flanker) on detection of both types of changes. An analysis of variance on sensitivity values was performed.

Position changes were detected with a higher accuracy for moving objects. Furthermore, saccadic status played no role in detecting these changes. For the stationary object, detection was only high in saccade-target conditions. Concerning orientation changes, performance was almost equal for stationary and moving objects. For both types of objects, detection was always better for the saccade target. For detection of changes in stationary objects, it is thus very important that the object is also the saccade target. For moving objects, this is only the case for in-depth-orientation changes. Even when a moving object is not the saccade target, we can keep track of its path and detect changes in that path.

- **Flickering retinal signal induces larger saccade-contingent mislocalisation**

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Previous findings suggest that a saccade-contingent mislocalisation (SCM) originates from a difference between an extraretinal eye-position signal and a retinal signal. However, it has not been thoroughly investigated what kind of retinal signal affects SCM.

The purpose of this study was to examine whether the magnitude of SCM is influenced by the difference between a flickering and a continuous target. In a dark room, four subjects were required to perform a task under two conditions: the target LED was made to flicker at 200 Hz (flicker condition) or was continuously lit (continuous condition). The task given was to make 20 deg horizontal saccades and to localise both endpoints of perceived dashed or solid lines during a rightward saccade. The fixation LED was placed 10 deg to the left of the target LED, and another LED, the intended goal of saccades, was placed 10 deg to the right of the target. When the saccade amplitude exceeded 5 deg, the target LED was presented for 31 ms.

Results showed that the magnitude of SCM under the flicker condition was larger than that under the continuous condition.

## LEARNING, MEMORY, AND DEVELOPMENT

- **Induced categorical perception of novel, real-world, complex stimuli**

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Categorical perception can be demonstrated by enhanced inter-category discrimination of items that are equally spaced along physical continua (eg colour categories and wavelength). Research with novel stimuli has shown changes in the dimensional structure of adults' perceptual similarity space following category learning: induced categorical perception. However, this work has used relatively simple stimuli, artificially constructed complex stimuli, or familiar complex stimuli. In a series of studies we examined induced categorical perception using images of cervical cells. These 'natural' stimuli represent multi-faceted, highly variable and complex data, novel to most adults, thus offering the further advantage of exploring the effect of categorisation experience uncontaminated by previous image exposure.

Experiment 1 showed that the structure of perceptual similarity space varied with expertise at categorising cervical cells. In experiment 2 we used a perceptual similarity measure to explore naïve observers' perception of cervical cells, before and after category learning.

Results showed a post-training increase in between-category dissimilarity on categorisation-relevant dimensions, indicating induced categorical perception. Taken together, our results indicate that induced categorical perception effects are not restricted to simple, artificially constructed or familiar complex stimuli. Current experiments are designed to investigate the effect of different types of categorisation experience, and the level of perceptual processing at which changes occur.

- **The role of visual information on control of simple low-level motor movements in Alzheimer's disease patients**

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Previous findings indicate that Alzheimer's disease (AD) patients are more dependent on visual feedback for accurate performance of a complex motor skill than healthy older adults. In this study we examined whether AD patients also rely on visual feedback to accurately perform simple ballistic aiming movements.

Thirty AD patients and thirty healthy older adults performed a rapid goal-directed aiming movement with their dominant arm. Each subject received 'full vision' practice trials and 'partial vision' post-test trials.

We found that the AD patients were slower and less accurate than the normals. The AD patients also made more corrective sub-movements to reach the target and made significantly fewer ballistic movements. The movements of AD patients were significantly less accurate than those of the healthy older adults under partial vision conditions. AD patients are thus more dependent on visual feedback than the healthy adults for the control of simple motor movements.

- **The role of the tool in Michotte's 'tool effect': Evidence from representational momentum**

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In the 'tool effect', a moving stimulus (the launcher) contacts a stationary stimulus (the intermediary), which then begins to move and subsequently contacts a different stationary stimulus (the target), which then begins to move [Michotte, 1951, reprinted in Thinès et al, 1991 *Michotte's Experimental Phenomenology of Perception* (Hillsdale, NJ: Lawrence Erlbaum Associates)]. Three experiments were performed to test a naïve impetus explanation for Hubbard and Favretto's (1999 *Perception* 28 Supplement, 44a) finding that representational momentum [displacement of remembered target position in the direction of target motion] of targets in tool-effect displays is decreased relative to representational momentum of targets in isolation.

Experiment 1 presented an invisible intermediary. Experiment 2 presented a stationary intermediary that filled the gap between the final location of the launcher and the initial location of the target. Experiment 3 presented a stationary intermediary that contacted either (but not both) the launcher or target. In all experiments, the launcher, intermediary (if visible), and target vanished simultaneously, and observers indicated the vanishing point of the target. Decreases in representational momentum occurred only when a visible (stationary or moving) intermediary contacted both the launcher and target.

The data suggest that the decreased representational momentum of a target in a tool-effect display results from the perceived impetus of the launcher being conveyed through the intermediary to the target.

## MOTION PERCEPTION AND OPTIC FLOW

- **Estimating internal noise for human visual-motion-detection mechanisms**

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Two problems in determining equivalent noise for motion processing are: manipulating signal-to-noise ratio, while keeping mean luminance and contrast of the stimuli constant, and appropriately measuring sensitivity of motion detection. Random-dot kinematograms were generated by superimposing motion and dynamic-noise components.

In one experiment, observers decided the location (2AFC) of a motion-defined object; each run was at a fixed level of noise and the size of the region of coherent motion was varied to allow estimation of detection thresholds. In a second experiment, observers decided in which of two regions of coherently moving dots noise was present; this same experiment was performed for two velocities of motion and for two areas of motion.

Threshold area for detecting coherent motion was constant when external-noise level was low but increased at high levels of external noise; thresholds were greater for higher-velocity coherent motion. Threshold-noise-detection levels were higher when the area of coherent motion was smaller and they were higher when the velocity of the coherent motion was higher. We have



tested novel methods for estimating internal noise associated with visual-motion-processing mechanisms using stimuli that were motion-defined only.

- **Two-system model of the transition from dichoptic motion rivalry to motion transparency**  
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Dichoptic motion rivalry gives way to transparency if one eye sees a low-speed and the other eye a high-speed random texture. Motion transparency then prevails, while rivalry is found if both moving patterns have low-speed or high-speed. This is one of many indications that there are separate low-speed and high-speed motion systems. They can be tapped separately by the motion aftereffect (MAE): dynamic noise reads out the fast channel (MAE duration  $T_d$ ), static spatial noise reads out the slow channel (MAE-duration  $T_s$ ).

From  $T_d$  and  $T_s$  we calculate total adaptational excitation as a function of speed. We hypothesise that mutual contrast between two speeds in one channel during dichoptic stimulation has to exceed a threshold to attain dominance. If one of the dichoptic stimuli dominates the fast and the other the slow channel, we expect motion transparency, otherwise motion rivalry. Transparency probability is thus predicted for any chosen pair of dichoptic speeds for each of our subjects from their MAE durations. The predictions match independently measured psychophysical results, supporting the hypotheses, including that MAE durations can provide valid measures of total excitation in each channel during adaptation.

- **The detection of orientation and motion-direction differences relative to a radial pattern**  
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We compared detection of independent object motion in a self-motion display with that of differences in line orientation in a matched static display as a function of presentation time. To probe the spatial scale at which these features are analysed by the visual system, we also examined the effect of local cues.

The self-motion display consisted of an expanding pattern simulating self-motion (speed  $8 \text{ m s}^{-1}$ , random heading direction). The static display was matched with the self-motion display in that line length was equal to dot trajectory length for a given presentation time (varying between 149 ms and 745 ms). In the local-cue condition, the element that deviated from the rest of the display was presented simultaneously with a 'correct' element at the same location.

Results showed that the local cue lowered detection thresholds in both displays, indicating that local cues contribute to the detection of differences in both orientation and motion in radial patterns. Thresholds decreased with presentation time, but more strongly for line orientation than for motion direction. Given the increasing probability of intersecting elements with presentation time, these results suggest that the visual system is more sensitive to intersecting lines than intersecting trajectories of moving dots.

- **Flash lag effect is larger when flashed objects are presented at the onset of a moving object**  
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Briefly flashed objects were perceived to spatially lag behind a continuously moving object when they were physically aligned [Nijhawan, 1994 *Nature (London)* **370** 256–257]. This phenomenon is called the 'flash lag effect' (FL). Although in the original study a rotating bar was presented, in the present study a bar moving horizontally was used. In experiment 1, SOA between the moving bar and the flashed bars was manipulated (0, 400, 800, 1200, and 1600 ms). The moving bar moved always leftward.

The results showed that FL was larger at SOA 0 ms than at the other SOAs. This trend of data was unchanged when participants were asked to pursue the moving bar (experiment 2a) or to fixate the fixation point (experiment 2b). In experiment 3, the direction of the moving bar was randomly altered trial by trial (leftward or rightward). FL at SOA 0 ms in the random condition was larger than in the control condition (always leftward).

These results suggest that FL at SOA 0 ms has different characteristics than at the other SOAs, and that FL at SOA 0 ms is influenced by the predictability of the directions of the moving bar.

- **Contribution of extra-retinal signals to the scaling of object distance during self-motion**  
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We investigated the contribution of extra-retinal signals to the scaling of visual information generated by self-movement. A large field display facility, a head tracker and a graphic station were used to generate dynamic stimulation.

Monocular observers performed frontoparallel head movements to estimate the absolute distance of objects positioned at different locations in depth. The objects were spheres covered with random dots. Their diameter was 6, 15, or 30 deg, and they were presented at eye height in isolation or superposed on a ground plane. Their apparent angular size was kept constant by covarying the size and distance parameters. Hence the only distance cues available to the observer were the motion parallax and the extra-retinal information about the observer's self-movement. Eight subjects had to indicate whether the apparent distance of the object was larger or smaller than established thresholds (50, 100, 200 cm). Perceived distances were correlated with simulated distances for all conditions, with a general tendency to underestimation. This effect was highest for smaller objects (6 or 15 deg) presented in isolation, with errors ranging in the 50–70 cm interval. The presence of the ground plane improved subjects' performance only in the case of small objects (6 deg).

- **Optical information for catching fly balls**  
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Catching a fly ball requires that the catcher gets at the interception location at or before the time the ball arrives there. Running such that the optical velocity of the ball is constant brings the catcher at the interception location, without the need to know about that location or the ball flight time. Previous research has suggested that this strategy is used in catching fly balls travelling along the sagittal plane. However, in those studies, the implied optical information could not be manipulated directly. This would be possible with the use of virtual-reality techniques, such as a CAVE. For this reason, we are studying the catching of virtual fly balls in a CAVE.

In the first experiment, participants had to intercept virtual balls with their hand or had to judge whether virtual balls would land in front of them or behind them. The timing of the judgments appeared to be related to optical acceleration profiles, a finding corroborated in the second experiment. A third experiment aimed at further establishing optical acceleration as a basis for the judgment timing, as well as testing an improved interception task: in this experiment participants had to have virtual balls hit their forehead.

## NATURAL IMAGES, BIOLOGICAL MOTION, AND FACES

- **Lateralised processing of the internal and external facial features of personally familiar and unfamiliar faces: a visual half-field study**  
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In this visual half-field experiment, we investigated possible differences between the left and the right hemisphere in the processing of the internal and external features of familiar and unfamiliar faces. On the basis of previous studies in which famous and unknown faces have been used, it was hypothesised that the right hemisphere is superior to the left hemisphere and that both hemispheres use the same qualitative mode of processing; that is the internal features are more important for the matching of familiar faces, while external and internal features are equally important for the matching of unfamiliar faces.

In this experiment, personally familiar faces, rather than famous faces, have been used. There are several reasons why personally familiar faces are more appropriate stimuli to investigate face processing, and recent studies with personally familiar faces have produced new insights. The results of the present study showed that, under these experimental conditions, no overall visual field effect occurred, but, more importantly, that face processing in the left hemisphere differed qualitatively from that in the right hemisphere.

- **The role of facial parts in facial expression judgment**

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Physical changes in facial parts are reliable information sources for judging facial expression. However, it is not clear whether every facial part is equally helpful. We conducted serial experiments that differed in the number of transformed facial parts (one part, two parts, and four parts) in which we investigated how partial transformation affected the strength of facial expressions (anger, sadness, smile, and surprise). We morphed facial images to exchange their parts for the same parts of the same individual's expressive faces. Those images and their labels of four expressions were randomly presented. Participants rated each image on a 7-point scale (1 as the weakest, and 7 as the strongest).

The results provided two meaningful suggestions. First, each of the four facial expressions has its own most effective part for judgment. Presumably, this finding indicates that we can recognise a facial expression by giving attention to only one informative part when the context implies information about the probable expression. The other suggestion is that the strength of a facial expression does not become linearly stronger by adding morphed parts: sometimes the mean value of a two-part-morphed face was less than the value of a one-part-morphed face.

- **Gender bias in Rembrandt's portraits reveals hemispheric asymmetries**

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For centuries painters have predominantly painted portraits with the model's left cheek facing the viewer. This occurs more with portraits of females (~ 68%) than males (~ 56%). Numerous portraits painted by Rembrandt typify this unexplained phenomenon. In a preliminary experiment, subjects judged twenty-four emotional and social character traits in twenty portraits painted by Rembrandt. A factor analysis revealed that females with their left cheek exposed were judged to be much less socially appealing than less commonly painted right-cheeked females. Conversely, the more commonly painted right-cheeked males were judged to be more socially appealing than either left-cheeked males or females facing either direction.

It is hypothesised that hemispheric asymmetries regulating emotional facial displays of approach and avoidance influenced the side of the face Rembrandt's models exposed in accordance with prevailing social norms. A second experiment had different subjects judge a different collection of twenty portraits painted by Rembrandt and their mirror images. Mirror-reversed images produced the same pattern of results as their original-orientation counterparts. Consequently, hemispheric asymmetries that specify the emotional expression on each side of the face are posited to account for the obtained results.

## SHAPE

- **An oblique benefit: Kanizsa squares versus diamonds with misaligned edges**

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It is well known that Vernier acuity is lower for oblique lines than for the cardinal axes. Since illusory-contour lines do not depend on adjacent line-ends, an increase in distance between the Vernier lines allows for the inference that Kanizsa squares with misaligned edges should retain the illusory quality of the square better when the entire display is rotated 45° than real contour squares. To test this prediction we used two types of inducers (circles and irregular shapes) with six different edge alignments: 0°, 6°, 8°, 10°, 12°, and 14°. Kanizsa squares with both types of inducers at all alignments were judged by trained observers using a 'goodness-of-square' magnitude estimation task, with the squares at both the cardinal and oblique orientations. All figures were presented, in a random order, on a high-resolution computer screen.

