

“. . . On the Basis of Velocity Clues Alone": Some Perceptual Themes 1946–1996

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Three factors that have transformed perceptual research in the last fifty years are the digital computer, single-unit electrophysiology, and molecular biology. Amongst the developments in which members of the Experimental Psychology Society have been central are: the recognition of the role of optic flow in spatial vision; the demonstration that our perceptual systems contain parallel pathways extracting different information from the sensory array; the identification of specific detectors that can be selectively adapted in psychophysical experiments; and the transfer of the concepts of fourier analysis from audition to vision. The history of Opponent Process Theory offers an example where experimental psychologists have been misled by too simple an interpretation of physiological recordings.

I begin with a sad story and one not previously recorded in print. In 1950, J.J. Gibson published his *Perception of the Visual World*. In an argument that then seemed novel, he suggested that our perceptual systems directly recognize higher-order dimensions of the world. The best example was our ability to derive depth directly from texture gradients and velocity gradients. Suppose that a pilot is flying an aeroplane on a level path beneath an overcast sky and that he or she is looking in the direction of travel. Texture will flow across our pilot's retina at different velocities in different parts of the visual field. There will be one point, towards which the observer is moving, where the velocity is zero. From this point there will be a gradient of velocities increasing to a maximum above and below the observer. If now our pilot observer makes a landing glide towards the runway, the point of zero velocity moves to a point on the runway; it tells the pilot where the plane will land if it continues the glide, and the rate of optic flow in the peripheral field indicates distance from the ground. Figure 1 represents this situation: the lengths of the arrow vectors indicate velocity. If the observer makes a pursuit eye movement and tracks a point on the ground, then a constant is added to all the velocities in the array but the gradients remain the same (Gibson, 1950).

This paper is based on an invited presentation to the Experimental Psychology Society in Cambridge, July 1996, in celebration of the 50th anniversary of the founding of the Experimental Psychology Group, from which the Society subsequently evolved.

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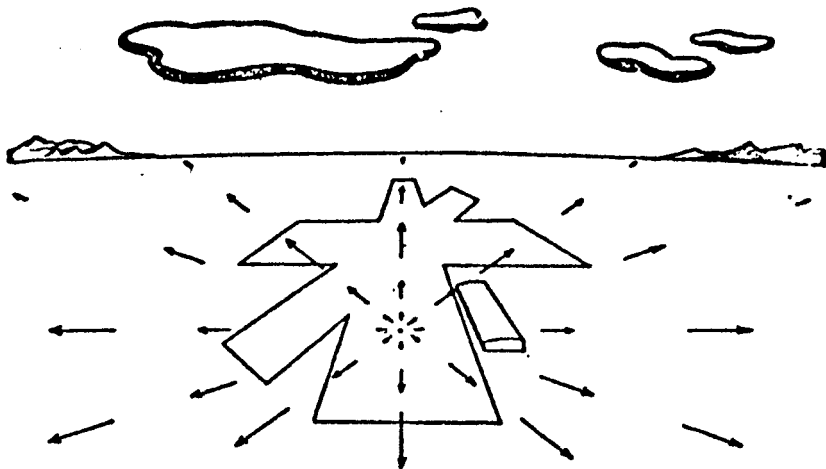


FIG. 1. A figure from J.J. Gibson's mimeographed report of 1947, later reproduced in *The perception of the visual world*. The arrow vectors represent the velocities of texture flow in different parts of a pilot's visual field as the plane makes a landing glide.

What was the origin of Gibson's revolutionary ideas? I shall argue that he took the concept of optic flow from an unpublished report by G.C. Grindley. Much loved by those who knew him but nowadays underestimated, Grindley was a founder member of the Experimental Psychology Group, and it was his anonymous donation that allowed this *Journal* to be started (Zangwill, 1977). He was universally known as "C". The account that follows was first mentioned to me in a letter of 1978 from another founder member, Bernard Babington Smith (known, in his turn, as "BBS"). He learnt it from C. Grindley at a meeting in Cambridge in 1959, and my account is based on written notes that Babington Smith prepared for me.

