Analysis of the Mechanisms of Human Visual Processing

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Education:

Institution	Degree	Conferred	Field of Study
University of Leicester, U.K.	B.A.	1966	Psychology
University of Aston, U.K.	M.Sc.	1967	Applied Psychology
University of Keele, U.K.	Ph.D.	1970	Communications

Reseach and Professional Experience:

1990-2003	Associate Director, Smith-Kettlewell Eye Res. Institute, San Francisco, CA.
1981-	Senior Scientist, Smith-Kettlewell Eye Res. Institute, San Francisco, CA.
1977-	External Doctoral Thesis Advisor, Dept. of Psychology, University of California, Berkeley.
1986-87	Adjunct Professor, School of Optometry, University of California, Berkeley.
1985-89	Visiting Professor, UCLA Medical Center, Jules Stein Institute.
1978-80	External Doctoral Thesis Advisor, Dept. of Psychology, Stanford University, Stanford, CA.
1978-82	Honorary Res. Associate, Institute of Ophthalmology, London, U.K.
1975-81	Scientist, Smith-Kettlewell Eye Res. Institute, San Francisco, CA.
1974-75	Res. Fellow, Dept. of Sensory and Perceptual Processes, Bell Laboratories, Murray Hill, NJ.
1973-74	Res. Fellow, Dept. of Psychology, University of Bristol, U.K.
1972-73	Assistant Professor, Northeastern University, Boston, MA. (Psychology Courses: Experimental, Introductory, History, Social Issues, Vision).
1972	Visiting Assistant Professor, Dept. of Psychology, University of California, Los Angeles, CA. (Course: Perception).
1970-72	Res. Fellow, Dept. of Psychology, Northeastern University, Boston, MA.

Dissertations

M.Sc. A study of the electrical activity of the brain in a simple decision task. University of Aston, Birmingham (1967). (Supervisor: G. Harding)

Ph.D. A psychophysical study of the dynamics of colour vision using wavelength modulated light. University of Keele, Staffs (1970). (Supervisor: D.M.Regan)

Honors:

The William A. Kettlewell Chair of Res. in Visual Science (2002-03).
The Catherine D. Kettlewell Endowed Chair (1995-96).
The William A. Kettlewell Chair of Res. in Visual Science (1984-85).

1982 Garland Clay Award, Editorial Council of the American Academy of Optometry for "Binocular Facilitation in the Visual-Evoked Potential of Strabismic Amblyopia" with P. Apkarian and D. Levi.

Post-doctoral Fellowships -
Dynamic analysis of the brain during intensity, real and apparent movement, and stereoscopic movement stimulation, Foundation Fund for Res. in Psychiatry, 70-481 (1970-72) Northeastern University, Boston, MA.
Visual Psychophysics (1973-74) University of Bristol, U.K.
Stereoscopic Vision (1974-75) Bell Laboratories, New Jersey.

Travel Fellowships:
Retinitis Pigmentosa Foundation (1978);
Wellcome Foundation (1980).

Grants Awarded (Direct Costs):
Etiology and Diagnosis of Visual Disorders, EY 2124 ($124,000, 1977-1980).

Normal and Abnormal Spatial Development in Children, EY 3622 ($222,000, 1981-1984).

Spatial Organization of Human Vision, EY 3884 ($224,000, 1981-1984) (with K. Nakayama).

Normal and Abnormal Spatial Development in Infants, EY 3622 ($504,000, 1984-1988) (with A.M. Norcia).

Temporal Visuogram as a Diagnostic Technique in Glaucoma, EY 6555 ($278,000, 1986-1991).

Temporal Mechanisms of the Retinal Light Response, NSF BNS-85-11099 ($103,500, 1985-1987).

Linearity and Non-linearity in the Retinal Light Response, NSF BNS-87-11217 ($213,000, 1987-1990).

Contrast, Disparity and Stereopsis, NIH EY 7890 ($390,000, 1991-1995).

A Generalized Autocorrelation Theory for Image Analysis, NIMH MH49044 ($545,000, 1991-1997).

Contrast, Disparity and Stereopsis, NIH EY 7890 ($640,000, 1995-2000).

Structure of the Human Cortical Depth Map, NIH EY 7890 ($1,509,754, 2001-2005).

Long-range Processing in Dorsal Occipital Cortex, NIH EY 13025 ($1,497,372, 2002-2006).

Core Grant for Vision Research, NIH EY EY6883 ($1,500,000, 2003-2008).

National Research Service Award Fellowship Program NIH EY T32-14536 ($1,000,000).

Editorships:
Associate Editor, Vision Res. (1999-)
Distributing Editor, Perception (1999-)
Feature Editor, Spatial Vision (1994-95).
Associate Editor, Perception & Psychophysics (1985-93).

Professional Society Memberships:
Vision Sciences Society
Association for Research in Vision and Ophthalmology
Psychonomic Society
Optical Society of America
Society for Neuroscience
Society of Photo-Optical Instrumentation Engineers

Grant Reviews:
National Institutes of Health
National Science Foundation
National Institute of Mental Health
Science Research. Council, Canada
Science Research. Council, Australia

Journal Reviews:
American Journal of Optometry and Physiological Optics
Bulletin of the Psychonomic Society
Investigative Ophthalmology and Visual Science
Glaucoma
Journal of Comparative Neurology
Journal of Experimental Psychology
Journal of the Optical Society of America
Nature
Perception
Perception & Psychophysics
Psychological Reviews
Quarterly Journal of Experimental Psychology
Science
Spatial Vision
Vision Research

Professional Society Activities:
Organizer, Fall Vision Meeting, San Francisco (2002)
Vision Sciences Society Review Panel (2002)
European Conference On Visual Perception Review Panel (2001, 2003)
Section Chair, Visual Psychophysics, ARVO (1997)
Chair, Noninvasive Assessment of the Visual System, OSA Topical Meeting.
        (1994-95)
Section Chair (Binocular Vision), Annual Interdisciplinary Conference (1978).

Committee Member: Committee to Evaluate "Investigative Ophthalmology and Visual Science".

Invited Colloquia:

Bell Laboratories; Brandeis University; Bristol University; Cambridge University; Columbia University; Dalhousie University; Harvard University; Institute of Ophthalmology, London; Johns Hopkins University; Massachusetts College of Optometry; Massachusetts Institute of Technology; McGill University; University of Montreal; New York University; University of Nevada; Northwestern University; Rochester University; Rockefeller University; Saint Andrews University; Stanford University; State University of New York, School of Optometry; University of Amsterdam; University of California (Berkeley, Los Angeles, Santa Barbara and San Diego); University of Chicago; Vanderbilt University; Yale University; York University

Festschrift Participations

Matthew Alpern
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Analysis of the Mechanisms of Human Visual Processing

Introduction

The processing of visual information is often said to occupy 80% of the human brain. While this estimate is of unknown origin and doubtful validation, it provides some concept of the importance of visual processing in the scheme of human brain function. Vast amounts of the information we need for reading, writing, computing, office work, factory work, driving, sports and entertainment are predominantly visual (although the deeper contextual and social meaning is often carried by the auditory speech channel). The past half-century has seen an extraordinary proliferation of studies on the nature of multifarious aspects of visual processing both in humans and in many other species.

At the time of my dissertation research at Keele, one could identify two streams of advances in the study of visual processing. One, emanating principally from The Netherlands and from the University of Cambridge, was the application of rigorous techniques of engineering systems analysis to basic visual processing of luminance and colour variations. The other, more general, approach was the study of complex perceptual variables such as motion, stereoscopic space perception, navigation and texture perception by a variety of techniques. One of these techniques was the application of the methods of noise, or stochastic generation processes, to perceptual processing, principally by Donald MacKay, founder of the Department of Neurocommunication at Keele, and by Bela Julesz at Bell Laboratories, NJ, USA. I was lucky, therefore, to have completed my doctorate at Keele and, subsequently, to have obtained a post-doctoral fellowship with Julesz.