The results showed a highly significant difference between the square and diamond orientations at 6°, 8°, and 10° for the Kanizsa squares. These findings indicate that the latter benefit from the oblique effect; real contour squares lose their 'squareness' at both the orthogonal and the oblique orientation when line misalignment reaches about 4°.

- **Why is RT of mental flipping shorter than that of mental spinning in mental rotation?**

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When an inverted image was mentally rotated to upright, Murray (1997 *Memory and Cognition* 25 96–105) showed that RT of mental flipping (rotating in depth about the  $x$ -axis) was shorter than that of mental spinning (rotating in the picture plane). We hypothesised that the absence of representation at the midway position in the mental flipping led to the previous finding.

The purpose of the present study was to investigate this hypothesis by the priming paradigm. The rotation task was followed by the same–different task in one trial. In the rotation task, subjects were asked to mentally rotate an inverted image to upright. In the same–different task, they were asked to judge whether two images simultaneously presented were the same or different. Only the flipping in the rotation task did not prime the same–different task, and the result in the rotation task was consistent with the previous finding. It is speculated that there is no representation midway in the flipping. This result could indicate that flipping is not a continuous rotation, which might explain why flipping is faster.

- **Perceptual completion in horizontal and vertical directions at the blind spot**

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We examined perceptual completion across the blind spot in horizontal and vertical directions. A pair of lines, the lengths of which were varied, was presented to the horizontal or vertical borders of the blind spot for 200 ms. The two independent variables were the orientation of the line (horizontal and vertical) and the width of the line (1–5 mm). Subjects reported whether the line appeared ‘complete’ or ‘gapped’ when compared to the reference line presented simultaneously to the temporal retina.

The results for seven subjects showed that the mean minimum length of line sufficient for the completion in the vertical direction was 4.03 deg (SD = 1.41 deg), and that in the horizontal direction was 2.85 deg (SD = 0.98 deg); the difference between these means was statistically significant ( $p < 0.001$ ). The mean vertical and horizontal extents of the blind spot averaged over the subjects was 6.58 deg and 6.00 deg, respectively. The horizontal/vertical ratio of the mean minimum lengths of the lines has no correlation ( $r = 0.083$ ) to the horizontal/vertical ratio of the extent of the blind spot. These results suggest that the perceptual completion in the horizontal and vertical directions is mediated differently at the blind spot.

- **Differential structure as a source of information about the orientation of planar shapes in depth**

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We investigated the influence of the perceived orientation of planar elliptical shapes on the perception of these shapes. Because the perception of the metric properties of these shapes is ambiguous without additional information about their orientation in depth, we projected these shapes via a laser on the surface of a real, perfect sphere. The orientation of the elliptical shape was then defined by the differential structure of the sphere at the particular point of the sphere. Because the perceived orientation does not necessarily coincide with the objective orientation, and because there is some uncertainty about the perceived orientation, we found that the perception of these shapes (ie which ellipse out of the set of projected ellipses was interpreted as being a circle) depends on the particular point of the sphere where the ellipses were projected.

In a second experiment we manipulate the perceived orientation by projecting the ellipses not on a real sphere but on a sphere projected on a monitor. We expect the perception of the ellipses to be influenced by slant, which will be underestimated under these conditions (ie more circular interpretations for ellipses with a larger aspect ratio).

## SPATIAL FREQUENCY AND CONTRAST

- **Contrast dependence of high-speed apparent motion**

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We have previously shown that perceived speed of sequences of Gabor patches depends on their orientation relative to the motion path. We described both an overestimation of apparent speed

for collinear sequences and an underestimation for parallel ones (Georges et al, 1999 *Perception* 28 Supplement, 80c).

Here, we examined how these effects depend on contrast and phase. We used a 2IFC design to measure speed discrimination for apparent motion induced by rapid sequential presentation of oriented Gabor patches. The apparent speed of sequences composed of collinear Gabors is higher than that of parallel Gabors, independently of orientation and phase variations in the Gabor sequence. Surprisingly, Gabor patches collinear to the motion path (speed = 64 deg s<sup>-1</sup>) appear faster at low (8%) than at high (51%) contrast. This effect decreases with decreasing speed.

To account for our data, we developed a computational model of spatiotemporal interactions, in which a 'dynamic association field' integrates feedforward and lateral inputs. Lateral inputs shorten or lengthen response latencies, which induces modulation of apparent speed at a later stage. The model accurately simulates the contrast dependence, in that latency modulations are stronger at lower contrasts.

- **Contrast uncertainty effect on simple reaction time**

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Uncertainty effects have been used to discriminate whether a particular stimulus dimension is processed by a single channel or by multiple channels. Theories of pattern vision propose the existence of mechanisms selectively sensitive to spatial frequencies, motion directions, etc. The effects of uncertainty in the case of such stimulus parameters have, indeed, been described. It is not supposed that stimuli differing in contrast are processed by separate channels, hence contrast uncertainty should not alter performance.

In the present experiments, the reaction time (RT) to 100 ms sinusoidal gratings was measured in a series of experiments with constant or variable contrast. The spatial frequency was constant and ranged from 0.5 to 16 cycles deg<sup>-1</sup>. Stimulus contrast varied between 2.5% and 50%. Contrast uncertainty did not affect RT at low spatial frequencies (0.5 and 2 cycles deg<sup>-1</sup>), while increasing RT at higher spatial frequencies. Response failures were observed at the lowest contrast at high spatial frequencies (10, 12, 16 cycles deg<sup>-1</sup>). The failures were significantly higher in the variable-contrast series. In this spatial-frequency range, the uncertainty effect could be due to contrast-sensitivity reduction, reduced subjective stimulus probability, and a more conservative response strategy. Detection threshold was similar at 0.5, 5, and 8 cycles deg<sup>-1</sup>, yet contrast uncertainty affected RT at 5 and 8 cycles deg<sup>-1</sup> but not at 0.5 cycle deg<sup>-1</sup>. Another mechanism may be responsible for the uncertainty effect at these spatial frequencies.

- **Masking visual stimuli by transcranial magnetic stimulation: Comparison with masking by light**

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Transcranial magnetic stimulation (TMS) applied over the occipital pole is able to suppress the perception of visual stimuli. This suppression is based on a shift of the perception threshold. Here we compared the modulatory effect of a light flash with the suppression effect of TMS.

Subjects had to report the orientation of a flashed hook. At two different adaptation levels (0.3 and 3 cd m<sup>-2</sup>) we determined contrast thresholds by the method of constant stimuli. A light flash (15 or 150 cd m<sup>-2</sup> for the different adaptation levels) was applied with different SOAs after the appearance of the hook, and threshold shifts were measured. Similarly, threshold shifts due to focal TMS with SOAs from -25 to +195 ms were measured.

With high background intensity, TMS shifted thresholds up to 1.2 Weber contrast units (WC), and with low background intensity the shift was up to 6.6 WC. Latency for the maximal effect was shorter at the high background level (85 ms SOA) than at the lower level (115 ms SOA). We found similar effects on threshold shifts with light flashes at SOAs from 20 to 80 ms. Our results suggest that the masking effect of TMS might share similar mechanisms with a masking effect by light.

## VISUAL IMPAIRMENT

- **Visual effects of eye-lens fluorescence**

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Lens autofluorescence is of relevance to visual function of the individual. First of all, the fluorescent light itself emitted by the lens also stimulates the retina. This is visible as a veil

that may hinder observation of weakly illuminated objects (UV headlights). Apart from that, the autofluorescence is indicative for light losses in the lens and light scattering.

Isolated lenses were studied, normal and with cataracts, from donors aged 21 to 86 years. Light emitted by the lenses from a 4 mm diameter monochromatic, 380, 400, or 420 nm pencil beam was collected with a 0.7 deg radius diaphragm and measured as a function of angle and of wavelength. The number of fluorescent quanta was between 5% and 0.25% of that of incident quanta, dependent on age and wavelength. The dependence on wavelength of fluorescent emission was in accordance with literature.

Because of fluorescence of the eye lens, light with wavelengths of 420 nm and below is visually much more effective than one would deduce from the CIE luminosity function. Absolute values that can be derived from fluorophotometry can be used to assess an individual's visual hindrance from short-wavelength light and other lens-related disturbances.

- **Colour vision abnormalities in dysfunction of peripheral visual neurons**

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Colour vision testing is a sensitive method for detection of subjects affected by optic atrophy (Brown, 1997 *Archives of Ophthalmology* **115** 95–99). Eighty-two subjects with dysfunction of peripheral visual neurons were examined with the Farnsworth–Munsell test to determine the extent of colour perception defect. Dysfunctional and healthy control subjects tested ranged in age between 15 and 45 years. Error scores obtained in the Farnsworth–Munsell test correlated with the severity of dysfunction.

Colour vision defects increased markedly for subjects with a visual acuity below 0.6, but colour vision defects were also found in subjects with normal visual acuity and normal contrast sensitivity. Most subjects (45%) showed red colour abnormalities, blue colour abnormalities were in evidence in 40% of cases, and green colour abnormalities were present in only 7.5% of cases. Colour vision testing seems appropriate for the early detection of dysfunctional peripheral visual neurons.

- **Simulation of artificial vision: a setup for eccentric reading using a stabilised area of the visual field and first results**

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During the past few years, several research groups have initiated important projects aiming at the development of visual prostheses. In this context, one key question is, however, “what are the minimum requirements for useful artificial vision?”. We use simulations of artificial vision on normal subjects to answer this important question.

Retinal implants will be permanently implanted at a fixed (and probably eccentric) place in the retina. To simulate this condition, one needs to project stimuli on a defined stabilised area of the visual field. This can be achieved experimentally by online compensation of gaze position on a fast (160 Hz) computer display with a high-speed (250 Hz) video-based eye- and head-tracking system (SMI Eyelink, as used by Cornelissen et al). Images of various sizes and content can be pre-processed (eg pixelised) and projected to defined locations (eccentricities) in the visual field.

Initial experiments on reading four-letter words with various pixelisations and eccentricities showed that reading performance of normal subjects drops abruptly when the information content of the target is reduced below a certain threshold (expressed as the number of pixels). This value is highly dependent of the target eccentricity in the visual field. Under optimal conditions, at least about 250 pixels are necessary to code four-letter words.

- **Form and motion processing in autism**

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We report that motion coherence thresholds in children with autism are significantly higher than in matched controls. No corresponding difference in form coherence thresholds was found.

We interpret this as a specific deficit in dorsal stream function in autism. Perceptual abnormalities are frequently cited in reports of people with autism. Clumsiness or coordination deficits are also prevalent in children with autism. To examine the possibility of a neural basis for these perceptually based abnormalities we tested twenty-three children diagnosed with autistic disorder, in three different age groups, on two tasks specific to dorsal and ventral cortical stream functions: global motion coherence thresholds and form coherence thresholds.

The results provide the first evidence that autistic individuals have a specific impairment in dorsal stream functioning compared with VMA matched controls. We conclude that autism may have common features with other developmental disorders and with early stages of normal development, perhaps reflecting a greater vulnerability of the dorsal system.

## ORAL PRESENTATIONS

### ATTENTION IN DYNAMIC TASKS

#### ◆ Do we keep track of where we've been or what we've done?

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We explored the interaction between visual search, memory, and action using a simple visuomotor task. Stimuli were eight light-grey disks (targets;  $\sim 1$  deg diameter) on a medium-grey background. Targets were numbered 1–8, and placed randomly within a  $12 \text{ deg} \times 11.5 \text{ deg}$  rectangle. The task was to move a mouse pointer to each target and click on it in numerical order, as quickly as possible, starting with number 1. Twelve subjects performed 60 trials in each of two conditions: vanish—each target was removed from the screen after the subject clicked on it; no change—clicking on a target did not change the display. Reaction time (RT) decreased roughly linearly by 22.89 ms per item with each response (not counting RT to the first target). There was no effect of condition, nor an interaction.

We conclude that all targets initially compete at some level to control responses. Each response completely eliminates that target from competition. In a further study, we attempted to separate retrospective (what you did) and prospective (what you will do) elements of the task. We did this by scrambling items ahead of the current target after each response. Preliminary results suggest prospective memory may be driving the decrease in RT.

#### ◆ Shifts of spatial attention between continuous RSVP streams investigated by event-related fMRI

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We investigated the time course of the top–down biasing of early sensory representations using event-related fMRI in a paradigm based on rapid serial visual presentation (RSVP).

Subjects fixated centrally and monitored digits ('3' or '7') which appeared every 3–5 s among distractor letters in one of two laterally presented RSVP streams (200 ms per item). When the target was a '3', attention was held at that location, and otherwise ('7') shifted to the opposite location. The haemodynamic response was acquired by echoplanar imaging (TR = 1 s, 16 axial slices,  $6 \times 3.75 \times 3.75 \text{ mm}^3$  voxels). Time series were analysed by multiple regression with four regressors: hold left, hold right, shift left to right, shift right to left.

Significant event-related activations were observed in occipital, parietal, and prefrontal areas. Different events produced distinct time courses in the haemodynamic response depending on the preceding event. The results reveal properties of the time course of spatial attention shifts. We have demonstrated that small but significant event-related effects can be seen with rapid target presentation and overlapping haemodynamic functions, and that activations driven only by target identification, and not by a low-level feature such as an onset, can effectively be used in event-related paradigms.

#### ◆ Differential grouping of features

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'Flicker' displays were created where an original and a modified image continually alternated, with brief blanks between them. Each image was an array of simple rectangles, half having one value of a feature (eg horizontal), the rest a different value (eg vertical). In half the trials, one of the

items changed its value; in the remainder, no changes occurred. Observers were asked to detect whether a change was present in each trial.

As the display time in each alternation cycle is increased, search slopes become proportional to display time, with the proportionality constant a direct estimate of attentional capacity (Rensink, 2000 *Visual Cognition* 7 345–376). Two display times were examined here: 80 ms and 800 ms. For orientation changes, slopes for the two conditions differed significantly, with the long-display slope corresponding to a capacity of 5.3 items. However, for contrast polarity, slopes did not differ, indicating a capacity of at least 10. It is suggested that visual attention still has a capacity of 4–5 units, but that items of similar polarity are grouped such that they effectively form a single unit. Such grouping was also found for size and colour.

◆ **How the window of attention changes shape over time**

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When a brief blank is presented between two static images, attention is required to detect differences between those images (Rensink, 2000 *Visual Cognition* 7 345–376).

A study is reported in which attention either remained at fixation (no precue), or was drawn to one of four positions away from fixation at random by cuing for 50 ms. At a variable duration after cue offset, the whole screen blanked for 50 ms in order to induce ‘change blindness’. In the pre-flash image, red or green squares were placed on 50% of tested positions at random. In the post-flash image, a square was placed at one position that had previously been blank. Fixation was monitored. The proportion of answers above chance at a given point indicated the strength of attention there.