Grindley was unfit for service at the outbreak of war, but in 1941 Bartlett set him to studying the landing of aircraft on behalf of the Flying Personnel Selection Committee. Grindley went up in a trainer with an instructor called Peter May, and he asked May for advice on landing. May said, "You look at the point where you want to land and fly towards it till the ground explodes around it (making a gesture with his hands). Then you flatten out." Grindley realized the significance of this description of optic flow, carried out experiments and calculations, and submitted a secret report to the Air Ministry. When Babington Smith asked "C" whether Gibson would have seen the report, Grindley responded "He must have, my report went to him." At the time, Gibson was working for the American Air Force.

After Grindley's death, in 1976, Babington Smith prompted me to search for the report among C's papers. I couldn't find it. But BBS insisted and it was C's former assistant, Valerie Townsend, who recovered the yellowing report from the clutter at the bottom of C's filing cabinet. The document, marked "Secret" and numbered "F.P.R.C. 426", is entitled *Notes on the perception of movement in relation to the problem of landing an aeroplane*. It contains a clear description of how optic flow can be used in depth judgements. Figure 2 shows C's hand-drawn diagram. Gibson's later diagram looks derivative.

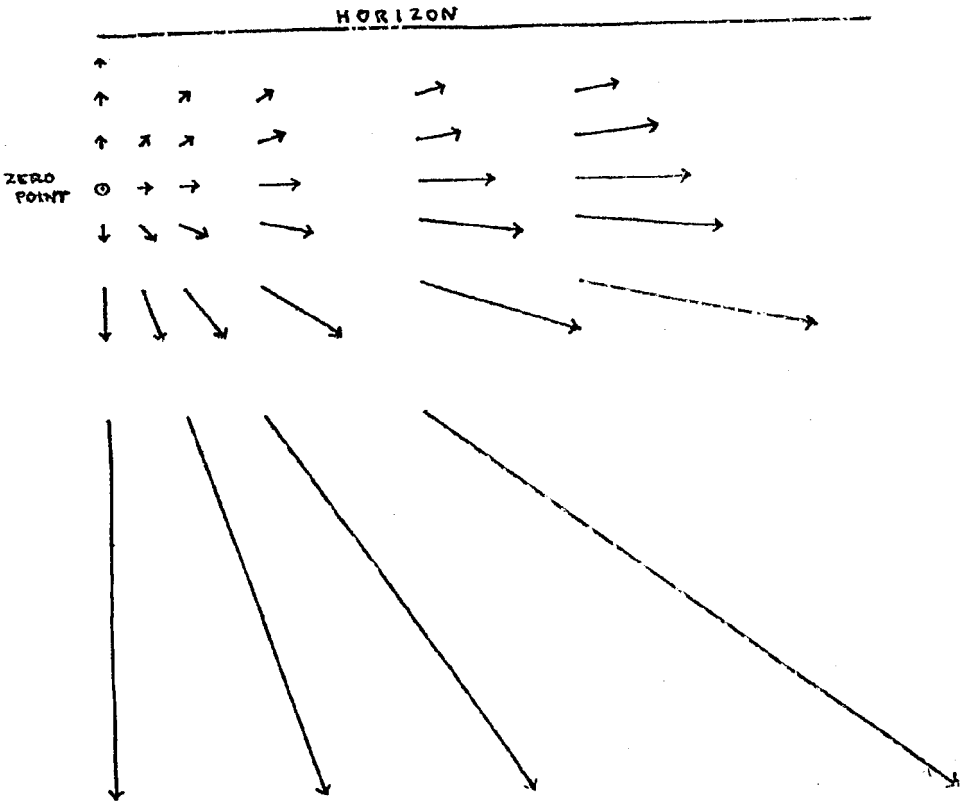


FIG. 2. A figure from G.C. Grindley's mimeographed report of 1941. The arrow vectors represent the velocities of texture flow in different parts of the pilot's visual field as the plane makes a landing glide.