On completing my doctorate, my goal was to employ the techniques of analytic systems analysis to the exploration of perceptual variables beyond those defined by luminance variations in the four receptor types (which was the major application of such techniques at the time). The idea was to pursue the rigorous analysis of quantifiable perceptual variables and their interactions up to the boundary with cognitive processing of the significance of the stimuli to the organism, which did not seem amenable to such an approach. This is the field is study that is now characterized as "mid-level vision", although it was viewed as rather high-level at the time.

Pathways of Analysis of Human Brain Function

There are many response pathways for the analysis of human brain function. To some extent, the predominant and most respected of these are the indirect ones: the anatomical, neurophysiological and biochemical analysis of the brains of lower species like the macaque monkey and the cat, since the most detailed information can be discovered in those species and then, presumably, extrapolated to human brain function. My view is that these brains are too dissimilar in many respects for the extrapolation to be very useful, and that it is obvious that such species lack large ranges of human neuronal processing (if only because they are no more than $1/10^{th}$ of the size of human brains). For this reason I have devoted my career to the study of explicitly human brain function. In this respect, there are six main pathways of information available:

Psychophysical A rich source of information is obtained from the measurement of the limits of detection and perception of sophisticated stimuli designed to stimulate particular subsystems of the neural processing array.

Anatomical The generic anatomy of the human brain has been well-known for over a century, so there is little more than can be derived from the study of anatomy alone.

Neuropathological One way to obtain information about the localisation of function in humans is to apply the psychophysical technique to patients with well-defined neuropathologies, when available. The visual loss with respect to normal may then be associated with the anatomical site of the brain disruption, as defined by an increasing variety of neuroimaging techniques.

Electrophysiological Another pathway from the neural signal processing is the microvolt graded electrical potentials recordable from the scalp. When averaged with respect to a stimulus event, they reveal temporal aspects of the underlying processing in the form of *visual evoked potentials*. Recent advances have increased the electrode coverage to as several hundred over the scalp surface.

Magnetoencephalic This approach uses supercooled magnetic sensors to pick up the magnetic component of the same graded neural potentials recorded by electroencephalography.

Functional brain imaging Beginning in the 1980s, whole-brain imaging techniques became available for use with humans, with submillimetre voxel resolution becoming available in recent years.

My own research over the past three decades has focused on four of these techniques: psychophysics, neuropathological studies, visual evoked potentials and fMRI imaging. Within these techniques, the main tool for characterizing visual function has been the systems analysis approach developed for the analysis of complex engineering systems. Two major themes have been pursued with these techniques – temporal aspects of visual processing deriving from my dissertation studies, and the extended investigation of stereoscopic space perception and also a corresponding spatial matching task – perception of symmetry. I have also ventured into related fields as the opportunity presented itself.

Techniques of Systems Analysis

Systems analysis consists of a powerful set of engineering tools designed for the characterization and analysis of complex linear and non-linear systems, such as electrical systems, mechanical systems, geological systems, atomic systems, and so on. Since it became increasingly obvious that the human brain is a complex electrical system, the main thrust of its investigations turned to cybernetics, the systems analysis of feedback control systems applied to the brain, soon after the cessation of World War II. Systems analysis may be divided into three subdivisions, each offering different advantages for the analysis of complex systems. In a linear, noise-free world, they would each provide the same answer, but in the presence of noise they emphasize different domains of system operation, and with nonlinear system one needs as many approaches as possible to triangulate the characterization of the system.

1. Impulse analysis This is a classical technique of activating the system with brief impulses, instantaneous steps and related stimuli. The response of a linear system to an infinitely brief impulse is termed the "impulse response," and can be used to characterize the response to *any* other stimulus by decomposing the stimulus into its constituent pulses and summing the responses to all those pulses. A strong test of the linearity of the system is to determine whether impulse-response summation can predict the response to an instantaneous step in stimulus intensity that remains indefinitely at the new level.

Electrophysiologically, measurement of the impulse response is straightforward. Psychophysically, it can be approached only through the summation function of the interaction between two brief pulse stimuli.

2. Steady-state frequency analysis This approach consists of perturbing the system with sinusoidal inputs spanning the usable frequency domain. For a linear system, the output must be a sinusoid of the same frequency, but its amplitude and phase characterize the visual processing that has taken place, which may be analysed under the concepts of linear filter theory. Again, for a linear system, the sinusoidal frequency response can be predicted as the Fourier transform of the impulse response, providing A strong test of system linearity. Any discrepancies reveal that there are dynamic parameter readjustments between the transient (impulse response) and steady-state (frequency-response) domains.

Electrophysiologically, measurement of the frequency response is again straightforward. Psychophysically, only the amplitude component of the frequency response can be measured, with the phase remaining indeterminate except through special techniques with limited domain of application In the fMRI technique, the limitations of the neural frequency response measurement is similar to that for psychophysics.

3. Noise analysis The third major approach to complex systems is through stimulation of the system with stochastic noise of some controlled random form – having binary, uniform or Gaussian amplitude distribution and a 'white', 'pink', 'blue' or narrowband characteristic of the amplitude spectrum in its domain of variation (not in the literal colour of its light). Noise is a broadband stimulus for which the readout of the temporal response provides the characterization of the input-output relations. It can also be used in interesting ways to establish correlations between different parts of the brain activation. Electrophysiologically, measurement of the noise response is again straightforward. Psychophysically, it can be approached only through masking and summation studies, as there is no direct readout of the noise time series (except for very slow processes).

The specific application of these techniques to a variety of basic and elaborated visual functions has been the thrust of my research enterprise. The presence of nonlinearities allows one to dissect the processing, or filter, characteristics of the mechanisms before and after the nonlinear stage, even in the case of a single output variable such as psychophysical probability of detection. The results are summarized in the logical sequence of the development of the ideas rather than in the dated order of their publication.

Significant Conceptual Advances

Science in general may be viewed as consisting of three types of activity – conceptual advances in the design of experiments, measurement of novel results in these new conceptual domains, and development of explanations in the form of mathematical or computational models of the underlying processes. The main text describes these functions in the research presented for this dissertation, but it is worth highlighting my conceptual advances in novel stimulus design that opened the way for much of the research described (since many of these have been subsequently adopted by the field with little explicit recognition).

Large-field light-emitting diode (LED) stimuli - allowing narrow-band wavelength stimulation of uniform fields with durations down to 1 microsecond.

Bit-stealing for full-resolution psychophysics and display – improved luminance resolution for typical 24-bit color graphics.

Clamping of the luminance gain – a procedure to inactivate the gain control mechanism that contaminated all previous measurements of the luminance transducer nonlinearity.

Stimuli scaled to cone density – a novel probe of eccentricity variations scaled to the retinal cone density, to determine any further deviation from this scaling by subsequent neural projections.

Realization of a model cortex – analogous to the model eye of physiological optics, allowing the easy design of stimuli equated for cortical area of activation.

Smooth time-windowing of brief large-area stimuli - to eliminate transient artifacts and frequency adaptation, to record the highest known human temporal frequency resolution of 107 Hz.

Transient-doublet and smoothed-lifetime dynamic noise stimuli - for cyclopean stereoscopic depth stimulation (invisible to monocular view), targeting the human magnocellular and parvocellular stereoscopic pathways, respectively.