The results show that while the shape of the ‘window of attention’ is approximately round in the no-precue condition, it resembles an ellipse with high aspect ratio in the cue conditions. This ‘ellipse’ is roughly centred at fixation and has the cued position near one end. Surprisingly, change detection is also enhanced on the opposite side of the fixation point from the cued location. The window seems to stretch like a sheet of latex both toward and away from the cued location simultaneously, before regaining its original form.

## **BINOCULAR ISSUES**

◆ **Binocular colour mixing in half-occlusions**

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When we view stereograms by using anaglyphs, we perceive an image that is remarkable in three ways. (i) We perceive a single image in stereoscopic depth, despite the different colours of the anaglyphs. (ii) The colour of the image is different from the colours of the anaglyphs. (iii) The image is of uniform colour. The last property is remarkable because one half-image of the stereogram may contain areas whose colours are not mixed with those of the counterparts in the other half-image. These areas represent half-occlusions in the stereoscopic scene.

We created coloured stereograms that contained two depth planes. We independently varied the hues of the backgrounds, foregrounds, and half-occlusions in each of the two half-images. In a dichoptic matching task, we found that the binocularly perceived colours of half-occlusions are mixtures of their monocular colours and the mixed colours of the neighbouring foreground and background in the other half-image. This result shows that half-occlusions in anaglyphs are special cases, which remain unnoticed because foregrounds and backgrounds have the same colour.

◆ **Are the same effects found for stereogram stimuli presented either with shutter-glasses or as red/green anaglyphs?**

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We used a repeated-measures design to investigate observers’ reliance on texture/outline cues and binocular cues in cue-consistent and cue-conflict parabolic ridge stereograms (Buckley and Frisby, 1993 *Vision Research* 33 919–934). As well as measuring judged ridge amplitudes we also measured reaction times to complex random-pattern stereograms. All stimuli were displayed at 57 cm with a Silicon Graphics machine. In half of the conditions Crystal-Eyes shutter-glasses were used to display the stereograms, in the remainder they were displayed as red/green anaglyphs.

In agreement with previous work (Brennand et al, 1998 *Perception* 27 Supplement, 31c), when judging amplitudes, some observers relied mainly on texture/outline cues, some mainly on binocular cues, whereas others relied on a combination of cues. Similarly those observers who



relied on texture/outline cues in conflict ridges were slow at seeing the objects depicted in complex stereograms, whereas those who relied on binocular cues were quicker. These individual differences were found to be stable across both red/green anaglyph and shutter-glasses presentation. Many aspects of these individual differences were, for all stimuli, significantly related to an observer's tonic accommodation (measured with a Canon R1 autorefractor). Therefore very similar effects are found for stimuli presented either as red/green anaglyphs or with shutter-glasses.

◆ **Suppression of rival binocular inputs induced by a blank-field priming stimulus**

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Permanent suppression of one eye is produced by presenting a blank field to that eye and a grating to the other eye (Ooi and Loop, 1994 *Vision Research* **34** 2997–3003). During permanent suppression the visible stimulus is continuous. Then, it is expected that the dominance of an eye receiving a preceding stimulus should persist after the onset of rival binocular stimuli. To test this assumption, we employed a priming method, which was similar to Wolfe's paradigm (Wolfe, 1984 *Vision Research* **24** 471–478).

As rival binocular stimuli we used colour rivalry (equivalent blue versus red squares). Immediately after the presentation of a priming stimulus (a blank field) to one eye alone for 1000 ms, the rival stimuli were simultaneously presented as test stimuli. Duration of the test stimuli varied from 10 ms to 200 ms.

We found that, for the stimuli lasting less than 50 ms, a colour presented to the primed eye was suppressed. In contrast, for the stimuli lasting more than 50 ms, a colour contralateral to the priming was suppressed. That is, the eye primed by a blank field keeps its sensitivity for the test stimuli of longer duration (> 50 ms). This is analogous to the continuous visibility during permanent suppression.

◆ **Paradoxical contrast processing in stereopsis, Vernier acuity, and motion perception**

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When contrast increases in both eyes, stereopsis improves, but when contrast increases in just one eye, stereopsis deteriorates. Not surprisingly, explanations of this 'contrast paradox' have been inherently binocular. But could the behaviour be a more general property of signal integration in vision and, thus, require a more general explanation?

We measured stereo, Vernier, and two-frame motion thresholds for Gabor patches that varied in contrast ratio across (i) eyes, (ii) Vernier break, or (iii) motion frames. The contrast paradox was indeed present in all tasks and, moreover, all showed a similar frequency dependence from 1 to 4 cycles deg<sup>-1</sup>. To determine if the paradox resulted from single-mechanism integration, we measured Vernier acuity versus the width of the gap defining the Vernier break. When gap width became sufficient to prevent single-mechanism integration, the paradox disappeared. Finally, we developed a model incorporating partial normalisation that reproduced the paradox. The model predicts the disappearance of the paradox at high added noise levels, and this prediction was confirmed by measuring Vernier acuity versus added noise.

In conclusion, the 'contrast paradox' seems to be a general property of single-mechanism integration, and can be modeled by endowing the underlying mechanisms with incomplete signal normalisation.

## ATTENTION, CUES, AND MASKING

◆ **Visual attention to colour cues**

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Can colour cues attract attention in a manner similar to those documented for luminance cues? To test this notion we used a COVERT cueing paradigm where the possible location of a forthcoming target (defined by luminance) was signalled by the presentation of a colour cue at this location, and measured the reaction time and errors made in identifying the orientation of the line target. Three cue validities (80%, 50%, and 20% valid) were tested in separate blocks, for three cue luminance values (dark, equiluminous, and light with respect to the background).

Equiluminance was defined by the minimum flicker for the same cues as used in the main experiment. All cues were presented on a background of dynamic visual noise so as to mask any small errors in the equiluminance point.

Cueing effects were similar for the equiluminance cues as for the luminance cues in all conditions tested. This was true for red cues on a green background, and blue cues on a yellow background. Therefore colour cues behave like luminance cues even when they are purely exogenous (automatic), and even when the observer is searching for targets defined by luminance.

◆ **Effects of attentional cueing on the identification of laterally masked targets**

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Lateral masking is typically described as a low-level sensory process that impairs detection of objects in peripheral vision.

We looked for effects of attentional cueing on the detection of laterally masked targets. Subjects searched a crowded (360 elements; blue or green lines oriented at 45° or 135°) display while maintaining fixation centrally. The target was defined as the 'odd one out' by a conjunction of orientation and colour. Targets appeared in one of the 48 display locations (1 of 6 positions along the upper, lower, left, and right axes and diagonals) most likely to be affected by lateral masking. On each trial, target presence/absence judgments were made and target attributes were reported. Cues giving the exact or global location of the target were presented at the beginning of each trial. In half of each type of location-cue trial, the identity of the target was also cued. 50 ms separated the cue and stimulus displays. Exact location cues led to significantly better performance than global cues, and cueing the identity of the target also improved the ability to detect the target. We conclude that there are clear effects of attention in identification of laterally masked stimuli.

◆ **The role of lateral masking in visual search**

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The relation between lateral masking and reaction time (RT) in visual search was examined. Targets were grey or white vertical or horizontal lines. Target type was crossed with search type (disjunctive or conjunctive) and set size (16, 32, or 64 elements), resulting in 24 conditions.

In a search experiment, position of the target (when present) was randomised, and accuracy and RT to make target-present/absent judgments were recorded. Subsequently, the strength of lateral masking was measured in all 24 conditions by the following method. Subjects were instructed to move their gaze to the left or right of a centrally presented target, following a fixation cross, and to indicate when they no longer could identify the target. The distance between target and fixation cross was taken as a measure of lateral masking. The same factors that increased lateral masking also increased RT in visual search. Lateral masking accounted for 40% to 90% of the variance in visual-search RT as a function of set size, search type, and target attributes.

We argue that future models need to take into account lateral masking as a factor determining performance in visual-search tasks.

◆ **Do spatial precues affect preattentive vision when accuracy is the measure?**

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The detection of primitive visual features is generally thought to occur preattentively in parallel across the visual field. Visual-search data showing that time to determine the presence or absence of a target defined by a primitive feature is independent of the number of items in the display have been taken as evidence that preattentive vision operates free of attentional capacity limits.

Recently, however, it was reported by Theeuwes et al (1999 *Journal of Experimental Psychology: Human Perception and Performance* **25** 341–347) that the allocation of attention to a particular region of the visual field speeds up search in that region. The finding that precueing a particular region speeds up detection responses for targets in that region is important because it runs directly contrary to the assumption of capacity-unlimited preattentive processing. However, patterns of reaction-time data are always open to the challenge that they reflect response factors rather than purely perceptual processes. Therefore, we studied detection accuracy for a masked red target among masked green distractors using precueing of particular regions of the visual field. Our results are fully consistent with the reaction-time data.

## ASYMMETRIES IN STEREOPSIS

### ◆ Stereoanomaly explains inter-subject differences in various stereoscopic depth experiments

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Stereoanomaly is the inability to process the complete spectrum of crossed and uncrossed disparities. Since stereoanomaly was first discovered (Richards, 1971 *Journal of the Optical Society of America* **61** 410–414), few psychophysical studies have taken advantage of the deficit as a tool for understanding depth perception. Recently, two easy-to-use stereoanomaly tests have been introduced (van Ee and Richards, 2000, submitted).

Here we report for thirteen subjects that performance in the stereoanomaly tests correlates quite well with performance in (at least) two types of experiments involving stereoscopic depth perception. One of them involves volumetric depth judgments based on the integration of motion and disparity (van Ee, 2000, submitted); the other one involves perceived 3-D-depth relief under monocular, binocular, and synoptic viewing conditions (Koenderink et al, 1995 *Perception* **24** 115–126).

The results indicate that volumetric depth percepts require a comparison between pooled activities over the crossed and uncrossed disparity ranges. Given that as much as 30% of the population is stereoanomalous, we propose that, generally, the interpretation of stereoscopic experiments would be more meaningful if observers were characterised with regard to their stereo abilities.

### ◆ Stereoacuity thresholds are not symmetrical about the fixation plane in the presence of a reference surface

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With isolated stereo targets, the best depth discrimination is found in the fixation plane [eg Blakemore, 1970 *Journal of Physiology (London)* **211** 599–622].

We measured stereoacuity thresholds in the presence and absence of a frontoparallel reference surface to determine whether the plane of maximal stereoacuity was altered by the reference surface. Subjects judged the depth of a vertical target line presented above a comparison line in a blank window within a random-dot field. Exposure duration was 150 ms and psychometric functions with different conditions were interleaved to reduce the likelihood of anticipatory vergence movements. Without a reference surface, thresholds rose as the target and comparison were moved away from the horopter. With a reference surface, stereo thresholds were (i) lowered by adding the surface at the same depth as the comparison line, and (ii) no longer symmetrical about the fixation plane. Thus, they were consistently lower for pedestal disparities with the same sign as the reference surface. The implication is that the reference surface has influenced the stereoscopic system at a level that is often assumed to be anatomically hard-wired.

### ◆ Modal and amodal surface interpolation

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New phenomena are presented that reveal asymmetries between modal and amodal completion. We show that modally completed surfaces depend critically on the luminance and contrast relationships in the scene, whereas amodally completed surfaces do not. Sinusoidal gratings were viewed stereoscopically through multiple circular apertures on a homogeneously coloured surround, and a relative disparity was introduced between the aperture boundaries and the gratings. When the disparity relationships placed the grating behind the aperture boundaries, and the phases of the gratings were aligned, the gratings appeared as a single interpolated surface. This percept was independent of the luminance of the adjacent surround. But when the disparity relationships were reversed, the grating appeared to split into multiple depth planes, appearing as stripes that completed in front of uniform discs. In contrast to the amodal case, completion was only observed when the luminance of the adjacent surround fell outside the luminance values within the grating. Using a 2AFC procedure, we found that observers were more accurate in discriminating the relative phases of the gratings when completion was observed.

It is argued that the mechanisms underlying modal and amodal completion must differ because of the different constraints imposed by partial occlusion and camouflage.

◆ **The reasons for anisotropy in stereoscopic slant contrast**

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 Van Ee and Erkelens (1996 *Vision Research* **36** 2253–2262) and Pierce et al (1998 *Perception* **27** 87–103) found greater stereo slant contrast for horizontal slant when the inducer is above/below the test surface than when it is left/right. Van Ee and Erkelens attribute this to the different effect contrast has on perceived axes of slant in the two cases. Neither group considers the possibility that the contrast effect has a different basis in the two cases.

We have argued that up/down, but not left/right, inducers enhance slant and contrast by introducing a gradient of shear along the boundary. Van Ee and Erkelens found a contrast effect for overlapping left/right inducers which is consistent with the view that this gradient is the critical feature. We measured slant contrast for up/down and left/right inducer/test arrangements in a variety of configurations including those with the axes of the inducer and test at different depths (ruling out the van Ee–Erkelens explanation). The contrast effect was much greater in the up/down case, regardless of whether one or two flanking surfaces were present. This supports the view that slant enhancement and contrast arise because a second surface provides a gradient of shear along the boundary.

## POSTER SESSION 6

### ATTENTION, TEXTURE, AND VISUAL SEARCH

● **Spatiotemporal discrimination thresholds for dynamic random fractal ( $1/f$ ) textures**

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Natural scenes are fractal in space (ie they have  $1/f^B$  spatial frequency spectra) and time ( $1/f^A$  temporal spectra), and can be compellingly mimicked by fractal textures. If dynamic fractal texture statistics are used to describe natural scenes, then data on discriminability of such textures are required.

The smallest detectable change was measured separately for 10 spatial (0.4 to 2.2) and 8 temporal exponents (static, and 0.2 to 1.4) with an adaptive staircase. Computational constraints limited each fractal to 64 frames ( $\sim 2$  s) of  $64 \times 64$  pixel images. Spatial discriminations were easiest when the spatial exponent  $B$  was  $\sim 1.6$  and were similar across all temporal exponents. Temporal discriminations were easiest when the temporal exponent  $A$  was  $\sim 0.8$ , and increased in difficulty as the spatial exponent increased.

This similarity in spatial discrimination thresholds for static and dynamic fractals suggests that the spatial and temporal dimensions are independent in dynamic fractals (at least for spatial judgments), as is often assumed. The dependence of temporal judgments on the coarseness of the texture (ie on the spatial exponent) is understandable, as a 1 mm change in position is more noticeable for a 1 mm object than for a 100 m object.

● **Texture orientation detection: visual field and spatial frequency effects**

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The visual field factor is important in a spatial pre-cueing task with discrimination of Landolt squares, 'broken-line', and Vernier target (Carrasco and Yeshurun, 1999 *Vision Research* **39** 293–306).