C makes the point, that later turns up in *Perception of the Visual World*, about a constant being added to all velocities if one tracks a point in the field. C also did laboratory experiments to assess how well observers could judge absolute velocity—one of his subjects was G.C. Drew, another founder member—and he gives simple trigonometry for working out the velocities in the stimulus field. He concludes: "... the experiments would suggest that a pilot could land an aeroplane safely *on the basis of velocity clues alone*" [italics in the original].

But can we prove that Gibson saw Grindley's report? Yes, we can. Gibson wrote an unpublished postwar report of his own in 1947, in which he discusses optic flow. I have examined this report. On page 227 there is a slight footnote, citing Grindley but in a way that implies C's contribution was tangential:

G.C. Grindley has described this and some other aspects of the phenomenon in a brief report to the British Flying Personnel Research Committee. Whether a discussion of the phenomenon has been published could not be determined at the time of writing this report.

The Perception of the Visual World contains no reference to Grindley, but there is no denying that it has been one of the most influential books in the last fifty years of perceptual research.

The Computer and Perceptual Psychology

The remainder of this paper must necessarily be selective, and I concentrate unashamedly on developments in which members of the Experimental Psychology Society have had a part. But it is a machine, not an individual person, that is responsible for the most salient changes in our field since 1946. That machine is the digital computer, and it is worth distinguishing its several roles:

1. *A Metaphor for the Human Mind.* Most importantly of all, the computer has provided models for man in general and for the operation of particular neural subsystems. In 1946, except among the specialist groups such as the Experimental Psychology Group, people did not think of human beings as information-processing systems. Nowadays, such a view is commonplace for any television viewer.
2. *Machine Recognition.* Attempts to build machines that parse the visual world, or recognize objects or speech, have obliged us to define much more specifically the problems our perceptual systems must overcome. Sometimes this field of Artificial Intelligence has drawn its solutions from those favoured by the brain; sometimes the solutions adopted by programmers have suggested how the brain solves the equivalent task.
3. *Laboratory Instrument.* The computer has become the main instrument in psychology and has replaced the tachistoscopes, millisecond clocks, and other specialist devices that once furnished the perceptual laboratory. As a postdoc with John Krauskopf at Bell Telephone Labs in 1970, I was introduced to the use of a Varian computer to control the shutters and stepping motors of a Maxwellian-view optical system: the Varian had 8K of RAM, but my assembly-language programs never filled it.
 - 3.1. *Complexity of Stimuli.* Even a modest machine such as John Krauskopf's Varian allowed the use of complex adaptive procedures—multiple staircases—that adjust successive stimuli according to the history of the subject's responses (Cornsweet, 1962). By thus allowing the stimuli to centre themselves on the subject's threshold or on the Point of Subjective Equality, we maximize the efficiency of the experiment, and we also avoid the biases that are introduced by using the fixed set of stimuli of the Method of Constant Stimuli (Sekuler & Erlebacher, 1971). More recently the coming of the computer-controlled display has allowed us to present, and to modify from trial to trial, stimuli that are spatially complex or even naturalistic but yet are controlled in their statistical structure (e.g. Tadmor & Tolhurst, 1994). Needless to say, the computer-controlled display, like the electronic tachistoscope before it (Mollon & Polden, 1978), has brought with it snares for the unwary, and many artifacts masquerade in the literature as honest effects (Jonides, Irwin, & Yantis, 1983; Mollon & Baker, 1995).

3.2. *Separation of Experimenter and Subject.* The computer releases the experimenter from the need to record responses manually and to manipulate apparatus. This may save labour (some of us spent the best years of our youth feeding cards into a tachistoscope), and it allows the experimenter, without dependence on an assistant, to measure his or her own discrimination with randomized stimuli; but more importantly the computer saves us from Rosenthal effects—the subtle class of artifacts that derive from the experimenter's expectations. And another type of experimenter effect deserves mention: when hemifield differences in verbal tasks were classically measured with tachistoscopes, the experimenter typically sat to one side, feeding the cards, recording responses—and surely biasing the subject's attention.