Ultra-brief temporal stimuli – specialized waveforms whose perceptual time course is shorter than that of the briefest physical flash of light

Electronic sweep VEP – parameter sweep in 10 sec with overlapping analysis bins to allow measurement of visual acuity and other visual functions in preverbal infants (Developed independently of other forms of sweep VEP by D Regan).

Two-dimensional spatial modulation – stimuli of sinusoidal modulation in two orthogonal dimensions, producing second-order modulation of the contrast envelope.

Biased Gabor functions – sinusoidal modulation in a Gaussian envelope with a half-amplitude Gaussian luminance bias to generate either all-bright or all-dark bars, for the measurement of sign-specific nonlinearities.

Stereogratings – sinusoidal corrugations of the binocular disparity of a random-dot field.

Autostereograms – single-image random-dot patterns that could be free-fused to form a binocular disparity image of any definable surface.

Cyclopean stereomotion stimuli – disparity planes defined in dynamic noise and modulating in disparity to form cyclopean z-axis stereomotion, with no visible monocular cues to the disparity change.

Cyclopean luster stimuli – dynamic-noise fields defining dichoptic correlation, decorrelation and anticorrelation down to frame durations of 1.5 msec, for the study of prestereoscopic processes of binocular combination.

Disparity Gabor functions - sinusoidal modulation of random disparity in a Gaussian disparity envelope for the measurement of stereoscopic mechanisms of disparity profile analysis.

Kinetic gratings – sinusoidal corrugations of the motion vector field of a random-dot array.

Research Description

I. Temporal processing of luminance information

The most basic application of systems analysis techniques is in the temporal processing of luminance variations in a uniform patch of light Pioneered by Ives (1922) and de Lange (1958), these techniques revealed that human vision operates linearly at high frequencies. Tyler (1991a) developed a rapid automated staircase method of measuring the temporal tuning function that was robust to error and have a stable distribution across temporal frequency. Anstis, Kontsevich & Tyler (1999) developed a direct observational method of measuring the temporal tuning function by exhibiting a two-dimensional array of sinusoidal temporal frequencies and modulation depths on a computer screen. A basic issue in temporal processing is the complete reconstruction of the human temporal impulse response by measurement of the phase as well as the amplitude component of the Fourier representation. Tyler (1992a) and Tyler & Kontsevich (1993) developed the first successful approach to measurement of the phase function, providing a complete impulse response reconstruction for the long-wavelength cone pathway. Contrary to most previous assumptions, it was a triphasic function, in accord with two-pulse estimates by Roufs & Blommaert (1981) and Manahilov (1999) by different approaches. This triangulation gives an unorthodox view of human temporal processing, which has yet to be incorporated in most vision models.

Tyler (1975a) evaluated flicker sensitivity as a function of luminance level and unearthed the nonlinear effects of two distinguishable subsystems in the frequency response to sinusoidal luminance flicker. The analysis showed that the two subsystems exhibited different nonlinear behaviors as a function of mean luminance level, characteristic of the magnocellular and parvocellular subsystems of the retinal response. Tyler & Liu (1996) went on to use the temporal response as an index of the operation of luminance gain control. The normal variation in two-pulse temporal summation time-course in a small (7') test field was clamped by the presence of a fixed-luminance surround, implying that the luminance gain control mechanism had been inactivated. This procedure allowed the first accurate estimation of the nonlinearity luminance transducer function, which proved to be a hyperbolic compression function rather than the logarithmic function commonly assumed.

The role of systems with different temporal characteristics was studied in a pulse-summation study of sinusoidal spatial modulation by Gorea & Tyler (1986). Contrary to previous work on temporal summation, realistic computational modeling revealed that the summation was linear at short durations and could be predicted by varying the weight of temporal inhibition as a function of spatial frequency, without any other change in temporal parameters. The model employed the novel concept of a limited temporal integrator for probabilistic summation over time, explaining the paradoxical reduction in sensitivity often observed at long pulse durations. Fulton, Hansen, Yeh & Tyler (1991) showed that the temporal summation function in human infants was substantially prolonged relative to that of adults. Lawton & Tyler (1994) then extended the issue of temporal processing to the domain of suprathreshold contrast processing by the contrast-

masking paradigm. Under all test conditions, there was no detectable difference between as spatially in-phase and a spatially quadrature mask, implying that the masking was entirely due to gain control rather than transducer nonlinearities (since the quadrature mask would be invisible to the dominant population of simple cells responding to the test grating).

The temporal characteristics of the visual evoked potential (VEP) response recorded from the occipital scalp region was studied in conjunction with the properties as a function of contrast, spatial frequency and retinal eccentricity. Stimulus-evoked activity could be found up to 90 Hz for uniform-field stimulation (Tyler, Apkarian & Nakayama, 1980), an about 50 Hz for pattern reversal stimuli (Tyler & Apkarian, 1982), confirming the magno/parvo split of the psychophysical analysis. In addition, the activation levels supported the concept of a 'model' magnification function in which equal cortical areas of about 1 sq cm received projections from octant annuli doubling in eccentricity from the central 1/4° - 1/2° out to the most peripheral 32° - 64° (Tyler & Apkarian, 1982). This model cortex is extremely useful for approximation analysis of the effectiveness and homogeneity of standard stimuli. For example, few vision scientists realize that a stimulus of only 4° radius projects to about half of the cortex in each visual projection area, and contains cortical scaling of about 16:1 within it.

In a series of papers, the temporal processing of local retinal regions with stimulation of equal numbers of one photoreceptor type – long-wave sensitive cones. For this purpose, an accurate equation was developed to fit the cone density reduction (and far peripheral increase) with eccentricity (Tyler, 1985a; 1997a). Sensitivity was established as a function of temporal frequency, retinal location and mean luminance (Tyler 1985a, 1987a; Tyler & Hamer, 1990, 1993). No previous study had isolated all these variables and the results were surprising – rather than degrading with eccentricity, temporal resolution almost doubled from the central foveola to the far periphery, and the maximum resolvable frequency f_L as a function of mean luminance L accurately followed the Ferry-Porter Law of $f_L = k.\log L$ under all conditions. In the process of these studies, we determined that the region of maximal retinal sensitivity was determined to lie at about 40° retinal eccentricity (except near the upper vertical meridian), and recorded flicker detection to 107 Hz, the highest frequency ever reported. Such high temporal frequency responses are completely incompatible with the temporal characteristics recorded from human cones *in vitro* (Schnapf, Kraft & Baylor, 1987), implying that there are serious deficiencies in the physiological paradigms for cone recording.

The specificity of these response characteristics in human cones prompted an examination of the literature on direct recording of the cones of non-human primates. In addition to other problems, we found that the analytic modeling of the data by Schnapf & Baylor (1989), if taken literally, was inaccurate by six orders of magnitude. This lapse led to the development of an analytic model for cone function that fully explained the details of the response onset as a function of luminance within about 0.1 log units accuracy (Tyler & Hamer, 1995; Hamer & Tyler, 1995, 1996). (Thus inspired, my coauthor in this endeavor has gone on to collaborate with many of the key photoreceptor

biophysicists in developing the most complete analysis of rod and cone function now available.)

II. Clinical applications of temporal modulation sensitivity

A study of the development of temporal processing throughout the life span, as a baseline for clinical evaluations, involved temporal frequency response data from 1400 observers (Tyler, Clarke & Hawker, 1988; Tyler, 1989a). This large subject pool allowed analysis as fine as two-year age bins, which is probably unique in the annals of research into visual aging. The long-wavelength test target isolated sensitivity variations from neural, as opposed to optical, sources. Two complementary processes of neural development were identified – a uniform increase in visual sensitivity from age 5 to age 15, and a progressive high-frequency decline from age 15 to 70. However, the latter decline corresponding to a slowing of the derived temporal impulse response of only 15%, so temporal sensitivity is one of the visual processes most resistant to aging effects.