In our study, the visual field factor was tested in a texture orientation detection task. Two experiments were conducted. In the first, our subjects were detecting the orientation of horizontal and vertical lines, on five textures with different line density (spatial frequency factor) using 17 positions on the screen (visual field factor). In order to disable rapid eye movements, the visual stimulus was exposed for only 50 ms followed by masking. Subjects used a mouse key to indicate one of the two possible texture orientations (horizontal or vertical). The second experiment was conducted in the same manner as the first, with the exception of the line order which was random in the second experiment.

An ANOVA showed that both visual field and spatial frequency factors were statistically significant. The line order, as a grouping factor, did not reach statistical significance. The spatial frequency was shown to be a statistically significant predictor of RT. In a texture orientation detection task, the spatial frequency was facilitating (ie the higher spatial frequency, the shorter RT).

- **Inhibition of return and visual masking at invisible objects behind occluders**

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When an object moves behind another object and goes out of sight, we do not think of it as ceasing to exist but as still existing in the visual environment. Such experience suggests that occluded objects might show similar perceptual/attentional effects to visible objects. To explore this possibility, we tested if inhibition of return (IOR) and visual masking can be observed with occluded objects.

In experiment 1, one of two moving objects was cued when they disappeared behind occluders. Then a target appeared at one of four locations (cued/uncued  $\times$  location/object) when the two moving objects reappeared. IOR was found at the cued object as well as at the cued location, contrary to a previous study (Tipper et al, 1994 *Journal of Experimental Psychology: Human Perception and Performance* **20** 478–499). In experiment 2, a cue and a target appeared when moving objects were occluded. We found IOR again at the cued locations and invisible objects behind occluders. Moreover, visual masking was found at blank locations where objects were occluded. These results suggest that occluded objects are represented in a similar way to visible ones and that early visual processing can be influenced by higher visual representations.

- **Discriminating networks for spatial and selective attention in visual search—A correlational fMRI study**

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We investigated the interplay of visuospatial and selective attention in visual search. Whereas usually different paradigms are used to localise these functions in the brain, we activated both networks simultaneously and discriminated which area serves which attentional process with a correlational analysis.

With our reaction-time model STRAVIS (Müller-Plath, 1998 *Perception* **27** Supplement, 36c), a visual-search process can be decomposed into distinct subprocesses and described quantitatively by individually estimated parameters. In the present study, we validated the model with an RT experiment. In the following fMRI experiment, we related estimated model parameters to BOLD responses.

We found activations correlating with the parameter ‘attention dwell time’, eg in the right dorsolateral prefrontal cortex (rDLPFC), the intraparietal sulcus (IPS), and extrastriate visual areas. We concluded that these areas are involved in selective attention to stimulus features. Activations correlating with ‘movements of attention’ were found also in the rDLPFC and the IPS, but in each anterior to the above mentioned areas. These areas may be involved in visuospatial attention. Additionally, in extrastriate visual areas and the IPS we observed lateralisations of activations corresponding to the attentional focus size. This finding may contribute to the discussion on global and local stimulus processing in the two hemispheres.

- **Quantifying target conspicuity**

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Target conspicuity can operationally be defined as the maximal angular distance between target and eye fixation at which the target can be distinguished. TNO Human Factors recently developed a simple and efficient psychophysical procedure to quantify the visual conspicuity of a target in a complex scene. This method can be used in situ, with full prior knowledge of the target and its location in the scene.

Visual conspicuity and search time were measured for a large number of military vehicles in different rural backgrounds, both for observers viewing the actual scenes (in the field) and for observers viewing slide projections of the same scenes (in the laboratory). The results show a linear relation between the logarithmic values of the conspicuity and the mean search time. Also, target conspicuity measured in the field agrees with measurements done on projections of photographic slides.

The first result means that conspicuity determines (predicts) human visual-search performance in realistic (complex) scenarios. The second result implies that target conspicuity can be determined from photographic reproductions of a scene. Photosimulation studies can therefore be used to optimise the conspicuity of a target. Examples are shown of applications of this method to a range of different practical problems.

## BINOCULAR AND SPATIAL VISION

### ● Influence of local orientation distractors on Vernier acuity

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In psychophysical experiments we studied how Vernier acuity depends on local distracting lines having different orientations. A Vernier stimulus was formed by two thin (1 min of arc) horizontal lines (10 min of arc long). The two lines were either abutting or had a gap of 2.5 or 5 min of arc. One line served as a referent and was presented alone or in the presence of two symmetrical distracting lines (5 min of arc long). The distracting lines formed an arrow pointing to the middle of the stimulus. The angles changed from 0° (when the distractors were parallel to and separated by 2 min of arc from the line) to 90° in 15° steps. The observers' task was to indicate the direction of the offset of the test line.

We found that offset discrimination thresholds depend on the orientation of the distractors: the thresholds rose at angles up to 45° (for abutting stimuli) and 60° (for stimuli having 5 min of arc gap) and then returned to the thresholds measured for an isolated stimulus. For the stimulus having 2.5 min of arc gap, the thresholds increased, but did not depend on the orientation of the distractors. The results are discussed in terms of local interactions between the parts of activated visual field.

### ● Spatial summation of orientation information across gaps: no influence of stereoscopic occlusion cues

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Orientation discrimination for a patch of grating is greatly improved when there are two separated but collinear patches instead of one (Guest and Georgeson, 1999 *Perception* **28** Supplement, 101c).

What process links the information from the two patches? Some cells in the visual cortex responded well to a pair of separated, collinear line segments that fell outside the classical receptive field, but only when the gap was filled by a blank region that was stereoscopically nearer than the lines [Sugita, 1999 *Nature (London)* **401** 269–272]. Thus, as early as V1, stereo cues may enable neural responses that correspond to amodal completion of contours. We measured orientation discriminability ( $d'$ ) for pairs of collinear luminance-modulated or contrast-modulated gratings (2 cycles deg<sup>-1</sup>, 1 deg aperture) shown for 80 ms in a 7 deg field of binary spatial noise. A rectangular strip of noise (1.3 deg high) between the gratings had crossed, zero or uncrossed disparity in different blocks of trials. Across several experiments we found that  $d'$  for two gratings was often 2–4 times better than for a single grating, but the stereo depth of the gap region had little or no effect. Thus we found no role for stereoscopic occlusion cues in this form of contour integration.

### ● Effect of a head-mounted visual frame on the subjective vertical

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When instructed to adjust a visual rod surrounded by a tilted frame to the vertical, observers tend to set the rod in an intermediate direction between the gravitational vertical and the axis of the frame (the rod-and-frame illusion). Tilting the head results in larger errors, suggesting increased weighting of the visual reference.

In the present experiment we aimed to investigate the influence of a head-centric visual frame with the use of a head-mounted display. This equipment allowed a strict collinearity between the axis of the head and the vertical symmetry axis of the frame while the subject was performing free head movements. After the head was tilted at given angles, the subject set the rod to the perceived vertical. Subject performance following active or passive head movements, with or without vision of the frame during the movement, was contrasted with the effect of head tilt and visual frame alone. Results are discussed in the conceptual framework of visual, vestibular, and postural integration for spatial orientation.

- **Plaid motion coherence can be achieved under dichoptic viewing**

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Plaid motion coherence was studied with orthogonal spatial-frequency components presented separately to each eye. In order to characterise the limits for binocular fusion, plaid motion coherence was assessed as a function of the difference in spatial frequency between the components. Plaid patterns composed of two square-wave drifting gratings (same contrast, velocity, and phase) were presented dichoptically through LCD shutter glasses. Interoocular spatial-frequency differences were introduced by keeping the spatial frequency of one component constant at 5 cycles deg<sup>-1</sup>, and varying the spatial frequency of the other component in steps of 1/4 octave. The component gratings were oriented +45° and -45° from the horizontal axis so that, when binocular fusion of the two components was achieved, observers perceived horizontal coherent motion.

Results showed that, when both components were of identical spatial frequency, the subjects perceived coherent plaid motion. However, the binocular fusion broke down rapidly as the difference in spatial frequency between the components exceeded 1/4 octave. Overall, these findings suggest that plaid motion coherence can occur from combined inputs from each eye, but that this binocular fusion can tolerate only narrow spatial-frequency differences.

[Supported by FCAR and NSERC.]

- **Neuronal connections within and between cortical areas 17 and 18 of the cat**

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We reported previously (Toporova et al, 1999 *Perception* **28** Supplement, 97d) that areal distributions of the population of cells sending axons to a single cortical column of the same area are orthogonal in areas 17 and 18. We have tried to find out whether these peculiarities of intrinsic connections are reflected in neuronal connections between these areas.

Horseradish peroxidase was microiontophoretically injected in one of these areas and retrogradely labelled cell region in the other area was reconstructed. Areal distribution of labelling (in tangential plane) was elongated in area 17 along the representation of the horizontal meridian of the visual field and in area 18 along the representation of the vertical meridian. Such projection patterns appear to be common throughout the central 10 deg for various elevations (from -40° to 0°) of the visual-field representation in these cortical areas. Thus, spatial arrangements of extrinsic connections (from area 17 to 18 and from area 18 to 17) are orthogonal as well. The following visual information exchange scheme may be suggested. Area 17 may supply area 18 with more detailed information on the horizontal component of the visual image, and the information on the vertical component of the same image may be supplied in the opposite direction.

[Supported by RFBR grant 00-04-49289.]

## COLOUR AND BRIGHTNESS

- **Colour constancy redefined and an invariance hypothesis for saturation**

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The AMBEGUJAS phenomenon is a reversible 3-D figure (cf the Necker cube), where the two phases appear different even in colour. The chromatic surface colours of phase A disappear in phase B, where the chromatic colours appear as a chromatic illumination and shadow. The shift of the mode of appearance of colour is synchronised with the reversal of the 3-D figure (Jakobsson et al, 1997 *Perception* **26** 531–547; Bergström et al, 1999 *Perception* **28** Supplement, 65a).

Classical colour constancy is defined as an invariance of perceived surface colour under varying illumination. This seems to be a special case of the mode of appearance of colour: the perceived surface colour is locked to the distal stimulus (veridicality, 'regression to the real object'). As a consequence of the AMBEGUJAS phenomenon, a different definition of colour constancy is proposed, which is totally perceptual (in the subjective domain). The phenomenon is demonstrated and psychophysical measurements of surface and illumination saturations are presented to try to state an invariance hypothesis for these two modes of appearance of colour.

● **Spectral and thermal properties of visual pigments bear no simple relation**

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It is generally assumed that the tuning of spectral absorbance by structural factors in the visual-pigment (rhodopsin) molecule is equivalent to tuning the transition energy ( $E_a$ ) for isomerisation of the chromophore. The assumption that the wavelength of peak absorbance ( $\lambda_{\max}$ ) is inversely related to  $E_a$  was originally proposed by Barlow [1957 *Nature (London)* **179** 255–256], following a simple physical idea of Stiles. Further, the probability for purely thermal activation of rhodopsin, producing a noise component that must necessarily limit absolute visual sensitivity, would also be inversely related to  $E_a$ . Thus a ‘red-sensitive’ rhodopsin would always be noisier than a ‘blue-sensitive’ one.

Using microspectrophotometric and electrophysiological measurements from photoreceptor cells, we have studied the relation between  $\lambda_{\max}$  and  $E_a$  for several amphibian rod and cone rhodopsins, considering also the apparent rate of thermal activation if available (ie for rod pigments). We find that frog 502-nm rod pigment and 562-nm cone pigment have similar  $E_a$  (ca 45.5 kcal mol<sup>-1</sup>), but 502-nm rod pigments of frog and European toad have significantly different  $E_a$ , as is true also of the rod pigments of European toad ( $E_a$  ca 49 kcal mol<sup>-1</sup>) and cane toad ( $E_a$  ca 43 kcal mol<sup>-1</sup>), which have indistinguishable rates of thermal activation.

● **The effect of SOA on brightness under glare condition**

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Previous studies have shown the effect of brief exposures to glare on brightness, related to scotopic–mesopic range of adaptation (Colombo et al, 1999 *SPIE* **3749** 504–505). The perceived brightness is reduced when a test patch is presented under glare condition. In this work, we measured the effect of SOA on brightness for several glare intensities.

Subjects had to compare brightness of two uniform luminance fields sequentially displayed, one of which was presented under a glare condition produced by shining a bright light on the eyes. The observer reported which field was brighter with respect to another. A forced-choice paradigm with the method of constant stimuli was adopted to determine the luminance corresponding to the perceptual matching luminance. The experiment was carried out for values of SOA between 0 and 500 ms and glare intensities of 15, 30, and 60 lx measured at a point between the two pupil centres.

Results show that the effect of transient glare on the matching luminance is less as SOA increases, suggesting that the time course of rapid events of adaptation affects the evaluation of brightness.

● **Colour perception deficiency in demyelinating processes of visual system**

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Menage stated that Farnsworth–Munsell 100 data for demyelinating optic neuritis revealed abnormality in the blue–yellow axis [Menage, 1993 *British Journal Ophthalmology* **77**(2) 68–74].

Forty-eight subjects with opticoneuromyelitis were tested with computerised Farnsworth–Munsell test. The zones of colour confusion and degrees of colour discrimination were measured. Contrast sensitivity testing and ophthalmological examination were also performed. Colour deficiency was identified by bipolarity and clustering of maximum errors in two regions which were nearly opposite. The regions in which the errors were made were used to identify the type of colour deficiency.

The patients were divided into three classes according to the number of mistakes they made: normal—between 20 and 100 mistakes (20.1%); average—more than 100 mistakes (57.2%); and poor—more than 300 mistakes (22.1%). Colour deficiency for red was 46.2%, deficiency for blue 38.5%, and for green 11.5% of cases. It is concluded that demyelinating processes revealed abnormalities in the perception of red and blue colours when the visual acuity and contrast sensitivity remained unchanged.



- **Effects of  $+G_z$  on colour vision**

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The US Air Force is developing colour helmet-mounted displays and night-vision goggles for use in tactical aircraft. One of the main purposes of this development is to provide colour-coded weapons-targeting information, which must remain intact perceptually if it is to serve its intended purpose during the high- $G$  turns that are often required during combat. Surprisingly, there seems to be essentially no scientific literature documenting the effects of  $G$ -forces on colour vision.

Recent research at the Air Force Research Laboratory, however, has shown that colour perception is altered when human observers are subjected to high  $+G_z$ . Specifically, colour stimuli become desaturated and their hues may shift as  $+G_z$  increases; furthermore, colour vision is lost altogether at  $+G_z$  levels near the observer's gray-out point. Results from psychophysical investigations of the effects of luminance contrast and saturation on colour perception under  $+G_z$  are presented, and experiments are described that more realistically simulate tasks requiring accurate colour perception that might be performed by pilots. These results hold the important promise that display-design guidelines can be developed that will ensure sufficiently accurate colour perception at  $+G_z$  levels up to the point at which all vision is lost.