I'll take just one example of how it was before computers were available to the experimental psychologist. In the late 1950s the *Quarterly Journal* had a section happily called "Miscellanea"—it may never have been formally abolished—and in there we find a paper by Carolus Oldfield and colleagues, which describes the preparation of a random black-and-white pattern (Laner, Morris, & Oldfield, 1957). Figure 3 shows a fragment of the finished product. But let me quote the authors' account of how the pattern was constructed:

The procedure adopted was to fill in or leave blank successive squares on a sheet of 1/12 in. graph paper, 27 in. × 40 in., in accordance with a random series of scale of two digits incorporating the desired statistical distribution. In its original form the screen thus contains 155,000 elements. Pencil was found to be the best and easiest medium for filling in the squares. This original screen was then copied by a photostat process having a non-linear contrast characteristic which results in the dark squares being very greatly intensified, while the faint lines of the graph paper disappear. This intensified screen was then photographed in as contrasty a manner as possible.



FIG. 3. A fragment of the random pattern prepared manually by Laner, Morris, and Oldfield and later used in masking experiments by Kinsbourne and Warrington.

It happened that, for the purposes in mind, an equal number of black and white squares was not desired, but instead a black/white ratio of 29:71. . . . The necessary random sequence was obtained by a method similar to that used by Kendall and Babington-Smith (1938). A card-board disc was rotated on a horizontal axis at 2,000 r.p.m. immediately behind a vertical screen with a narrow slit in it radially situated with respect to the disc. The edge of the disc was cut out, by an amount equal to the length of the slit, over an angle of 104° (corresponding to the fraction 0.29). Behind the disc and the slit in the screen was placed a Strobeflash lamp set to operate on a single flash. . . . The operator watched the slit and at intervals irregular in relation to the speed of rotation, pressed the Strobeflash control button. If the light was seen through the slit he recorded (on a typewriter) a symbol for black: if not, another symbol for white. These typewritten records of random sequences . . . were then used to fill in squares on the graph paper.

Within two years of this heroic exercise, Bela Julesz, with the resources of Bell Telephone Labs behind him, used an IBM-704 computer to generate random-dot stereograms on tape, which could then be displayed on a television monitor by means of a digital-to-analogue converter. However, the Oldfield pattern did serve in one classical British study, published in the *Quarterly Journal*—that of Kinsbourne and Warrington (1962a, 1962b). This was one of the first parametric investigations of backward pattern masking, and I mention it to highlight another trend of the last three decades, the interest in the temporal aspect of perceptual processes. Kinsbourne and Warrington found that an after-coming random-pattern mask could prevent recognition of a letter target presented up to 64 msec earlier. These experiments, and those of George Sperling, were to initiate a large field of research on visual information processing. A distinction has not always been made, however, between true backward masking, where the target is not detectable, and the use of random-pattern masks to "terminate the processing" of suprathreshold stimuli. Experiments of the latter kind rest on unsafe assumptions, for the icon may be four-dimensional, preserving the temporal sequence of events (Mollon, 1969), and subjects may learn where to attend within this four-dimensional representation. It is interesting that representations in echoic memory are implicitly assumed to preserve temporal sequence, whereas this assumption is seldom made in the case of the analogous visual store.

The Independent Analysis of Sensory Attributes

In 1946 the visual system was often—though not by everyone—thought of as a homogeneous channel delivering a single representation of the retinal image to the cortex. We now believe instead that the array of retinal receptors is examined in parallel by different post-receptoral channels, which extract different features of the image. Different information is carried by morphologically distinct ganglion cells and projects via anatomically distinct pathways to different cortical and subcortical destinations. Different sub-regions of prestriate cortex appear to be devoted to the analysis of different attributes (Cowey, 1979; Zeki, 1977).

It would be wrong to suppose, of course, that such ideas were absolutely unknown in 1946. As early as 1869, J.J. Chisholm of Charleston, South Carolina, described the case of a 35-year-old woman who suffered an acute attack of optic neuritis and whose spatial resolution recovered much more completely than did her colour vision: he asked explicitly

‘‘whether there are special nerve fibres, for the recognition of special colours, independent of those used in the clear definition of objects’’ (Chisholm, 1869). And before the nineteenth century was closed, Sigmund Exner was offering detailed models of how particular stimulus attributes (such as movement) might be recognized by specific neural subsystems (Exner, 1894). Nevertheless, it is in the last four decades that the concepts of feature detectors and parallel channels have become central to perceptual theory. To earlier evidence from pathology has been added evidence from physiology, psychology, and, more recently, brain imaging.