In conjunction with the basic studies, the concept of systems analysis was applied to the analysis of visual deficits in glaucoma (Tyler, 1981a), showing that losses of the order of one log unit in specific temporal frequency bands could often be in patients showing normal Goldmann field sensitivity. The glaucomatous lesion of the optic nerve showed a characteristic loss of sensitivity around 20 Hz, presumably reflecting reduced magnocellular function (Tyler, Hardage & Stamper, 1994). The same form of loss could be seen in association with the variation in intraocular pressure in normal population (Tyler, Ryu & Stamper, 1984), and the degree of loss was predictive (90%) of progression to Goldmann Field loss within five years (Tyler, Stamper & Hawker, 1992). Other optic neuropathies showed residual parvocellular losses focussed around 1 Hz in both eyes after recovery from a magnocellular deficit in the affected eye (Tyler, Katz & Hardage, 1994). A study of nicotine, alcohol and progesterone intake in the normal population (Tyler, 1991b) showed that only the first of these had a significant (though small) impact on flicker sensitivity.

In retinitis pigmentosa of one genetic form, Tyler, Ernst & Lyness (1984) found a uniform form of temporal sensitivity loss that could not be explained either by an effective luminance reduction or photoreceptor drop-out. An extensive survey of patients with retinitis pigmentosa (Tyler & Ernst, 1986) gave the remarkable result that numerous different genetic subtypes of the disease showed distinctive patterns of temporal loss, even though no other clinical differentiation are known (except for time of onset). Autosomal dominant patients showed a uniform loss over frequency, regardless of the severity of the loss. Autosomal recessive patients showed a progressive loss at high frequencies and even a gain in sensitivity relative to normal at the lowest frequencies. X-linked patients showed an extremely steep cut in temporal function around 15 Hz, while the X-linked carriers showed a significant loss despite normal visual function on clinical tests. Patients with mild Usher's syndrome, although genetically autosomal recessive, showed a unique pattern of temporal loss with supernormal sensitivity at high frequencies, while more severely affected patients showed a pattern of high-frequency loss more reminiscent of glaucoma (Tyler, 1991c). Patients with optic nerve head drusen

and acute papilledema both showed predominantly low-frequency losses implicating the parvocellular system alone (Tyler, Katz & Hardage, 1994).

III. Temporal processing of colour information

In the temporal processing of colour, Regan and I confirmed de Lange's (1958) result that wavelength had little effect on temporal luminance processing but we showed that the temporal characteristics of equiluminant chromatic modulation varied dramatically with mean wavelength, measured with both sinusoidal and pulse test probes (Regan & Tyler, 1971a,b,c). We developed a circuit model of the temporal properties of opponent processing that accounted for these results Subsequent studies of the isolated cone pathways (Hamer & Tyler, 1992) revealed that the Ferry-Porter relation describing the temporal response with luminance had a time-constant 25% faster for the middle-wavelength than for the long-wavelength pathway (a result also found but unrecognised in four previous studies). The difference could be cancelled by appropriate luminance adjustment at any given frequency, opening serious questions as to whether luminance should be defined (as is current practice) by heterochromatic flicker photometry. An analysis of cone thresholds (Tyler & Liu, 1992) suggested that 'green' cones must be more prevalent than implied by other techniques.

In characterizing the temporal sensitivity for chromatic motion, Tyler & Cavanagh (1991) showed that the temporal characteristics of lateral oscillatory motion in chromatic sensitivity were lowpass, similar to those for chromatic flicker. This property contrasted with the sensitivity for luminance motion, which was bandpass, similar to that for luminance flicker. They suggested the novel hypothesis that the chromatic opponent pathways have co-opted the lateral inhibitory connections used for inhibitory sharpening of the tuning function, making lateral opponent connections across cone types in order to generate the color code, and losing the inhibitory property in the process.

IV. Temporal and spatial processing of lateral motion

Beyond the basic retinal processing of luminance and colour stimuli lies the domain of perceptual processing of more complex stimulus properties. The simplest of these may be motion of a line. Observation of a line alternating between two positions revealed two antagonistic forms of apparent motion – standard phi motion of the lines, and what may be termed omega motion of a patch of background alternately covering the two lines now seen as stationary (Tyler, 1972). Although previously described, the two processes were now shown to have inherently different temporal characteristics, implying separate motion processing mechanisms rather than different inputs into the same processing mechanism.

The temporal and spatial properties of motion processing were analyzed for single direction-selective neurons in a collaborative study (Jagadeesh, Wheat, Kontsevich, Tyler & Ferster, 1997). Intracellular patch-clamp recordings were obtained from single cells in layers 3 & 4 of area 17 of cat visual cortex in response to sinusoidal counterphase-modulating gratings at a range of contrasts and spatial phases at the optimal spatial and temporal frequency. The intracellular neuronal responses could be described as arising

from accurately linear summation between two spatial subunits with a temporal phase shift between their highly nonlinear responses.

It has often been claimed that the periphery is more sensitive to motion than is the fovea. This claim was borne out in terms of generic temporal processing (see Section I) but had not been evaluated in terms of specific motion stimuli. Tyler & Torres (1972) used oscillatory motion of lines to measure motion acuity and found that the periphery is dramatically *less* sensitive to motion at all temporal frequencies, a result that has yet to be incorporated into textbook accounts. Nakayama & Tyler (1981) looked at the spatial interactions between pairs of lines oscillating in counterphase (making and expansion/contraction gap figure) and an interposed pair of stationary lines. Motion was induced from the moving to the stationary lines, establishing for the first time that induced motion is a direct cortical phenomenon rather than being attributable to eye-movement tracking of the inducing stimulus. The frequency response of the induced lateral motion showed a reduced sensitivity together with a high temporal frequency limitation, implying that the induction process was both distinct from and slower than the core motion generation process.

Nakayama & Tyler (1979) extended the motion analysis to spatial and temporal properties of line and random-dot motion fields. A field of random dots was given a sinusoidal corrugation of motion shear, generating the first motion-defined gratings. Because the relative position of particular dots was indistinguishable, random-dot motion stimuli provide a pure probe of motion processing, whereas motion of line stimuli include a dominant position cue. Motion detection thresholds for line stimuli were invariant with temporal frequency (below some integration limit), as a result of the presence of the *position* cue, but those for random-dot motion degraded as temporal frequency was reduced because they were governed solely by a *velocity* limit (the position cue having been silenced). For line stimuli, the threshold degraded at low spatial frequencies because it was limited by the minimum spatial gradient in the sinusoid. For random-dot fields, the threshold improved over the same range (below 2 cy/deg), implying that greater spatial integration was required to extract the global motion signal from the field of dots when local position cues were masked.

Ramachandran & Gregory (1980) showed that there is a deficit in global motion processing for coloured random-dot stimuli at the equiluminance point (although the local dot correspondences still seemed to support motion). One may ask whether this equiluminant behavior is due to a loss in the ability to cohere the global configuration in the spatial noise stimuli that they used, or is a fundamental property of the motion processing system. Cavanagh, Tyler & Favreau (1984) consequently applied the paradigm of sinusoidal drifting gratings in homogeneous perifoveal retina to show that the perceived velocity near equiluminance could slow markedly or even drop entirely to zero (stationarity). This *motion-slowing* of colored stimuli at equiluminance implies that motion is purely a property of the luminance response, and many studies of equiluminant motion processing and its deficiency in the colour-dominated parvocellular system have ensued.