## EYE MOVEMENTS

- **Incidence rates of eye dominance in various fields of professional activity**

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Eye dominance was investigated in 251 surgeons (urology), 144 musicians, 57 Alpine skiers (German National Team), and in 53 handball or basketball players. Together with handedness, it was assessed in each subject by a German adaptation of Coren's questionnaire (Coren, 1993 *Bulletin of the Psychonomic Society* 31 1–3) and by Walls' pointing test (Walls, 1951 *Archives of Ophthalmology* 45 387–412). The resulting incidence rates were compared with those of a representative reference sample of 3372 unselected persons.

While surgeons and Alpine skiers did not differ in their incidence rates from the reference sample (20%), significantly higher rates for left-side eye dominance were found in musicians and ball players (30% and 36%). No differences in handedness were found. Eye dominance assessed by the questionnaire did not always conform with that found experimentally, revealing a right-side bias (dependent on handedness) for the questionnaire data.

The results suggest that different fields of professional activity and their respective differential requirements of sensory–motor skills (which need to be further investigated and identified) favour persons with left-side or right-side eye dominance.

- **Isoluminance makes saccade programming more difficult**

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Although many recent studies have been devoted to the magnocellular part of the visual system, the role of magnocells in programming eye movements is still largely unknown.

In an explorative experiment under isoluminous and nonisoluminous conditions, subjects were asked to do a speeded task that required making accurate saccades only. During each trial, four horizontal lines were presented that crossed each other at various locations. The lines were approximately equal in length and ended at the right in the numbers 1, 2, 3, and 4. The subject was asked to follow the line marked by an arrow from left to right in order to arrive at the correct number. Subjects needed approximately 500 ms longer to respond when the lines were presented isoluminously than when they were nonisoluminous (response times were between 2 s and 3 s for most subjects). There were no differences between conditions in the number of errors. To perform the task, subjects only needed to program their saccades accurately.

The considerably longer time needed for tracking the line under isoluminance suggests that magnocellular input is important for programming saccades. Whether the absence of luminance contrast increases the number of saccades or the fixation durations is currently under investigation.

- **Evidence for a psychological refractory period in a visual – auditory countermanding task**  
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In the countermanding paradigm, the primary task for subjects is to perform saccadic eye movements toward eccentric targets (go-task) but to inhibit their reaction whenever a stop-signal is presented with one of several delays after target presentation (stop-task). A widely accepted assumption, formalised in an influential model (Logan and Cowan, 1984 *Psychological Review* **91** 295–327) holds that internal inhibitory and reaction processes are largely independent. Whereas most experimental data are consistent with this assumption, one of the findings indicating a violation is that of unexpected long reaction times for short-delay conditions. This finding is usually ignored, as only few reactions occur for such delays.

To study the effects of auditory stop-signals presented shortly after a visual go-stimulus subjects were required to react at a speed level determined in a previously run experiment without stop-signals. With these rapid reactions, enough responses could be collected for the short-delay conditions. We found significantly delayed responses for the short-delay conditions, decreasing with increasing stop-signal delay. This is interpreted as a psychological refractory effect in terms of an enlarged stop-signal processing time, enabling relatively long reactions to escape inhibition. Altogether, the results suggest a serious violation of the independence assumption of the Logan–Cowan model.

## LEARNING, MEMORY, AND DEVELOPMENT

- **Visual motion processing deficits in dyslexia**  
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Recent findings indicate that motion processing is impaired in a large proportion of poor readers. These results have been interpreted as reflecting a magnocellular deficit in dyslexia.

In this study, we tested adult dyslexic and control subjects on a variety of visual-motion tasks, asking: (a) whether difficulties occur in all motion-processing tasks; and (b) whether the difficulties are consistent across tasks. The minimal interval required to detect direction of apparent motion of a single dot moving horizontally between the right and left visual fields was significantly longer in dyslexics. In a coherent-motion task, a significant group difference was found when the adaptive variable was presentation time, but not when the adaptive variable was coherence. Motion detection posed difficulties for about 50% of the dyslexics tested (at least when the adaptive parameter was stimulus duration). Motion detection measures were only moderately correlated with one another and with reading, and only marginally correlated with contrast sensitivity in the range governed by the magnocellular system.

We conclude that associating difficulties in motion detection, contrast detection, and reading with a single magnocellular deficit is questionable.

- **Face-specific processes during visual discrimination learning in monkeys with bilateral cortex lesions**  
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To identify a possible cortical mechanism in rhesus monkeys intended for face recognition, we studied the characteristics of learning processes involving visual discrimination of stimuli with different animal body parts and faces, as well as with various spatial relationships between these body parts. The prefrontal cortex sulcus principalis was removed bilaterally in animals of one group, and the parietal cortex 7 area was removed bilaterally in monkeys of another group. The remaining animals served as unoperated controls.

Monkeys' decisions and motor reaction times were recorded. Bilateral extirpation of sulcus principalis did not influence learning characteristics for different animal faces, nor for various spatial relationship between these body parts. After bilateral lesions of the parietal cortex 7 area, these learning characteristics for different animal body parts also were not changed; however, learning to discriminate different spatial relationships between animal faces and body parts was dramatically impaired.

From the above results and the learning deficit shown recently after the bilateral lesions of sulcus principalis for visual discrimination learning of nonface objects and their spatial relationships (Chueva et al 1999 *Perception* **28** Supplement, 92a), we suggest the existence of a special mechanism of face recognition separate from nonface object-recognition structures.

[Supported by the Russian Foundation for Basic Research, grant 99-04-49645.]

- **Colour and luminance interference effects on object and location recognition**

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There is substantial evidence for separate cerebral processing of visuospatial information and visual recognition. In this experiment we were interested in the relative contributions of the P channel and the M channel to these different processes.

We studied interference effects of colour or luminance peripheral flicker (in order to saturate either the parvocellular or the magnocellular stream) on object-identity and spatial-location memory. The results showed that colour flicker interfered with object-identity recognition, whereas luminance flicker affected memory for spatial location. Moreover, it was found that overall performance was worse if coloured compared to grey-scaled objects were used in the stimulus display. There was no selective effect of colour flicker affecting coloured objects and achromatic flicker affecting achromatic objects. These results provide strong evidence for the theoretical position that the 'what' pathway relies heavily on information derived from the P stream and the 'where' pathways on that derived from the M stream.

New research is currently being conducted on the stage during which interference is effective (during presentation or during a subsequent delay) and on the critical flicker frequencies.

## MOTION PERCEPTION AND OPTIC FLOW

- **Time course of the lower threshold of motion during rapid events of adaptation**

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To examine how the time course of rapid events of adaptation affects motion vision, we measured the lower threshold of motion (LTM) for temporally windowed sine gratings (300 ms stimulus duration) in the presence of steady and transient glare caused by shining a bright light on the eyes. Glare and stimulus were presented separated in time by a variable interval (SOA: 50–450 ms). We adopted a 2AFC paradigm using the constant-stimuli method for LTM measurements. We found that transient LTM (LTMT) is greater than steady LTM (LTMS) and follows the typical Crawford's time course of adaptation (Crawford, 1947 *Proceedings of the Royal Society of London, Series B* **134** 283–302).

We hypothesised that the increment of LTM is caused by: (i) a reduction of the effective stimulus duration due to the sudden onset of glare, and (ii) an increment of the minimum displacement due to the increase in the contrast threshold for displacing gratings, according to the proposal of Nakayama and Silverman (1985 *Journal of the Optical Society of America A* **2** 267–274). In order to check these hypotheses, we measured LTM using an additional stimulus duration (500 ms). Results show that the LTMT/LTMS ratios are similar for both stimulus durations which strengthens the hypothesis of increasing contrast threshold.

- **Spatial displacement limits for stereoscopic and luminance apparent motion with random patterns**

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Spatial displacement limits in stereoscopic (cyclopean) apparent motion were measured from random-depth patterns consisting of rectangular elements of various sizes, and then compared with those in luminance-defined apparent motion. The stereoscopic random patterns consisted of rectangular elements, each of which had an alternative depth position (near or far), while the luminance-defined patterns consisted of elements each of which had an alternative luminance (bright or dark). The first frame pattern was presented for 182 ms and, then, the second frame pattern that was displaced to the right or to the left was presented without ISI. The subjects' task was 2AFC of the perceived motion direction of the sequentially presented random patterns.

The result was that  $D_{\max}$  (75% correct responses) with stereoscopic patterns became larger in proportion to increases in the size of the elements. The  $D_{\max}$  values were consistent with those measured from luminance-defined patterns with the same element sizes. This result suggests that the strategy for the discrimination of motion direction of random patterns is the same in both stereoscopic and luminance-defined apparent motion.

- **Whether target speed influences a hitting movement from the start depends on the target velocity**  
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When executing a fast hit, the hand starts to move about 250 ms after the target appears. The position of the target at the reaction time (RT) influences the subject's initial movement direction. A change in the target position takes less time to influence the hand movement than does a change in the target speed (110 ms vs 200 ms).

In the present study, we asked whether the target speed also influences the initial movement direction. Subjects had to hit targets moving at different speeds. Targets were matched to have the same position at RT despite moving at different speeds. Movements towards targets of low and intermediate speed differed in starting direction, implying that velocity information was used for deciding where to aim. On the other hand, movements towards targets of intermediate and high speed started in the same direction, implying that the speed was not used for deciding where to aim. This seems counterintuitive, considering that faster movement is detected more quickly.

- **An oblique viewpoint improves wayfinding performance, but not cognitive-map acquisition**  
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- Although it has been believed that for successful navigation in real-world environment a cognitive map, namely allocentric representation of an environment, should be learned, it is not clear what information is indispensable for the acquisition of a cognitive map.

Here, a study is reported of the effects of different viewpoints, an oblique viewpoint with semi-bird's eye view and frontal viewpoint, on cognitive-map learning. Landmarks were presented randomly at intersections of streets in a virtual maze with a hexagonal layout. Observers were instructed to find a way to reach designated landmarks consecutively. Although many landmarks were visible from the oblique viewpoint, only one landmark was visible from the frontal viewpoint. The results showed that time spent on wayfinding was significantly shorter under the oblique-viewing condition. On the other hand, there was a statistically significant improvement of the quality of the acquired cognitive map under the frontal viewing condition. This trend was heightened for larger size of virtual maze.

These results suggest that presenting an oblique viewpoint, which has become so popular in in-vehicle route-guidance systems, does not necessarily improve acquisition of a cognitive map even though it facilitates wayfinding performance.

- **False depth and motion in Hughes's reverspectives: the role of pictorial cues**  
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In Patrick Hughes's sculptured paintings ('reverspectives'), pictorial cues compete with the actual depth configuration. Because of this, reverspectives appear in reverse depth, and turn vividly as viewers move in front of them. To isolate the role of pictorial cues in eliciting these false percepts, I compared results obtained with a fully painted reverspective to those obtained with two versions of the same sculptured surface: one containing only perspective edges, and one that was unpainted.

Observers retreated from or approached the art piece, and reported the critical distance  $D$  at which the depth percept switched from veridical to reverse, or vice versa, respectively. Both monocular and binocular viewing was tried. The role of perspective cues was significant; the false percept was not obtained at all for the unpainted version by some observers, but always obtained for the other two versions. A strong hysteresis effect was obtained across conditions:  $D$  was significantly larger when retreating from than when approaching the surface.  $D$  was reduced significantly with practice, indicating learning effects.

A model that accounts for the false motion of reverspectives as a consequence of the false depth percept is presented. The model can also explain false motion in the hollow-mask illusion and in stereograms.

- **An illusion of relative motion dependent upon figure – ground segregation**  
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In the Ouchi illusion, two regions spatially in register and of the same depth appear to move relative to each other with one region (disk) floating behind the other (ring). Although the illusion is well documented, the underlying mechanisms are not well understood.

We examined the role of figure-ground segregation in Ouchi-type motion. A central array of solid black circles is presented within a larger surround of empty circles, the two regions being separated by a square frame. Under these conditions, the central array is perceived as lying behind the surround. If the stimulus is moved, subjects report floating motion of the central region. When the polarity of the circles is reversed, the central array is now seen floating not behind, but in front of the surround. We manipulated the strength of figure-ground segregation by varying the shape, orientation, and colour of the elements, as well as the distinctness of the frame. Ouchi-type floating motion increased with increasing figure-ground segregation, suggesting that the two are intimately related.

The results may be explained by a competitive network of spatially overlapping ON and OFF receptive fields responding to different stimulus properties and interacting to produce an unstable representation of element position.

## NATURAL IMAGES, BIOLOGICAL MOTION, AND FACES

### ● **Spiral pattern as an attractor of human visual attention**

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In designs of various cultures and periods we can find many spiral patterns that remind us of patterns in nature. It seems that the reason why there are so many spiral patterns in our designs is that spiral patterns catch human attention. In order to confirm this experimentally and to analyse how these patterns lead our attention, eye movements were recorded with an eye camera under apposition of a spiral pattern and a non-spiral control pattern. Texture spiral patterns made from natural textures by image processing were used, and illusory spiral patterns as well as typical geometric spiral patterns.

Duration of fixation on the two patterns and first fixation point indicate that the spiral pattern attracts our attention. In the case of apposition of a texture spiral pattern and its original texture, the texture spiral pattern attracted fixation significantly more than the original texture with few exceptions. Illusory spiral patterns that are not spiral at all also attracted fixation significantly more than corresponding very similar concentric circles that do not induce an illusion of a spiral. These results suggest that the spiral or spiral-like patterns that we find in nature as patterns of animals, plants, and water attract our attention.

### ● **Spatial inference in scene perception for 3-D scenes**

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Physiological constraints prevent viewers from seeing an entire surrounding scene at once. Successive views are the input. How does the visual system integrate these views to yield perception of a stable, continuous world?

One possibility is that visuospatial expectancies guide and facilitate integration. Indeed, when remembering a photograph of a natural scene, viewers remember having seen the area that existed just outside the picture's boundaries (Intraub and Richardson, 1989 *Journal of Experimental Psychology: Learning, Memory, and Cognition* 5 179–187). This spatial extrapolation appears to be rapid and automatic. Is it limited to pictures or does it occur in perception of real scenes? Is there an analogue in touch perception?

Subjects viewed or touched (while blindfolded) 6–7 common scenes for 30 s each. Shortly thereafter, subjects adjusted scene boundaries to their remembered location (recall or recognition). In all conditions, subjects remembered exploring a greater expanse of the scene than they actually had. Vision subjects remembered seeing 29–79% more area and touch subjects remembered having felt 11%–29% more area. Mental extrapolation of spatial expanse appears to be inherent in memory for scenes regardless of whether the primary modality is vision or touch. Implications for scene perception and cross-modal representation are discussed.

[Supported by grant NIH R01MH54688.]

### ● **Movement duration influences judgments of affect for point-light displays of simple arm movements**

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Although human observers appear able to discriminate between different styles of movement, the physical properties on which such discriminations are based are not well known. We examined the role of velocity (as mediated through movement duration) in the categorisation of affective biological-motion displays.