With regard to the physiology, a seminal paper was that of Horace Barlow, delivered to the Experimental Psychology Group in 1952 and printed for the first time on the occasion of the 50th Anniversary of the Society (Barlow, 1996). Horace Barlow's experience with this paper illustrates a central tension in the Experimental Psychology Group: some wanted it to be a private discussion group, others wanted it to become a national society. Barlow thought he was speaking to a private club, but a representative of the American naval attaché, elected a Visiting Foreign Member, disseminated an account of the talk to all holders of ONR grants in the United States. The paper was titled ‘‘The psychology of the frog's retina’’. Barlow recorded from different types of ganglion cell in the frog retina and showed that one type, the on-off, was best stimulated by a small black moving object. When the target extended beyond the primary receptive field, the response of the cell declined, even though stimulation of the outer region on its own attracted no response. Similarly, the response to a spot within the receptive field was attenuated if a second spot was present outside the receptive field. Barlow ended his paper to the Experimental Psychology Group with the explicit suggestion that the cell was a feature detector—indeed, a fly detector. This paper, of course, antedates by seven years the later paper by Lettvin, Maturana, McCullough, and Pitts (1959) entitled ‘‘What the frog's eye tells the frog's brain’’.

Hubel and Wiesel's work on visual feature detectors in cat and primate cortex is justly celebrated and had great influence (Hubel & Wiesel, 1959; 1968). But I should like to mention here the auditory analogue of Hubel and Wiesel's findings, as work in that field has been much less extensive, and the pioneering experiments were by two members of the Experimental Psychology Society, Whitfield and Evans. They recorded from single units in the auditory cortex of the cat and identified a subset of cells that did not respond to pure tones but did respond to modulations of frequency—warbles—or to ramps of frequencies. Figure 4 shows an example of such a cell: no action potentials are evoked by a tone of 2.5 kHz (upper trace), but there is a response to a stimulus modulated around this frequency, and the response always occurs in the same phase of modulation (Whitfield & Evans, 1965).

Let me turn to psychological evidence for the existence of independent channels within the visual system. A nice example, often now forgotten, is described in a paper in the *Quarterly Journal* by Anne Treisman; it was part of her D.Phil. work in the Oxford Institute of Experimental Psychology (Treisman, 1962). She presented to one eye two rings—a red ring enclosing a green ring. To the other eye she presented a green ring enclosing a red (Figure 5, colour plate). Relative to the outer rings, the inner rings were binocularly disparate. Under these circumstances, the rings never combine to give a binocular yellow. Rather, they exhibit an unstable rivalry of colour, parts appearing red

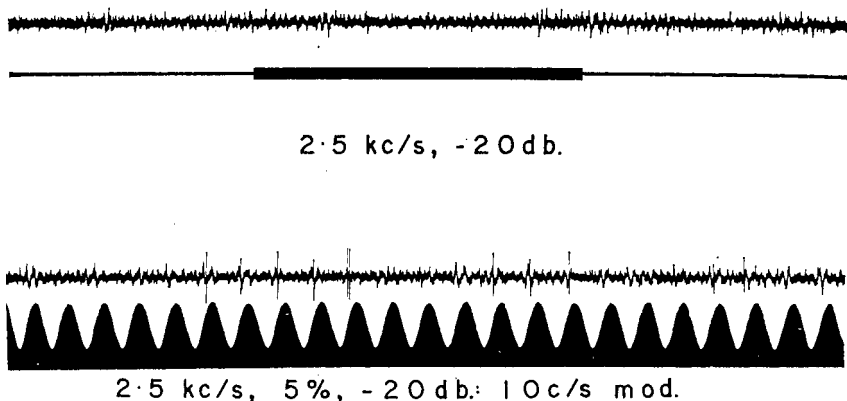


FIG. 4. Records of a neuron in auditory cortex, from Whitfield and Evans (1965). The neuron shows no response (uppermost trace) during the presentation of a steady tone, indicated by the thick bar immediately below. In the lower trace the neuron is seen to respond to a modulation of frequency, indicated by the sinusoidal pattern. Notice that the action potentials occur only when the frequency is changing in one direction.

and parts green. Nevertheless, the subject enjoys a steady impression of depth, in that the disparate inner ring appears in a different plane from the outer.