V. Temporal processing of stereomotion

Tyler (1971) took the temporal line motion approach a step further to compare the frequency response of stereomotion, derived from lines oscillating in spatial counterphase in corresponding locations in the two eyes. The temporal sensitivity for stereoscopic depth motion (stereomotion) had much the same form as for lateral motion, implying that the stereomotion system was no slower than the lateral motion system. Surprisingly, however, at all temporal frequencies the sensitivity for stereomotion was lower than for its monocular constituents, despite the fact that twice as much motion information was being presented to the two retinas. This *stereomotion suppression effect* was attributed to the mechanism of binocular fusion, since the same sensitivity reduction was found for vertical disparity modulation of horizontal lines (Tyler, 1975b). The same stereomotion suppression behavior was found for transient pulses of disparity displacement, but not for transient presentations of disparate lines in an empty region of the retina (Tyler & Foley, 1974; Foley & Tyler, 1976). Stereomotion suppression was degraded in the peripheral visual field and eliminated at low temporal frequencies by the presence of a paired stereomotions in counterphase at nearby spatial locations (Tyler, 1975b). Such spatial interactions in stereomotion processing are amplified by the recent finding of stereomotion induction from a stereomoving surround into a stationary central regions (Likova & Tyler, 2003a,b). The induced stereomotion was robust, showing almost linear degrees of cancellation with physical stereomotion in the target region. An analytic model of the details of the cancellation behavior as a function of the relative disparity between target and surround revealed a complex of dynamic interactions mechanisms involved in the motion interaction processing, including reference frame, elastic rebound and dynamic rigidity principles.

Norcia & Tyler (1984) and Norcia, Sutter & Tyler (1985) showed for the first time that purely stereoscopic, or cyclopean, stereomotion mechanisms could be activated by specification of a random-dot plane in dynamic noise that alternated between two disparities. (Julesz, 1971, had used cyclopean stereoscopic targets but had only investigated their lateral motion.) These stereomotion stimuli allowed the study of stereomotion characteristics to be extended to purely stereoscopic stimuli with no visible monocular events. Electrophysiological measures showed a large temporal resonance at about 3 Hz, falling rapidly to a limit near 5 Hz that matched the psychophysical limit for perceiving stereomotion between the two disparities. Beyond this level, hints of disparity change were perceived and recordable signals obtained up to about 15 Hz in both cases, beyond which frequency the stimulus was indistinguishable from two stationary transparent planes.

The processing of object rigidity could also be investigated in the context of stereoscopic motion. Using a stepped-pyramid figure in a random-dot stereogram, Tyler (1974a) showed that oscillating the figure in depth around a vertical axis induced a perceived relative motion between adjacent steps of the pyramid, despite the impossibility of relative motion in the physical stimulus plane. This perceived motion was attributed to the operation of an object constancy mechanism based on the expectation that motion of real objects is typically rigid. The failure of this rigidity assumption would be interpreted as relative motion between the 'steps'. The temporal frequency response of the perceived

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relative motion was both less sensitive and slower than for the primary depth motion of the object, revealing the temporal limitations of object constancy processing.

VI. Spatial processing of luminance information

By the time I entered the field, the study of spatial processing of luminance variations was already well advanced. However, I published the first investigation of two-dimensional spatial processing of sinusoidal variations (Tyler, 1978a). The two dimensions were not separable in terms of sensitivity, and this stimulus allowed me to make the first observations on second-order properties of spatial modulation (modulated gratings). This concept was expanded into a series of papers on the spatial summation of Gabor patches. Polat & Tyler (1999) studied the summation of the length (baguettes) and width (tigertails) of elliptical Gabor patches. Summation extended over several cycle units of length but only one cycle of width. Chen & Tyler (1999) found that, in foveal view, summation occurred over several Gabor patches regardless of phase, implying that the summation mechanism is second-order (contrast energy summation). In the periphery, on the other hand, summation was much greater for in-phase Gabors than for alternating counterphase Gabors, implying that peripheral summation is a first-order process. Liu, Tyler & Schor (1992) examined the summation of low-contrast gratings of different orientation in the two eyes, finding full dichoptic summation into a grid at all spatial frequencies, rather than binocular rivalry. Tyler & Chen (2000) extended the summation concept to complex stimuli such as faces, finding that there is full linear summation of face information up to about 3° diameter, beyond which the face information does not play a part in detection. The implication is that there is only a single matching filter for dace detection, whereas noise detection improved more gradually at all sizes.

To make such measurements psychophysically, one needs resolution of the luminance variations down to contrast levels of the order of 0.1% (three $\log_{10}$ units); for flexible investigation, this resolution needs to be available at all luminances and chromaticities. Even today, most video monitors have 24-bit color graphics, which can provide luminance modulation down to only about 1%. Tyler, Chan, Liu, McBride & Kontsevich (1992), Tyler & McBride (1996, 1997) and Tyler (1997) described a "bit-stealing" method of jittering the contribution of the color channels below perceptual threshold for each pixel, to improve luminance resolution by about a factor of 10 for both grey-scale and full-color images. This method is incorporated in a software package (Morphonome Image Psychophysics) that is in use in many vision laboratories around the world.

Through consideration of the tuning properties of a multiple channel system, Tyler, Chen & Kontsevich (2000) realized that there was much confusion in the literature about how the signals from arrays of channels could combine to form the system response, and how this behavior could be revealed under Signal Detection Theory with noise-limited choice behavior. They therefore developed, for the first time, an extensive analysis of the channel combination rules under various detection models within Signal Detection Theory. These analyses have formed the basis for a book under contract with Lawrence Erlbaum Associates, entitled *Principles of Vision Science*, which is intended to set the

theoretical framework for the next phase multiple channel analysis in psychophysical, neurophysiological, EEG and fMRI analyses of sensory function.

Chen & Tyler (2001) examined the suprathreshold spatial integration processes by looking at the interactions between flanking Gabors and the contrast discrimination behavior of a central test Gabor target. The interactions were phase-insensitive and could not be explained by a long-range inhibition model. Instead, a *sensitivity modulation* model was developed that has now been adopted by many groups studying long-range interactions. Chen & Tyler (2002) extended these results as a function of flanker orientation, finding that the flanker interactions are orientation-selective, in contrast to the orientation-invariant predictions of the Carandini & Heeger (1994) model (see also Carandini, Heeger & Senn, 2002), and again support the sensitivity modulation concept.

VII. Spatial-temporal processing of luminance information and its development in infants

Corwin, Volpe & Tyler (1976) showed that positive and negative afterimage durations depended differentially on spatial frequency. Tyler (1978b) observed unexpected structure in the simple afterimage of a luminance grating. With this homogeneous pattern as a probe, it became obvious that the afterimage showed pronounced fluctuations between a macula-sized ellipse about 3° diameter and the remainder of the stimulated field, as though the two regions were fluctuating independently in separate cortical regions. Tyler & Nakayama (1981) observed spatial-frequency interactions after prolonged observation of counterphase flickering gratings. A fine-grain aftereffect was induced throughout the peripheral field, with and orientation aligned to the grating but very high, invariant spatial frequency. Tyler (1974c) published a model of the spatial-frequency doubling of temporally modulated sinusoidal gratings, which formed the first observations on second-order visual processing. This second-order process was later incorporated by Kelly (1981) into his comprehensive model of spatiotemporal visual processing.