A three-dimensional position analysis system was used to record the arm movements of actors as they expressed different affects in their actions. In the data, the sad movements had a longer duration than the angry movements, and from these original movement data new movements of different duration, but identical spatial displacement, were created with an interpolation algorithm. This technique yielded re-sampled stimuli with movement durations ranging from the original angry duration to the original sad duration for each affect. Observers viewed the movements as point light displays. Their task was to rate the movements on a 100-point scale from sad to angry.

Results of the rating task showed that, when sad movements were played at a shorter duration, the ratings of sadness decreased relative to the original sad movement. In a similar fashion, when the angry movements were played at a longer duration, the anger ratings decreased relative to the original angry movement.

- **The role of attention in the processing of biological motion**

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Previous studies have shown that some forms of biological-motion displays—specifically those in which bottom-up integration is possible—can be processed very effectively when attention is allocated to a demanding secondary task (Thornton et al, 1998 *Perception* Supplement, 68b; Thornton et al, 1999 *Perception* Supplement, 35c).

Here we further explore the role of attention in biological-motion processing using visual search and flanker interference paradigms. Even in the absence of masking elements, detection of a target walker amongst distractor walkers (set size ranged between 1 and 4 walkers) was always slow and effortful, requiring approximately 116 ms per item when the target was defined in terms of direction of locomotion (left-facing walker amongst right-facing walkers or vice versa), and close to 200 ms per item when the nature of target motion was varied (phase-scrambled versus phase-normal walkers).

These findings suggest that the individuation of walking figures in these displays requires attention. We are currently using a concurrent flanker task to explore whether this reallocation of attention is a controlled or automatic process.

## SHAPE

- **The influence of environmental cues on pictorial relief**

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In pictorial perception, strict shape constancy does not hold. It has been shown that pictorial relief is subject-dependent and that it is highly influenced by the viewing conditions, the task, or the rendering.

In this study, the effects of background and frame on pictorial relief were investigated. The relation between background and object in the picture was manipulated by changing the illumination conditions of each of them. In this way, contrast and contour visibility of the object were varied in a systematic way. The relation between frame and object in the picture was manipulated by systematically changing form, size, and contrast of the frames surrounding the pictures. Pictorial relief was quantified via a probe for surface attitude: a gauge figure had to be adjusted such that it appeared as a circle painted upon the surface of the object. In this way, slant and tilt values were sampled at many locations. The stimuli were scanned (gray-scale) photographs of mannequins used for shop windows and (gray-scale) photographs of triaxial ellipsoids finished matte-white and approximating Lambertian diffuse reflection.

We find that the presence of a frame tends to flatten pictorial relief in a systematic fashion. The background is also of influence.

- **Visual form perceived purely on temporal features**

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Within the last decade, several groups have addressed the question whether one can perceive a visual form created solely from temporal structure. However, positive results have usually turned out to be explainable by means of 'classical' cues like brightness or motion. By thorough analysis of the criticisms we created a design that avoids these artifacts.

Subjects looked at a screen filled by  $20 \times 20$  randomly oriented colons which flipped to their orthogonal orientation once within every cycle. Those constituting the background flipped in phase whereas those within the target area flipped in counter-phase. Subjects had to report at which of four sites the target had been shown. We (a) systematically increased the temporal frequency from 8 Hz to 32 Hz (and thus reduced the delay from 60 to 15 ms) and (b) decreased target size from  $6 \times 6$  to  $2 \times 2$  colons.

Results indicate great inter-individual variance but show uniformly (a) that performance decreases with increasing frequency (from nearly 100% at 8 Hz to chance level at around 30 Hz) and (b) that smaller stimuli cannot be seen as reliably as bigger ones. Thus, the visual system is actually able to group elements to a figure by temporal structure, though this process appears to be limited to delays of more than 15 ms.

- **Object recognition in the mental rotation of line-drawn and dot-defined objects**

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We examined whether mental-rotation performance is preserved with dot-defined objects, represented only by isolated points at the vertices of cubes, either with or without stereo information and with or without opacity information (Nakayama and Mather, 1998 *Perception* 27 Supplement, 122a). Experiments were conducted to examine whether identification could be achieved when pairs of line-drawn and dot-defined objects are presented in our previous experimental design.

In the first experiment, both objects were presented with or without stereo cues. All percentages of correct responses except one were significantly higher than chance. Reaction time (RT) increased with angular difference for most presentations, as in previous experiments. The exception was 2-D presentation of depth rotations. Here responses were at chance, and RT did not rise monotonically. Most subjects suggested that some vertex points looked both in near and far positions. In the second experiment, one object was presented with stereo and the other was presented without stereo. RTs for all presentations increased with angular difference because depth cues were given by either object. There was no difference in RTs between depth and picture-plane rotations in most conditions.

The results from both experiments provide evidence that line-drawn and dot-defined objects share a common underlying representation.

- **Closure under equiluminance: a comparison between two-tone and equiluminous coloured Mooney faces**

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Closure is described by the Gestalt law as contours that form a closed region tending to be attracted to each other and forming a figure. To what extent closure is dependent on luminance is to be questioned.

Closure can be assessed by the Mooney-faces test in which a face becomes a two-tone perceptual puzzle that has to be solved by closure; accuracy of the perceptual Gestalt is tested by judging the gender and age. We created 200 two-tone Mooney-like faces in which the exchange of black and white parts (positive versus negative) made judgments still possible. This set of faces was used in two conditions. In the first, chromatic, condition, the faces were orange/green and yellow/green and were presented at five different luminance contrasts (-10%, -5%, 0%, 5%, and 10%). In the second, achromatic, condition, the normal black-and-white faces were presented in the same polarity of luminance-contrast. The judgment of the subjects in the two conditions were evaluated for their consistency.

The results show that subjects are less consistent in judging age and gender when the luminance contrast between the two colours decreases. This study shows that at equiluminance the judgment based on closure was clearly less consistent.

## SPATIAL FREQUENCY AND CONTRAST

- **Different contrast response functions underlying contrast adaptation and the tilt aftereffect**

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What can we learn from aftereffects about the selectivity, contrast response, and adaptive properties of visual coding mechanisms?

I modelled the tilt aftereffect (TAE) by assuming that the response of each orientation-selective neuron is represented by a contrast-gain-control equation in which the divisive term contains a pattern-selective effect of adapting contrast and a nonselective effect of test contrast. Encoded orientation was the vector sum of responses across cells. The TAE was measured by a nulling method for gratings of 2 cycles  $\text{deg}^{-1}$ , with adapting and test contrasts from 4% to 64%. The TAE peaked around  $\pm 20^\circ$  adapting orientation and grew almost linearly with log adapt: test contrast ratio. Data were well fit ( $r = 0.97$ ) by the model with Gaussian orientation tuning of each unit ( $\sigma = 7.2^\circ$ ) but only when the response was compressive over the whole contrast range. This is very different from the accelerating response at low contrasts that is required to model contrast discrimination and the loss of perceived contrast after adaptation, and is shown by V1 cells. Thus the TAE may reflect a later, more contrast-invariant stage whose role is orientation coding, not contrast coding. The finding of substantial TAE transfer between first-order and second-order gratings further supports this view.

- **Does spatial-frequency or contrast uncertainty influence reaction time?**

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Reaction time (RT) is often measured in mixed blocks with randomly varying spatial frequency and contrast, ie under conditions of uncertainty. The effect of uncertainty on RT was studied with the use of two gratings with different spatial frequencies or contrasts.

We found that spatial-frequency uncertainty increased RT and its standard deviation when: (i) spatial frequencies of the two stimuli were within two different ranges, below 3–4 cycles  $\text{deg}^{-1}$  for one of the gratings and above this critical value for the other grating; (ii) stimulus contrast was low. When spatial frequencies of both gratings were within the same range, or the contrast was higher, no effect of spatial-frequency uncertainty on RT was observed. It was also found that contrast uncertainty increased RT for higher spatial frequencies only and at low contrast of one of the gratings. The results support our previous suggestion that RT is determined by two mechanisms (transient and sustained) at a near-threshold contrast, and by one (transient) mechanism at a higher contrast.

[Supported by the NSF, Bulgaria, Contract L809/98.]

## VISUAL IMPAIRMENT

- **The role of visual experience in early motor development**

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The motor development of infants aged from 4 to 18 months with heavy visual deprivation was studied by observation and testing. The subjects were 17 infants with diagnosed retinopathy of prematurity (ROP), optic nerve hypoplasia, and retinal disorders other than ROP; their visual acuity ranged from 0 to 0.2.

Their results were compared with two control samples of full-term and premature infants with normal vision. It was found that visually impaired infants were less successful in performing tasks that required auditory-motor integration, and also in self-initiated movements. The differences between infants with normal and poor vision in these cases were highly significant. At the same time, tests on maintaining balance revealed no differences between the groups. The same results were obtained when the movements were stimulated by tactile touching or took place within own body dimensions.

All this leads to the conclusion that visual afferentation provides necessary support to the development of auditory-motor coordination and stimulates external motor activity. Without visual experience the early motor development relies mostly on tactile and kinesthetic stimulation with the infant's body scheme as the integration factor.

[Supported by Russian Foundation for Humanitarian Research, grant N 98-06-08123.]

- **Natural variation in both position coding and visual attention affects visual word recognition**

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Letter-position coding is known to be important in text processing, and may be impaired in those with reading disability. We have studied the natural variability in, and possible relation between, relative-position coding (for non-word stimuli) and visual word recognition.

An unselected sample of fifty adults performed a series of tasks, including measurement of attentional dwell time, visual word recognition (assessed by a lexical decision task), coherent-motion



detection, colour detection, and relative-position coding. We measured the latter with a paradigm based on the lexical decision task, but which required the subject to process the relative order of a string of novel symbols.

Controlling for age, IQ, and reading ability, we found that accurate visual word recognition was best predicted by independent contributions from both the attentional-dwell-time and position-coding tasks. Previous findings were also replicated with regard to coherent-motion detection and lexical decision (Cornelissen et al, 1998 *Vision Research* **38** 2181–2191). Subjects' performance in colour detection was uncorrelated with their performance in the attention, motion, and position tasks. Since many developmental dyslexics exhibit poor performance on dynamic visual tasks, these findings may have implications for whether reading difficulties can be caused by visual-system impairment.

- **Visuospatial attention influences residual vision of patients with brain lesions and near-threshold vision of healthy subjects**

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We applied high-resolution suprathreshold campimetry repeatedly to determine partially defective visual-field areas (transition zones) in twenty-three brain-lesioned patients. The findings were compared with results from a campimetric attention test with a visuospatial cue used to direct subjects' attention to their visual-field border (Posner's paradigm). A matched group of normal subjects was tested with both methods with suprathreshold as well as near-threshold stimuli.

Stimulus detection and reaction times of the patients improved in valid trials in comparison with neutral (uncued) conditions, but we also observed facilitation in invalid trials indicating an unspecific effect of alertness. The extent of improvement depended upon the size of the transition zone, ie there was a higher gain in patients with soft visual-field borders. In normal subjects, this effect could be simulated in the near-threshold condition.

We hypothesise that thresholds of perception are increased in transition zones but that directing attention to the visual-field border reduces thresholds and thereby facilitates conscious perception. Presumably, partially lesioned regions of the visual cortex are the neuronal basis of transition zones, and attention induces short-term neuronal plasticity in areas of residual vision. This effect might have important implications for the rehabilitation of patients with visual-field defects.

- **Subjective experience of visual-field defects caused by cortical infarctions**

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Visual-field defects caused, for example, by infarction of the occipital cortex, are frequently not subjectively detected by the patient, similar to the blind spot. This lack of awareness regarding blind portions of the visual field is probably due to mechanisms of filling in, perceptually filling the defect with patterns present close to its borders.

In order to make patients aware of their defects, we presented 12 different stimuli to patients suffering from recent infarction in the occipital cortex. These stimuli, presented on a colour monitor, extended over a circular area of the visual field with a diameter of 60 deg. Luminance, colour, orientation, position, or stereoscopic depth of the stimulus elements varied rapidly in order to preferentially stimulate different submodalities of vision.

Patients indeed experienced, under appropriate conditions, their visual field defects when looking at these stimuli. The spatial extent of the defects experienced subjectively was generally somewhat smaller than the extent of the scotomata present in the Goldmann perimetry that was performed in all patients as a gold standard. Obviously, not for all types of stimuli, defects can be filled in and some people are able to perceive their blind spots when looking at our stimuli.

## THURSDAY

### STICHTING BLINDENPENNING LECTURE

#### ➤ **Vision multiplexing for vision rehabilitation: from basic research to applications and back**

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Low-vision is a fast growing problem due to the aging of the population. Vision research could and should provide insights that will help in the rehabilitation of impaired vision. Vision impairment usually affects either the central or the peripheral field. Visual aids frequently compensate for the loss in one function without attention to the need to reconstruct also the interplay of central and peripheral vision. Many aids impede the use of eye movements that are essential for this interplay in normal sight.

I have proposed a general paradigm for vision rehabilitation called vision multiplexing that explicitly emphasises this need. The implementation of various modes of vision multiplexing in the design of new optical and electronic aids for patients with hemianopia, severely restricted peripheral fields, and central field loss is illustrated. The principles as well as the specifics of various implementations derived insights from basic-research results. On the other hand, I argue and demonstrate that the development and testing of new visual aids provide an opportunity and impetus to further studies and understanding of vision in general.

### ORAL PRESENTATIONS

#### HEADING

##### ◆ **Heading in the right direction?**

B J Rogers (Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, UK; fax: +44 186 531 0447; e-mail: [bjr@psy.ox.ac.uk](mailto:bjr@psy.ox.ac.uk))

Using displacing prisms, Rushton et al (1998 *Current Biology* 8 1191) and Rogers and Allison (1999 *Perception* Supplement, 2a) showed that straight-line walking and cycling paths are determined principally by the egocentric direction of a target rather than the 'centre of outflow' or other optic-flow-field properties. Does this mean that optic flow plays no role in locomotor control?

Two issues were investigated in the present study. First, could the previous results have been an artifact of using displacing prisms; and, second, are walking paths (in the absence of prisms) significantly straighter when optic-flow information is available? To answer the first question we used mirror spectacles (which create none of the distortions associated with prisms) to displace egocentric visual direction. The results were identical to those found previously. To answer the second question, we measured the deviations from straightness of both walking and running paths towards either (i) a visual target in an otherwise dark room, (ii) a target located on a homogeneously textured ground plane, or (iii) a target in a cluttered environment. Locomotor paths were not significantly straighter in conditions (ii) and (iii), reinforcing our previous conclusion that optic flow plays no significant role in the control of straight-line locomotion.