One can modify Treisman's demonstration by fixating not centrally, but to one side or the other of the outer ring, so that the stimuli fall entirely on the nasal retina of one eye and on the temporal retina of the other. For many people one hemi-retina is prepotent in binocular rivalry (Barrell & Parks, 1969). The colour signals from one eye now dominate, so that the subject sees one ring as consistently red and the other as green. Yet the stereoscopic percept is as stable as ever. Thus the colour signal from one eye can apparently be suppressed while, at the same time, contour signals from both eyes are stably combined for the purposes of stereopsis. The implication is that the two aspects of subjective sensation depend on channels that at some stage are functionally independent.

In the 1960s, when the concept of parallel channels was becoming popular, it was sometimes referred to as the "assembly-line hypothesis", but this is not the happiest of terms, as signals that diverge as early as the outer plexiform layer—signals that are carried by different classes of bipolar cell—may travel over different pathways to control different aspects of behaviour without ever being assembled into a unitary central representation. The internal representations that guide our locomotion or our grasp may be distinct from those that underlie our phenomenological judgements.

Spatial Frequency Channels

One of the particularly influential ideas of the 1960s was the concept that there are independent visual channels for stimuli of different spatial frequency. The hypothesis that the visual system performs a Fourier analysis of the spatial distribution of light drew upon ideas from the auditory analysis of frequency and was largely initiated by three members of the Experimental Psychology Society—Fergus Campbell, John Robson, and Colin Blakemore (Blakemore & Campbell, 1969; Campbell & Robson, 1968). A famous demon-

stration supports this idea (Figure 6). The effect is known as the Blakemore–Sutton effect after its discoverers (Blakemore & Sutton, 1969), and it is analogous to the tilt after-effect, which had been studied earlier by J.J. Gibson (Gibson & Radner, 1937). If one adapts to a grating of a given frequency, a grating of lower frequency will afterwards look coarser than it normally would, whereas a grating of higher frequency will look finer than normal. These types of after-effect show what is called the "displacement paradox": the maximum distortion of our perception occurs not at the adapting frequency or adapting orientation, but at a point on the stimulus dimension a little way from the adapting position on the dimension. We now believe that such behaviour is characteristic of sensory dimensions that are coded by place (Mollon, 1977).

The modern theory of such displacement effects was first given by Stuart Sutherland in one of the most original papers published in the *Quarterly Journal*, although it has never enjoyed the recognition it deserved (Sutherland, 1961). The underlying concept had long before been introduced by von Békésy to explain distortions of auditory pitch (von Békésy, 1929), but Sutherland was the first to extend it to higher-order features. He himself applied the theory to Gibson's tilt after-effect,¹ but Figure 6 shows the same explanation applied to the case of spatial frequency. We must suppose that a sensory dimension such as spatial frequency or contour orientation is represented in the visual cortex by an array of neurons each tuned to a different position on the dimension but broad enough in their tuning that their sensitivity curves overlap with those of neurons responding maximally to neighbouring parts of the dimension. We are also asked to assume that the judged quality of the stimulus (its orientation or spatial frequency) depends on the overall distribution of activity in this array of neurons. Adaptation produces a depression of sensitivity that is centred on the neuron representing the adapting orientation or frequency. If now we look at a stimulus a little way away on the dimension, the normal distribution of activity will be skewed away from the adapted region, so giving rise to the after-effect (for a fuller account see Braddick, 1982).

Colour Vision

The Status of Opponent Process Theory

Now let me turn to an aspect of perceptual theory that has not shown a consistently Whiggish trend during the last half-century. For several years a false association between opponent hues and physiological channels diverted the understanding of colour perception into a cul-de-sac.