Electrophysiologically, the study of spatiotemporal modulation with counterphasing sinusoidal gratings revealed a rich landscape of mechanisms tuned narrowly in both spatial and temporal frequency (Tyler, Apkarian & Nakayama, 1978; Nakayama, Apkarian, Mackeben & Tyler, 1988). These mechanisms were also specialized for contrast and binocularity, with at least 6 different patterns of contrast function (accelerating, saturating, two-limbed and contrast-tuned) and binocular interaction (from independence through linear summation to facilitatory) (Apkarian, Nakayama & Tyler, 1981; Nakayama, Apkarian & Tyler, 1982).

Much of this variety of nonlinear contrast transducer functions was also revealed psychophysically as a function of spatial frequency of biased Gabor functions by Tyler, Chan & Liu (1992) and Kontsevich & Tyler (1999a). Both studies also showed marked asymmetries in the contrast transducer for luminance increments versus decrements, implying that low-frequency gratings are detected by their dark points but high-spatial frequency gratings by their bright points. The cortical circuits underlying this degree of

diversity and specificity remain unknown, but may soon be amenable to analysis with current source-localization techniques.

In the course of this work, I realised that one could measure visual acuity and other limits of visual processing by recording the VEP as the stimulus was swept at an appropriate rate from a condition of high visibility through the threshold level. The point at which the response disappeared into the noise would provide a measure of visual acuity or threshold for the swept stimulus variable (Tyler, Apkarian, Levi & Nakayama, 1979; Tyler, 1982; Norcia, Clarke & Tyler, 1985). This technique proved to be of great value in studies of preverbal infant vision, providing measures of the developmental time course of visual acuity (Tyler, 1982a, 1991; Norcia & Tyler, 1985a,b), monocular visual acuity (Hamer, Norcia, Tyler & Hsu-Winges, 1989), contrast sensitivity (Tyler, 1982a, 1987, 1991; Norcia, Tyler & Hamer, 1988; Norcia, Tyler, Hamer & Wesemann, 1989; Norcia, Tyler & Hamer, 1990), validation of the match between sweep VEP and psychophysical measures of contrast threshold (Allen, Norcia & Tyler, 1986; Norcia, Tyler & Allen, 1986; Tyler, 1993) and the differential time course of central and peripheral visual acuity (Allen, Tyler & Norcia, 1996). In addition, the swept acuity method was of great value in showing that acuity develops according to the duration of exposure to visual stimulation in normal prematurity (Tyler & Norcia, 1986), and in defining the abnormal acuity and its recovery in retinopathy of prematurity (Norcia, Tyler, Piecuch, Clyman & Grobstein, 1987). From these studies, Anthony Norcia and I designed a swept-parameter VEP system for digital infant visual assessment (the DIVA system) that is now in widespread use in vision laboratories around the world.

VIII. Systems analysis of spatial position processing

The limit of spatial vision is its vernier acuity, which is a hyperacuity because it is about an order of magnitude finer than the diameter of an individual foveal cone (Westheimer, 1987). As the first application of systems analysis methods to vernier acuity, Tyler (1973a) measured the detectability of sinusoidal position modulation in a line target, finding that sensitivity peaked at about 3 ripples/deg and degraded at both lower and higher ripple frequencies. The sinusoidal paradigm was relevant because the periodic vernier acuity improved substantially as the number of cycles of any given ripple frequency the increased, relative to resolution for a single cycle. The periodic vernier acuity paradigm also exhibited a strong oblique effect (Tyler & Mitchell, 1977). Line stimuli with a sawtooth rather than a sinusoidal waveform show a strong tilt illusion of the whole line with respect to the physical mean orientation (Oyama, 1975). Tyler & Nakayama (1984) showed that the tilt went in one direction (resembling the Fraser illusion) for small sawtooth angles and the opposite direction (resembling the Zöllner illusion but without a separate test line) for large angles. They developed a computational model of the fine-to-coarse orientation interactions that are needed to account for these data.

One may also consider position processing in terms of the phase of a sinusoidal grating Tyler & Gorea (1986) showed that the temporal integration time for phase discrimination was longer than for simple contrast detection, implying that a further stage of spatial is required to extract the phase information. Klein & Tyler (1986) developed a complete

framework for the analysis of phase coding through the autocorrelation function. Kontsevich & Tyler (1998) extended the issue to the discrimination of position in sampled images (of a Gaussian bar). Remarkably, once the sample spacings exceeded the local filter limit of 3 arc min specified by Watt & Morgan (1983), there was no degradation in position discrimination until the Nyquist limit of about 3 samples was reached. Four and 32 samples supported equally good performance, for example. It was concluded that localization operated by means of a spatial interpolation mechanism that could use no more than a few samples-worth of information, however much was available.

IX. Spatial processing of stereopsis

One may apply the concept of the sinusoidal systems analysis to stereoscopic depth perception in two basic ways. One may either ask about the filter characteristics of the luminance-domain inputs into the disparity-computation or one may evaluate the disparity-domain modulation characteristics of depth perception *per se* In terms of the luminance-domain inputs. In the luminance domain, Blakemore & Campbell (1969) had used the steady-state VEP to measure the neural orientation tuning of the spatial channels to have a half-width of about 12 deg. Tyler & Apkarian (1985) analyzed the orientation tuning of the binocular channels, finding a tuning of only about 3 deg around the vertical orientation, substantially wider at other orientations. Kontsevich & Tyler (1994) evaluated the channel structure for stereoscopic processing and concluded that there were multiple spatial-frequency-tuned channels at 1° eccentricity, but the lowest frequency at which any channel peaked was 2.5 cy/deg; all depth processing below this spatial frequency was supported by this 2.5-cy/deg channel. Apparent tunings below this spatial frequency could be explained by the effective contrast tuning within the same channel. (Schor, Edwards & Pope, 1998, subsequently found a single low-spatial-frequency channel specifically for transient stereopsis that exhibited the same behavior.) Tyler & Sutter (1979) evaluated the stereoscopic slant obtained when viewing sinusoidal gratings of different spatial frequencies in the two eyes. They found that this perceived depth persisted even when the gratings were drifting rapidly in opposite directions in the two eyes, inducing motion rivalry, and concluded that the disparity of interocular spatial frequency differences ('diffrequency') was a separate stereoscopic depth mechanism from that for positional disparity.

To study the filter properties of disparity processing *per se*, Tyler (1973b, 1975c) applied the concept of sinusoidal disparity ripple in binocular line targets, showed that stereoscopic sensitivity was severely limited relative to monocular sensitivity at high frequencies, although equally good at low frequencies. Under no conditions could sinusoidal ripple be resolved beyond about 3 cy/deg (while luminance resolution is about 30 cy/deg at the same luminance levels). The brain is configured to economize on the circuitry that would be required to provide stereoscopic resolution to such high levels. Moreover, there was an upper limit to both binocular fusion of the stereoscopic stimulus and the *amplitude* to which depth variations could be resolved. These two upper limits scaled with spatial ripple frequency in a uniform manner, when a maximum gradient of disparity change was reached. That gradient corresponded to a 45° angle between the monocular components of the disparate stimuli in the two eyes. Prior to these studies,

there was no indication of any such limitations in the spatial form of disparity processing. These limits were shown to be similar to those for motion by Tyler (1991d).