##### ◆ **Can we be forced off the road by the visual motion of snowflakes? Immediate and longer-term responses to visual perturbations**

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Several sources of information have been proposed for the perception of heading. Here, we independently varied two such sources (optic flow and viewing direction) to examine the influence of perceived heading on driving.

Participants were asked to stay in the middle of a straight road while driving through a snowstorm in a simulated, naturalistic environment. Subjects steered with a forced-feedback steering wheel in front of a large cylindrical screen. The flow field was varied by translating the snow field perpendicularly to the road, producing a second focus of expansion (FOE) with an offset of 15°, 30°, or 45°. The perceived direction was altered by changing the viewing direction 5°, 10°, or 15°. The onset time, direction, and magnitude of the two disturbances were pseudo-randomly ordered.

The translating snow field caused participants to steer towards the FOE of the snow, resulting in a significant lateral displacement on the road. This might be explained by induced motion. Specifically, the motion of the snow might have been misperceived as a translation of the road. On the other hand, changes in viewing direction resulted in subjects steering towards the road's new vantage point. While the effect of snow persisted over repeated exposures, the viewing-direction effect attenuated.

◆ **Heading encoding in MST during simulated eye movements**

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Eye rotations destroy the correspondence between the focus of expansion and the direction of heading. The retinal flow contains information for solving this problem. We used information theory to determine whether cells in macaque area MST can solve this problem from the retinal input, and whether they do so by decomposing the flow into translational and rotational components.

Spike data were gathered while a monkey viewed large-screen optic flow corresponding to a long trip ( $\sim 1$  h) through a 3-D cloud of dots. Trajectories included translations and eye rotations. We determined how much heading and gaze-change information is contained in the spike counts of cells. This was done for the whole data set, for the subset of pure translation trials and for the subset including eye rotations.

The cells in our sample of 45 on average encode  $0.7 \text{ bit s}^{-1}$  of heading information. Extraction of heading information was equally good in pure translation and rotation trials: MST cells provide significant heading information even in the presence of simulated eye rotation. MST cells also represent gaze-change information ( $0.3 \text{ bit s}^{-1}$  on average). This suggests that a full decomposition is not performed at the single-cell level, because information on gaze change is still present.

[Supported by HFSP]

◆ **Calibrated direction of heading**

A Glennerster, A W Fitzgibbon¶, M E Hansard# (Department of Physiology, University of Oxford, Parks Road, Oxford OX1 3PT, UK; ¶ Department of Engineering, University of Oxford, Parks Road, Oxford OX1 3PJ, UK; # Department of Computer Science, University College London, Gower Street, London WC1E 6BT, UK; fax: +44 186 527 2488; e-mail: [ag@physiol.ox.ac.uk](mailto:ag@physiol.ox.ac.uk))

It has long been assumed that the visual system analyses retinal flow by decomposing it into rotational and translational flow (Longuet-Higgins and Prazdny, 1980 *Proceedings of the Royal Society, Series B* **208** 385–397), where translational flow specifies heading direction. For a fixating observer, rotational and translational flow are tightly linked to one another, suggesting alternative heuristics may be used.

Here we show how the following information can be computed, with increasing levels of precision. For a set of translations in the base plane (containing the fixation point and the translating optic centre): (i) divide the translations into two groups with respect to the fixation point, for example 'left' and 'right'; (ii) recover the component of translation perpendicular to the line of sight up to some unknown scale factor ( $k_1$ ) and the component along the line of sight up to a different scale factor ( $k_2$ ); and (iii) recover the ratio  $k_1 : k_2$ , providing a fully calibrated estimate of the directions of heading. Two elements of this scheme support it as a biologically plausible hypothesis. First, it is valuable if the observer maintains fixation on a point as (s)he moves. Second, there are intermediate stages, each providing useful information.

**NOISE AND EFFICIENCY 1**

◆ **Introduction to noise and efficiency**

D G Pelli (Department of Psychology and Neural Science, New York University, 6 Washington Place, New York, NY 10003, USA; fax: +1 212 995 4701; e-mail: [denis@psych.nyu.edu](mailto:denis@psych.nyu.edu))

Noise limits all forms of communication, including vision. As an empirical matter, it is often useful to measure the human observer's threshold with and without a noise background added to the display, to disentangle the observer's ability from the observer's intrinsic noise. When we know how much noise there is, it is often useful to calculate ideal performance of the task at hand, as a benchmark for human performance. This strips away the intrinsic difficulty of the task to reveal a pure measure of human ability. The talks in this session, invited and submitted, exploit these measures—efficiency and equivalent noise—in the study of vision.

◆ **The equivalent input noise: what it tells us about intrinsic visual noise**

M Raghavan (Comprehensive Epilepsy Center and Department of Neurology, New York University School of Medicine, 560 1st Avenue, Rivergate 4th Floor, New York, NY 10016, USA; fax: +1 212 263 8342; e-mail: [raghavan@psych.nyu.edu](mailto:raghavan@psych.nyu.edu))

Noise arises at several different stages of visual processing from phototransduction onwards. But which of these noises determine visual sensitivity?

The intrinsic noise that limits visual detection can be characterised as an equivalent input noise added to the signal. The equivalent input noise of different sources of intrinsic noise has

characteristic dependencies on the spatiotemporal frequency of the signal, luminance, and number of eyes to which the signal is delivered. We compared the observer's equivalent input noise, measured as a function of spatiotemporal frequency, luminance, and monocular/binocular of the signal, with that expected for the thermal noise of photoreceptors, photon noise, ganglion-cell noise, and cortical neural noise.

We find that photopic visual sensitivity is limited by an intrinsic noise that is well modeled as the sum of the photon noise resulting from transduction of 2% of the incident light, and a neural noise arising in the visual cortex, with a  $1/f$  spatiotemporal spectrum. When the integrated light from the stimulus exceeds 7 td deg<sup>2</sup> s, the cortical noise dominates and threshold follows Weber's law. Below this, photon noise dominates and threshold follows the Rose–DeVries law.

◆ **Lesions to extrastriate visual cortex cause local increases in internal noise**

R D Hayes, W H Merigan¶ (Graduate Neuroscience Program, University of Rochester, 601 Elmwood Avenue, Rochester, NY 14642, USA; ¶ Department of Ophthalmology and Center for Visual Science, University of Rochester, 601 Elmwood Avenue, Rochester, NY 14642, USA; fax: +1 716 271 3043; e-mail: [hayes@cvs.rochester.edu](mailto:hayes@cvs.rochester.edu))

Lesions of ventral extrastriate visual cortex in two human subjects and two macaques caused moderate, retinotopic decreases in contrast sensitivity. We consider two possible mechanisms of this loss.

Complete removal of one parallel cortical pathway might eliminate functions specific to that pathway. Compared with lesions of the P and M inputs to cortex (Merigan and Maunsell, 1993 *Annual Review of Neuroscience* **16** 369–402), the loss after a cortical lesion was not sufficiently selective to suggest loss of some parallel pathways. A second possibility is that lesions reduce the efficiency of a cortical pathway. We tested this by adding graded amounts of noise to the stimuli. Slopes of noise-masking functions were elevated compared to the control part of the visual field. We estimated internal/external noise ratios in some of the subjects by measuring the consistency of their responses to a fixed sequence of noise-masked stimuli. At the same percentage of correct responses, subjects showed lower consistency in the lesioned visual field, suggesting that the lesion caused an increase in processing noise.

In the four subjects of this study, visual loss following cortical lesions is better thought of as impaired processing efficiency than as the complete loss of some cortical pathways.

◆ **An early-noise model of complex-pattern discrimination**

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A four-stage, late-noise model incorporating pooled gain-control processes followed by selective summing mechanisms (Olzak and Thomas, 1999 *Vision Research* **39** 231–256) accounts for a large body of discrimination data. When the task is a spatial-frequency discrimination made on plaids, however, both concurrent-response data and uncertainty data suggest that the Olzak and Thomas account is not fully adequate. In an earlier work, Thomas (1983 *Journal of the Optical Society of America* **73** 751–758) demonstrated that models incorporating early neural noise can provide a good quantitative account of how frequency discrimination performance varies with contrast.

We have developed a new quantitative model of this class which omits a pooled gain-control stage, yielding a simpler structure than the four-stage model of Olzak and Thomas. Using data from a concurrent-response discrimination task and analyses we previously developed, we reconstructed the underlying bivariate response space, permitting us to estimate parameters of the new model. We show how this model correctly predicts the pattern of masking and cue-summation discrimination data obtained with complex frequency judgments, and demonstrates that effects of early noise passed through nonlinear systems may mimic effects attributed to divisive gain control.

## VISUAL CONTROL OF ACTION

◆ **Use of target velocity in hitting moving objects**

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We investigated whether velocity information is used to predict target position when hitting moving targets. Subjects hit spiders which ran from left to right at three different velocities. The spiders disappeared from view after 150, 250, or 350 ms. For each presentation time, the distance that subjects hit ahead of the disappearance point depended on spider's velocity. This means that target velocity is used. However, spiders that disappeared at different times but

moved at the same speed were hit at different positions. This means that differences in target velocity are only partly accounted for.

Two models seem to be able to explain the present data reasonably well. The first assumes that velocity is not really used to predict target position, but that the position at which the target disappeared is misperceived in the direction of ocular pursuit. The second proposes that target velocity is used to predict the position at which to hit, but that such information becomes available only gradually during target presentation and therefore manifests itself only during the course of the movement.

◆ **Visually guided control of locomotor pointing: Importance of optical expansion of the target**

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Optical expansion of a target for pointing at is an element of optic flow that may be used for visually guided control of locomotor pointing (eg for pointing at a visible target on the floor with a foot while walking). But does it actually serve its purpose?

A virtual-reality setup (virtual environment coupled to a treadmill) permitted us to answer this question, by manipulating the target expansion. First, we confronted subjects with targets that provided no expansion (extensionless dots), and with targets that provided normal expansion at the point of observation. Locomotor pointing control and performance in these two conditions were found to be similar. Obviously, target expansion was not essential. This fact, however, remains compatible with the use of target expansion when it is available. Because visual restriction of target expansion puts a limit on testing its use, we further confronted subjects with targets that provided over-expansion, normal expansion, and under-expansion at the point of observation.

Differences were found in the mean locomotor patterns, depending on our manipulation of target expansion. We provide a functional explanation of those differences in terms of locomotor pointing control, based on a perceivable variable that takes into account target expansion.

◆ **First-order optic flow and the control of action**

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First-order optic flow—dilation, shear, and rotation—provides powerful information for the control of action, and can be accurately measured. The ‘forward problem’—calculating first-order flow from surface orientation, distance, and relative motion—is well understood (Koenderink, 1986 *Vision Research* **26** 161–179), and the result that immediacy is specified by dilation for an approaching surface has been investigated in depth. However, there is no simple solution to the ‘inverse problem’ of how to make general inferences from first-order flow. There has also been less attention to shear and rotation, and to oblique surfaces on non-collision courses, for which foreshortening becomes important.

This paper introduces a new theoretical framework for the interpretation of first-order flow. Five variables, readily related to the control of locomotion, are introduced. Two are temporal quantities like immediacy, two are angles, and the fifth is spin. I demonstrate (i) that the first-order flow plus any one of these determines the other four; and (ii) that this set of variables provides sufficient information for the precise control of manoeuvres such as docking in 3-D. The framework suggests ways in which visuomotor systems might exploit full first-order flow, and experiments that can test these ideas.

◆ **The influence of non-visual cues on steering behaviour**

G Wallis, J Tresilian, A Chatziastros<sup>¶</sup> (Human Movement Studies, University of Queensland, Connell Building, St Lucia, QLD 4072, Australia; <sup>¶</sup> Max Planck Institute for Biological Cybernetics, Spemannstrasse 38, D 72076 Tübingen, Germany; fax: +61 7 3365 6877; e-mail: [gwallis@hms.uq.edu.au](mailto:gwallis@hms.uq.edu.au))

In an earlier study of lane changing with a fixed-based simulator, Wallis et al (1997 *Perception* **26** Supplement, 100c) demonstrated that the manoeuvre comprises two, roughly antisymmetric phases. Failure to provide visual information midway through the manoeuvre prevents initiation of the second phase, causing the vehicle to career off the road. In a real car, the windscreen and bonnet provide a visual reference frame, and vehicle movement provides both visual and haptic information. To test the importance of these cues we repeated the earlier study using a driving simulator comprising a motion platform, car chassis, and all-round vision.

Subjects drove the length of a two-lane highway and were asked to change lanes to the left or to the right. Lane-changing was conducted either with full vision or in complete darkness. As in the previous study, in the absence of visual information a clear relation between direction of lane change and final heading emerged, owing to a failure to complete the manoeuvre ( $p < 0.002$ ).

We conclude that subjects have little appreciation of the effect movement of a steering wheel has on their heading, and that they rely heavily on intermittent visual feedback even in the presence of other sensory information.

## NOISE AND EFFICIENCY 2

### ◆ Efficiency and Gestalt

N Majaj¶, N Raizman#, E Kim§, C Christian‡, M Palomares¶‡, D G Pelli¶‡  
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The Gestaltists proposed several laws of grouping. For example, the Gestalt law of proximity says that things that are close together are grouped together.

We wanted to test the role of the Gestalt laws in letter identification. We constructed letters out of Gabor patches. We imagined that the observers will be able to identify these letters much more easily when they can group the Gabors together. We measured threshold contrast for identification of these letters in noise as a function of several variables: spacing, orientation, and phase. We computed efficiency by comparing human and ideal thresholds.

With the assumption that grouping contributes to efficiency, the law of proximity predicts that efficiency will fall as a function of spacing. Instead, we find that efficiency is a U-shaped function of spacing, first falling from 6% to 2%, only to rise again at the largest separation to 10%. It seems that efficiency drops in inverse proportion to the number of Gabors, but that proximity helps by grouping the Gabors into an effectively smaller number.

### ◆ Perceptual organisation and perceptual efficiency

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Perceptual organisation greatly affects performance in perceptual tasks, but little is known about *how* visual processing changes with the perceptual organisation of a stimulus. We addressed this question using a noisy cross-correlator model (Pelli and Farrell, 1999 *Journal of the Optical Society of America A* **16** 647–653).

We measured contrast thresholds for discrimination between two slightly warped Kanizsa squares embedded in noise. Stimuli were modally completed Kanizsa squares (Modal condition), amodally completed Kanizsa squares (Amodal), Kanizsa-like squares with luminance-defined edges (Real), and Kanizsa inducers arranged so as not to perceptually complete into a square (Fragmented) (Ringach and Shapley, 1996 *Vision Research* **36** 3037–3050). In each condition we determined observers' equivalent input noise, calculation efficiency, and classification images.