The systems analysis approach predicts that corresponding limitation would be found as a function of the width of spatial pulse stimuli. This prediction was tested and validated by Tyler (1975c), as was the effect of square and triangular waveforms in comparison with the sinusoidal waveform. These tests revealed that the gradient limit was implicit in the stimulus, in that perceived depth was limited by the point at which the *minimum* gradient implied by the stimulus reached a *maximum* value (since a square wave had infinite gradient, and therefore could generate no depth if the limitation was based on the physical gradient present in the stimulus). The upper spatial frequency limit and the gradient limit were again validated for sinusoidal disparity modulations in random-dot stereogram stimuli by Tyler (1974d, 1991e). Despite the absence of any contours or monocular information about the depth form (Tyler & Raibert, 1975), the same limitations were obtained, indicating that these were characteristics of the disparity-processing system unrelated to any properties of the monocular processing of periodic vernier acuity. In particular, the low frequency fall-off in sensitivity implied the operation of disparity-specific lateral inhibition, analogous to the spatial inhibition in the luminance system but operating at the level of cortical disparity processing rather than retinal luminance processing.

Tyler (1975d) took the question of the processing of depth form one step further by testing for aftereffects of adaptation to cyclopean gratings. Aftereffects of both orientation and spatial frequency were found, implying that there are mechanisms tuned to the structure of the cyclopean form, invisible to luminance processing of the retinal images. Tyler & Kontsevich (2000) extended the issue of the filter range for stereoscopic processing to the two-dimensional structure of the filters at each spatial frequency of disparity modulation. Beginning with a Gabor patch with a Gaussian envelope of one cycle width (at half-height) in each direction, we measured the improvement in detection threshold as a function of width in each direction (elliptical Gaussian envelopes), and in both directions together (circular Gaussian envelope). Only the horizontal extension of horizontal ripples showed an extended summation field.

Stevenson, Cormack, Schor & Tyler (1999) extended the question of the filter range of stereoscopic processing into the binocular disparity domain. This issue is equivalent to measuring the spatial impulse response of the cyclopean disparity processing mechanisms. By using a random-dot disparity plane as a mask, the effect on the visibility of a stereoscopic test plane could be measured as a function of the relative disparity between the two depth planes. The whole experiment was conducted with dynamic noise stimuli, so that the planes were defined purely by disparity and no stimulus structure was visible monocularly. The masking effect peaked at each masking disparity tested, implying the existence of a multiplicity of disparity-tuned mechanisms (rather than just three, as proposed originally by Richards, 1970). Each tuning function was about 20 arc min of disparity in width and showed extended inhibitory flanks beyond the excitatory range of the masking function.

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In the course of this work, I developed the algorithm for the random-dot autostereogram, a method of presenting 3D information in a single image rather than a stereopair (Tyler 1983, see Section V; Tyler & Clarke, 1990). This method allowed stereo pictures to be freely printed and viewed (with some difficulty) and was the basis for numerous popular 'Magic Eye' books in the 1990s, with many viewers reporting that it was the best stereopsis that they had ever experienced. Mirror, prism and lens stereoscopes have limited visual field, while colour anaglyph and polarizing methods have significant cross-talk, especially in the dynamic mode. The autostereogram technique folds the information required for stereopsis into a single image, which is viewed with a small angle of either crossed or uncrossed vergence. This computational technique that does not simply combine the two images, but incorporates the disparity field into a repetitive base pattern that allows any desired disparity image to be generated. It may be viewed at any size, even a 180º field if desired, without cross-talk or visual field restriction.

X. Spatiotemporal processing of stereopsis

The systems analysis approach was extended to the spatiotemporal processing of vernier and stereoscopic stimuli by modulating the amplitude of the spatial sinusoidal lines in a temporal sinusoid (Tyler, Schor & Coletta, 1992). While vernier acuity was relatively invariant with temporal frequency, stereoscopic line acuity showed a complex interaction with a peak at 2 Hz and 3 cy/deg. Kontsevich & Tyler (2000) then developed dynamic noise stimuli with either sustained or double-pulse transient properties that selectively activated the magnocellular and parvocellular systems derived from the effects of monkey LGN on behavior (Merigan & Maunsell, 1987). The selectivity was of the order of a log unit. (Note that, despite the confusion in the neurophysiological properties of these systems, they are clearly distinguishable in monkey behavior, presumably extrapolating to human behavior.) Kontsevich & Tyler (2000) found that the parvocellular stimuli dominated the stereoscopic response throughout its spatial and disparity range, with a small contribution of the magnocellular system at large disparities.

The same line modulation approach of Tyler (1983) was extended to spatiotemporal processing of the binocular fusion limit by Schor & Tyler (1981). In addition to the proportionate fall-off in the fusion limit with spatial frequency, it showed a shallow reduction with temporal frequency, so that the range of binocular fusion fell from about 20 arc min at low spatial and temporal frequencies to as little as 3 arc min at high spatial and temporal frequencies. Binocular fusion thus needs to be thought of as a dynamically adjusting function rather than a fixed limit, even for a particular line width. Schor, Heckmann & Tyler (1989) then went on to test whether binocular fusion was limited by the luminance gradient or the spatial-frequency content of the stimulus, design local stimuli with different luminance gradients from the same frequency content summed in different phases. Binocular fusion was governed entirely by the frequency content, regardless of contrast, luminance gradient of component phase relations.

Spatiotemporal shearing stereomotion is evoked by viewing dynamic noise with a neutral density filer over one eye (Ross, 1974). The intraocular delay introduces random spatial disparities associated with biased apparent motion, that can be shown to form the local basis of the effect (Tyler, 1974b, 1977). The local receptive field structure of underlying

shearing stereomotion was studied by Morgan & Tyler (1995). Stimuli were generated in the form of dynamic random elements consisting of vertical Gabor strips of varying vertical spatial frequency Stereoscopic rotation was induced by the Pulfrich phenomenon of a neutral-density filter over one eye. An advantage was found for elongated elements in the tigertails, implying that the monocular inputs into stereoscopic motion are elongated in the vertical direction to an extent matching the simple cell receptive fields in cortex.

XI. Systems analysis in strabismus and amblyopia.

Strabismus is the condition in which the visual axes of the eyes do not remain aligned at all times. In intermittent strabismus, alignment is maintained much of the time, but fails intermittently under certain conditions, such as tiredness or certain vergence requirements. The most common type is intermittent exotropia (with the eyes diverging) In constant (or concomitant) strabismus, the misalignment angle is maintained all the time. The most common type is concomitant esotropia, in which the eyes adopt a constant convergence angle. In both types, the visual function is typically preserved in both eyes, but in other types of strabismus, one eye rapidly loses acuity and exhibits amblyopia or degraded vision. Tyler & Kaitz (1977) showed that changes potentially associated with the suppression of amblyopia could be found in individuals with normal vision after 6 hours of light or even form deprivation. Apkarian, Levi & Tyler (1981) and Apkarian & Tyler (1981) found that the binocular facilitation seen in the counterphase grating VEP response for binocular versus monocular stimulation (Apkarian, Nakayama & Tyler, 1981) was substantially reduced in strabismic amblyopes, but could still be found under certain conditions, indicating the existence of residual binocular function.

In terms of psychophysical limits, an interesting approach to strabismic losses is available through the line disparity modulation paradigm of Tyler (1973c). Rather than just measuring a loss in stereoacuity, this paradigm allows the evaluation of a whole domain of potential losses. In fact, several subjects showed specific losses of high spatial frequency disparity modulation with no other kinds of loss (Schor, Bridgeman & Tyler, 1983; Schor, Tyler & Bridgeman, 1984). One subject showed normal threshold sensitivities at all spatial frequencies of disparity modulation but a loss of the disparity gradient limit where the maximum disparity hit an invariant limit at all spatial frequencies. Thus, the disparity modulation paradigm can reveal stereodeficiencies that are untapped by conventional stereotests.

XII. Noise analysis of spatial vision

Noise analysis may take many forms In perceptual studies, spatial noise is typical used in the form of random dots to provide a base stimulus with no predictable features. This concept was introduced by Julesz (1960, 1971), being originally known as a 'Julesz textures', and has gained widespread application since that time. Texture perception may be studied by measuring the detectability of structured deviations from the random texture, or by comparisons of the texture under different viewing conditions. Tyler (1975e) compared the perceptual properties of dynamic noise texture viewed with one eye or both eyes. On closing one eye, the dynamic noise appeared to scintillate at a faster rate and to have a grain of higher spatial frequency, though isotropic in both cases. This

observation implied that the binocular receptive fields are larger and have longer integration times than the monocular ones in human visual cortex.

The temporal properties of the detection of binocular correlation in dynamic noise fields was studied by Julesz & Tyler (1976) and Tyler & Julesz (1976).   There was a pronounced anisotropy in the detection of transitions in correlation events, with a decorrelation pulse being detectable for durations or a few msec, while a correlation pulse took an order of magnitude long for its detection.   A model for the detectability of transitions among various degrees of correlation was developed, indicating that binocular correlation has a highly nonlinear transducer function. Tyler & Julesz (1978) extended these results to the spatial domain, showing that the summation area for both types of transition was about 2°, four times larger than the summation area for discrimination of depth of from binocular disparity in the same dynamic noise stimuli (which varies with stimulus extent; Tyler & Julesz, 1980).   This divergence indicates that binocular correlation of spatial noise is a separate visual process from the disparity combination.

An interesting deviation from random spatial texture is the presence of repetition in otherwise random texture. Such repetition transcends spatial frequency analysis because it has energy throughout the Fourier spectrum, although restricted to narrow bands of equal spacing across the Fourier space in the direction of the repetition. In this respect, the repetitive random textures resemble the more commonly-used Glass patterns of random textures generated from randomly-placed dot pairs (Glass, 1969), whose Fourier spectrum is a sinusoid filling the Fourier space. Tyler & Chang (1977) found that the detectability of random-dot repetition in a random-noise mask improved with the square root of repetition frequency. This law of detectability was shown to correspond to Ideal-Observer performance in this task. They also developed forms of noise that uniformized the noise spectrum in the direction perpendicular to the repetition, permuted noise with the same dot density in different permutations on every line, and rotated noise with the same random pattern on every line, but rotated randomly in phase for each line. These three manipulations reduced the sensitivity to repetition somewhat, but were governed by the same square-root law of repetition frequency expected of the Ideal Observer.

A further analysis of deviation from random textures is the issue of the autocorrelation hyperspace, in which patterns repeated within a random texture are detectable regardless of their location (Tyler & Miller, 1994; Tyler, 1995). A model of the human preattentive processing mechanism, which can effortlessly identify the presence of arrays of repeated patterns such as leaves or faces without scrutiny, the hyperspace approach allows the identification of any kind of structure merely on the basis of its repeated presence in the texture. A related approach was taken to the question of the adaptive patterns on the skin of the Peacock flounder (Ramachandran, Tyler, Gregory, Rogers-Ramachandran, Pillsbury, Duensing & Ramachandran, 1996; Anderson, Baddeley, Osorio, Shashar, Tyler, Ramachandran, Crook & Hanlon, 2003). My contribution was to determine the information transfer by the flounder visual system from the random and other textured backgrounds to the flounder skin pattern by performing a Principal Components Analysis on the correlation between the frequency spectrum of the flounder pattern and that of the background. Three separate processing channels for skin texture were significantly

active, one mid-frequency, one with low/high antagonism, and one with a specialized frequency structure. The ubiquitous 1/f spectral property such as is seen in the flounder patterns was shown to be potentially attributable to pattern boundaries rather than numbers of objects (Balboa, Tyler & Grzywacz, 2001).

Inspired by the ability of flounders to match the pattern of their background, Ramachandran & Gregory (1991) had discovered that a dynamic twinkle pattern would be perceived to fill in across the human blind spot and, indeed, across a small uniform grey patch. They also noted that the twinkle exhibited a dynamic aftereffect upon switching to a uniform grey patch. Hardage & Tyler (1995) compared the two phenomena and found that they were strongly dissociated: the filling was strongest in the periphery and for small fields, while the aftereffect was induced throughout the retina in regions as large as 20º diameter. This induced-twinkle aftereffect was evidently a separate phenomenon of long-range contrast-domain inhibition, and was only found for twinkle of high temporal frequency, implying that it was a magnocellular function. This interpretation was confirmed by Tyler & Hardage (1998), who showed that the twinkle aftereffect disappeared for an inducing surround of equiluminant colour noise.

An important probe into the global properties of random form perception is the detection of symmetry in unpatterned (random-element) stimulus fields. The ability to match an unanticipated pattern within a presentation time of less than 100 msec (and therefore less time than required for an eye movement), reveals important properties of human pattern processing. The match between pairs of symmetric patterns is invisible in the Fourier amplitude spectrum and is an obscure property of the phase spectrum, depending on the location of the symmetry axis. Symmetry cannot, therefore, be extracted from differential activation in a particular spatial frequency channel, but requires specialized global matching properties. It is often said that symmetry is extracted by attention to a specialized signal along the axis of reflection. However, Tyler, Hardage & Miller (1995) showed that, with dots of 1 arc min, the symmetry could be detected even with randomization of an axial strip up to 5 deg wide, requiring pattern matching far beyond any plausible axis information. At least two separate processes could be identified in the detection functions for axial width. These processes control the low and high probability-of-detection portions of the psychometric function. It was therefore relevant to determine the eccentricity scaling functions of these detectability regions, for both static- and dynamic-noise symmetry, as a function of eccentricity. Using unscaled noise, Tyler (2001) showed that the full-symmetry sensitivity was remarkably robust to eccentricity, falling only about a factor of two out to 12º eccentricity (where eccentricity scaling would have predicted a loss of a factor of 32 or more). This result calls for a re-evaluation of the scaling study of Saarinen (1988), since his claim that symmetry scales with the standard cortical magnification function for detection using scaled stimuli did not test for the predicted reduction with unscaled stimuli. Moreover, Tyler (1999) found that the sensitivity to axial randomization as a function of eccentricity (in uniform random-dot noise) showed a *reverse* eccentricity scaling, becoming narrower with eccentricity rather than wider, as would be predicted by a scaled receptive-field model of symmetry processing. These results again support a global pattern-matching model rather than a local receptive-field model of symmetry processing.

Tyler & Hardage (1996) then extended this result using eccentricity-scaled stimuli to show that patches of scaled noise in the far periphery, from 32º to 64º eccentricity, could support symmetry detection for durations as short (~50 msec presentations with dynamic noise mask) as those at any eccentricity. These conditions involve patterns separated by 64º on the retina, implying a truly long-range pattern-matching capability. Other nonlinear and global properties of the noise-matching process revealed by symmetry detection tasks were also reported by Tyler & Hardage (1996). Patterns of one-tenth density could be detected more readily than those of full density, a property of second-order (rectifying) rather than first-order (linear filter) systems. This interpretation was tested by using patterns of opposite polarity across the symmetry axis (anti-symmetry), to which a second order mechanism should be impervious. Sensitivity was slightly reduced at high density, though still uniform across eccentricity. At low density, there was no significant reduction in sensitivity for opposite-polarity relative to same-polarity stimuli, supporting a dominant role for second-order processing of symmetry. As a result, a symmetry energy model was proposed, paralleling the well-established energy models for motion and disparity, to account for these and other results (Tyler, Proc Nat. Acad. Sci. USA, under revision). In summary, the symmetry detection results combine to reveal nonlinear, long-range, global mechanisms of pattern matching in noise stimuli, well outside these predicted from standard simple filter models.

Word count: 9,944

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