Classification images showed that observers used similar templates for Modal, Amodal, and Real stimuli, and a very different template for Fragmented. This template difference was reflected in calculation efficiency: efficiency was higher for Modal, Amodal, and Real than for Fragmented stimuli. Furthermore, efficiency was highly correlated with the similarity of an observer's template to the ideal observer's template. Equivalent input noise was the same in all conditions.

We conclude that perceptual organisation affects shape discrimination by changing the efficiency of observers' classification templates.

### ◆ Estimating the psychophysical receptive fields of edge detection mechanisms

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Orientation selectivity of neurons in primary visual cortex is believed to facilitate the detection of luminance edges. Here we examine the psychophysical efficiency of edge detection to elucidate properties of these early visual mechanisms.

In a 2AFC task, observers judged the polarity of a vertical luminance edge in additive white noise, windowed by a circular or elliptical aperture. In experiment 1 we measured contrast thresholds and efficiencies as a function of stimulus size for a circular aperture. Efficiency was found to decline dramatically as a function of aperture size. In experiment 2 we measured efficiency for elliptical apertures of equal area over a range of aspect ratios, elongated either along the edge or orthogonal to the edge. Results were found to depend upon the area of the stimulus.

For small stimuli ( $0.36 \text{ deg}^2$ ), efficiency was highest (30%–40%) for circular apertures, declining for elongation in either direction. For large stimuli ( $5.7 \text{ deg}^2$ ), efficiency increased dramatically as the aperture was extended along the edge, up to aspect ratios of 16 : 1, suggesting a narrowly orientation-tuned mechanism for the efficient detection of extended edges. These findings are related to receptive field structure of neurons in primary visual cortex of primate.

◆ **Multiple alternative mechanisms in the detection of collinear elements in noise**

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In recent experiments on the detection of a row of dots against a background of randomly placed dots we varied the number of collinear dots in the target and measured the background dot density required to mask it (Tripathy et al, 1999 *Vision Research* **39** 4161–4171). We concluded that the results do not fit any current theory about the method of detecting the target. Here we report additional experiments in which the arrangement of the masking random dots was varied, hoping that, by changing the resemblance between the masking dots and the target dots, we could change how effectively the target was masked. This expectation was fulfilled qualitatively, but the results also revealed some unexpected features of the system, and again we could not formulate a single theory to account for all the results. We now think that parallel and different mechanisms are used to detect the target in different circumstances. Parallel mechanisms used in such an opportunistic way make biological sense, but are difficult to model. The output from each mechanism would have to be assessed on each trial for its statistical significance for the tested hypothesis, and then combined appropriately with the equivalent outputs for the other mechanisms.

## SPECIAL SYMPOSIUM

### COMPUTATIONAL NEUROIMAGING OF THE HUMAN VISUAL SYSTEM

▶ **Computational neuroimaging: beyond modern phrenology**

G M Boynton (Department of Systems Neurobiology, The Salk Institute, 10010 N Torrey Pines Road, La Jolla, CA 92037-1099, USA; fax: +1 858 546 8526; e-mail: [boynton@salk.edu](mailto:boynton@salk.edu))

The majority of functional MRI (fMRI) studies employ a localisationist approach, which attempts to locate specific brain centres associated with various perceptual, motor, and cognitive functions. However, as equipment and techniques improve, more researchers are exploiting the continuous, quantitative nature of the raw fMRI signal to detect subtle covariations between the fMRI signal and various stimulus parameters.

I discuss recent applications of this quantitative approach to explore the mapping between the fMRI signal and parameters, such as position in the visual field (mapping retinotopy), stimulus strength and duration, and the behavioural performance from psychophysical tasks.

▶ **Using fMRI to infer the physiological properties of neurons**

A T Smith (Department of Psychology, Royal Holloway, University of London, Egham TW20 0EX, UK; fax: +44 1784 434 347; e-mail: [a.t.smith@rhbnc.ac.uk](mailto:a.t.smith@rhbnc.ac.uk))

fMRI has mainly been used to establish which brain regions are active when a subject performs a given cognitive task. In occipital cortex, fMRI can be used to assess physiological response properties of neurons, albeit averaged across sizeable neuron populations. An example is the estimation of average receptive field size in different visual areas.

Subjects viewed a flickering checkerboard ring which slowly and repeatedly expanded from the centre to the edge of the stimulus. The duty cycle of the fMRI response modulation obtained as the stimulus periodically traversed the receptive fields (RFs) of the cells in a given voxel was quantified by fitting a rectangular wave to the temporal response function. For small RFs, the duty cycle should simply reflect the proportion of time that the stimulus covers the RF. As RF size increases, the duty cycle is expected to increase, because activity will commence when the stimulus first enters the RF and subside only when the trailing edge leaves it.

The results show a gradual increase in RF size as eccentricity increases. Clear differences in RF size also occur among the various visual areas (V1 to V4). These results are discussed in relation to those of single-unit studies.

▶ **Linear and nonlinear models of brain activations and interactions**

C Buechel (Cognitive Neuroscience Laboratory, Department of Neurology, Hamburg University School of Medicine, Martinistrasse 52, D 20246 Hamburg, Germany; fax: +49 404 2803 5086; e-mail: [buechel@uke.uni-hamburg.de](mailto:buechel@uke.uni-hamburg.de))

Cortical organisation is based on the principles of functional specialisation and functional integration. Those two concepts exist at multiple spatial scales. For example, at a macroscopic

level, functionally segregated areas V1 and V5 are integrated within the dorsal visual stream. At a microscopic level, it is possible to infer the functional integration of (segregated) ocular dominance columns within area V1. At the macroscopic level, functional specialisation and integration can be tested with functional neuroimaging, by fMRI/PET or EEG/MEG.

A framework that allows making inferences on functional integration between brain regions from fMRI is presented. The common feature of all techniques within that framework is that they can incorporate second-order terms and therefore explicitly allow for contextual modulations. Two examples demonstrate how attention can modulate effective connectivity within the ventral and dorsal visual stream. Furthermore, these models can incorporate nonlinear modulatory (feedback) connections that can account for the increase in effective connectivity observed.

► **fMRI as tool for testing computational models of cortical processing: lessons from stereo**  
B T Backus (Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, PA 19104-6196, USA; fax: +1 215 898 7300; e-mail: [backus@psych.upenn.edu](mailto:backus@psych.upenn.edu))  
The response of neurons in cat and monkey primary visual cortex (V1) to binocular disparity is well studied. Yet there are disparity-sensitive neurons throughout the visual cortex. One hopes that fMRI can be used to help figure out what they are doing.

In recent fMRI experiments (Backus et al, 2000, in revision) fMRI has been used to characterise the response of different visual areas to a variety of stereoscopic stimuli. Different visual areas responded differently: V3A was relatively more sensitive to disparity, and V1 was relatively more sensitive to the presence of stimulus energy per se. This confirms that the neural composition of V1 and V3A is different, and shows that fMRI has some ability to distinguish between computational models of cortical disparity processing.

There remain significant challenges to the use of fMRI to decide between models that differ only subtly. fMRI measurements reflect the average activity of many neurons in a given area of cortex. There are multiple types of neuron, that respond differently, within an area. To be distinguished with fMRI, two models would have to take into account not only the relative responses of different neuron types, but also their relative numbers.

► **Mapping human ocular-dominance columns with 4 T fMRI**  
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Hirosawa 2-1, Wako, Saitama 351-0198, Japan; e-mail: [kcheng@mailman.riken.go.jp](mailto:kcheng@mailman.riken.go.jp))  
In the primary visual cortex (V1), neurons located in, and (to lesser extent) above and below layer IVc, are primarily driven by inputs from either the left or the right eye, and are organised in periodic left–right alternating stripes known as ocular-dominance columns (ODCs).

ODC provides an ideal model for testing the capability of functional magnetic resonance imaging (fMRI) at high spatial resolution. We have attempted to map ODCs in normal human subjects using high-field (4 T) fMRI with a segmented EPI technique. The differential responses to the left-eye or the right-eye stimulation could be reliably resolved in anatomically well defined sections of V1. The patterns of revealed ODCs conformed to those studied with cytochrome oxidase stain applied to the brains obtained after death from patients who had undergone enucleation of one eye many years before death (Horton et al, 1990 *Archives of Ophthalmology* 108 1025–1031). In addition, we have shown that mapped ODC patterns could be largely reproduced in different experiments conducted either within the same experimental session or over different sessions.

Our results demonstrate that high-field fMRI can be used for studying functions of living human brains at higher (< 1 mm) spatial resolution.

► **Time course of attentional modulation in the visual system**  
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Perceptual theories on vision claim that the visual system is hierarchically organised. Research on cortical connectivity indicates that the interaction of visual areas is even more complex. In support of this contention, the present paradigm provides evidence from a MEG and fMRI recorded spatial-attention task.

Subjects performed a symbolic cueing task that required complex visual discriminations at covertly attended locations. The results indicate that cue-related shifts of attention to different



locations (left or right visual fields) result in activity over frontal, parietal, and extrastriate areas. During the complex visual discrimination, additional attentional modulation appeared in different visual areas, including V1. Differential time courses were particularly revealing and are discussed in detail.

► **Event-related fMRI of cortical activity related to pro-saccades and anti-saccades**

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We compared the results of event-related fMRI to those of conventional block-design fMRI while subjects performed a saccade task. Five subjects viewed stimuli that were projected onto a screen attached to the back end of a MR scanner (Siemens Vision 1.5 T). Each trial started with a central blue fixation point, which changed colour and then disappeared. A colour change to green indicated that the subject should make a pro-saccade, whereas a change to red indicated that an anti-saccade should be executed. After a temporal gap (200 ms), a saccade target (1500 ms) appeared either 10 deg to the left or to the right of central fixation.

During task performance, the subject's eye movements were recorded by a newly developed infrared limbus-tracking technique (Kimmig et al, 1999 *Experimental Brain Research* **126** 443–449). Activation on each trial was measured ( $6 \times 128 \times 128$  voxels, 4 mm slices, TE = 66 ms, TR = 1.5 s) and averages of 10 trials were calculated. Analysis of eye-movement recordings determined the saccadic reaction time, and saccade amplitude and direction. The results indicate task-related activity in primary visual cortex, the frontal eye fields, and the supplementary motor area. We discuss the present results in relation to other studies on fMRI correlates of saccadic activity.

## SPECIAL SYMPOSIUM

### MODELS OF EARLY VISION: MECHANISMS CHALLENGED BY THE VISUAL ENVIRONMENT

► **Retinal responses to natural movies**

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The responses of retinal ganglion cells to natural stimuli were studied. Natural movie clips were made with a digital video camera from scenes around the Charles River in Cambridge, MA. These clips were played back to an isolated retina of the larval tiger salamander on a computer monitor, and spike trains from ganglion cells were measured with a multi-electrode array. Qualitatively, ganglion cells were silent most of the time and fired in precise firing events, similar to how they respond to flickering checkerboards.

A simple model of ganglion cell firing—the LN model, which convolutes the stimulus with a linear filter and follows it with a static nonlinearity—does a strikingly bad job. Responses to natural movies were compared with those to random flicker in order to investigate some of the sources of the poor performance of the LN model.

► **Fixed gain in human foveal cones**

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Superimposing on the retina two interference fringes of slightly different orientation creates illusory gratings (distortion products) at the site of a nonlinearity that lies proximal to the outer segments of foveal cones. The amplitude of the distortion grating is proportional to the product of the amplitudes of the fringes producing it. Then the visibility of the distortion grating is reduced in proportion to the square of any attenuation preceding the nonlinearity, but that of a single interference fringe of the same spatial frequency as the distortion grating is reduced in direct proportion to any such attenuation. The visibilities of both gratings are reduced equally by any attenuation following the nonlinearity. So the ratio of thresholds for the two kinds of gratings is proportional to any gain change preceding the nonlinearity.

Observations with static gratings of varying mean illuminance, and with gratings of constant illuminance flashed for 2 ms on backgrounds of varying illuminance, agree in limiting gain changes in the outer segments of foveal cones to negligible amounts over a 1000-fold change of illumination. Theoretical analysis shows that gain changes in foveal cones are not necessary to preserve discrimination over the normal range of light levels.

- **Coding of visual motion information from retina through primary visual cortex of the cat**  
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Directional selectivity in the cat visual system is first established in primary visual cortex, presumably through spatiotemporal correlations of low-level information. Measurements are reported of the temporal resolution for direction discrimination in cortical complex cells with the use of random pixel arrays alternately drifting in the preferred and nonpreferred directions. Data show that correlation is established very fast (within 100 ms). Motion sensitivity thus depends on similarity of response patterns on a relatively short time scale.

To study the available motion information at various time scales in retinal ganglion cells, the reproducibility of responses to different motion stimuli, including drifting sine gratings, moving random-line patterns, and movies of natural stimuli has been quantified. Differences in spike timings are quantified for repeated measurements, for the same cell, and among different cells. Next, a bilocal motion-detector model is used to assess the relevance of accurate spike timing for generating directional selectivity, and for determining the optimal time scale for spatio-temporal correlation. The results stress the importance of exact spike timing, rather than mean firing rates, for motion responses to natural stimuli.

- **The pleistochrome: optimal nonlinear codes and colour opponency**  
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The cone excitations are strongly correlated, because the cone sensitivities overlap, and also because naturally encountered spectral distributions are broad. But, as often noted, colour opponency can provide relatively uncorrelated measures of colour. The efficiency of a colour-opponent code depends on the distribution of cone excitations from natural colours. Although some fairly arbitrary assumptions have to be introduced, these considerations can provide a posteriori justification for the human colour code, including such features as the contribution of short-wavelength cones to redness.

In addition, since most natural colours are quite close to white, we can suppose that not only the direction, but also the thickness of the visual system's slicing of colour space fulfils principled criteria. Specifically, it is advantageous to slice the space more thinly near white than in the outlying regions. This is naturally done by a neural code in which responses are weak or absent to white, and increase in the usual nonlinearly compressed way as stimulus saturation increases. This supplies a rationale for opponent codes that is entirely independent of the decorrelation principle. A 'split range' code, where pairs of rectifying neurons represent complementary domains in colour space, increases efficiency further.

- **Adaptation and information transfer in the primate retina**  
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Two sets of experiments are reviewed. First, recent physiological data have shown that adaptation to changes in light level occurs at multiple sites through both outer and inner retina. In outer retina, horizontal cell recordings show that adaptation is both cone-specific and local, but falls short of Weber's law at low-photopic to mid-photopic levels. In inner retina, further gain-control mechanisms must be present, since cells of the magnocellular pathway achieve Weber's law, although those of the parvocellular pathway do not.

Together with other physiological studies, these results provide a framework for studying ganglion-cell responses to stimuli designed to mimic the temporal pattern of natural (chromatic) stimulation. Information transmission rates, and their partition to luminance and chromatic components of the stimulus, can be estimated for various cell types. The goal of these measurements is to establish and model how naturally occurring stimuli can be reconstructed on the basis of ganglion-cell spike trains.

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