In 1878 Hering had proposed that our colour experience depended on two neural processes, each bipolar: an antagonistic red–green process and an antagonistic yellow–blue process. The evidence then was phenomenological, and, I shall want to argue, it is

¹ Gibson (1937) had explicitly suggested that the orientation of a line was a primitive "immediately sensed" quality. It is curious that he later took so little interest in the neural apparatus of vision, despite the demonstrations that the orientation of contours and the density of texture were features extracted at a relatively distal level of our perceptual system.

still the only evidence today. There exist four hues in the spectrum that appear phenomenologically unmixed—a red, a green, a yellow, and a blue. Other hues, such as orange and cyan, are judged by most people to be mixtures of the primitives. Moreover, the possible mixtures are constrained: we never experience reddish greens or yellowish blues.

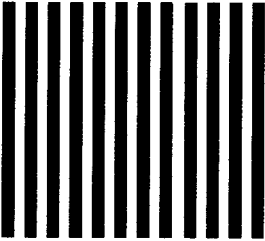
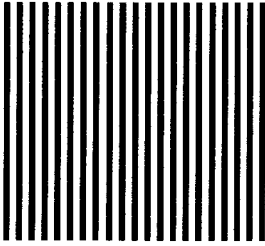
What is historically interesting in the period between 1946 and 1996 is what was taken as evidence for the Opponent Process Theory and what was not. Firm psychophysical evidence for chromatically antagonistic signals was provided by the British psychophysicist, W.S. Stiles, and it is derived from what are called "test interaction" experiments (Stiles, 1967). Stiles measured the threshold for detecting a brief flash on a steady background. The flash could be monochromatic or a compound of two wavelengths. Figure 7 reproduces Stiles' own slide. In this experiment the primary test flash is red and is presented on a bright green background. The abscissa of the graph shows the wavelength of a second flash, which is presented concurrently. The ordinate is an index of summation between the two flashes. Notice that when the second flash is green, the summation falls below even what would be predicted by probability summation, suggesting that the two flashes give signals that inhibit each other. Now this was the first non-phenomenological evidence for chromatic opponency in colour vision, and yet Stiles and his followers did not take it as evidence for classical Opponent Colours Theory, although they did recognize the possibility of channels that draw inputs of opposite sign from different types of cone.

What *was* taken as evidence for Hering's theory was the physiological work of De Valois and his collaborators (De Valois, 1965; De Valois, Abramov, & Jacobs, 1967). Recording from single units in the lateral geniculate nucleus of macaques, they found cells that were excited by one part of the spectrum and inhibited by other wavelengths. Such units appeared to fall into four classes and were quickly labelled with the initials of colour names: +R-G, +G-R, +B-Y and +Y-B. These findings led very widely to the idea that Hering had been vindicated and to the statement that the Young-Helmholtz trichromatic theory held at the level of the receptors while the Hering Opponent Colour theory held at a postreceptoral level. You still find this line in textbooks, and I know that it is taught to this day in more than one British university. Here is a case where psychologists were misled by physiology.

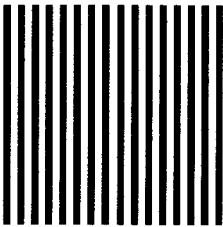
We still believe today that there are chromatically antagonistic channels in the early visual system—that is, channels that draw inputs of opposite sign from different classes of cone, but these channels simply do not correspond to the phenomenologically defined

FIG. 6. To the left are stimuli for obtaining the classical Blakemore-Sutton effect. First check that the two test gratings look equal in spatial frequency when you fixate the cross between them. Now adapt for at least one minute to the adapting gratings, letting your eye move to and fro along the solid bar between them. Now transfer your gaze deftly to the cross between the test gratings. Fleetinglly the upper grating will look coarser and the lower, finer. To the right is illustrated the von Békésy/Sutherland explanation of after-effects of this class. The stimulus dimension (here spatial frequency) is encoded by a set of neurons with overlapping sensitivity curves. The subjective percept depends on the distribution of activity in this array of neurons. Adaptation to a lower frequency depresses the sensitivity of neurons tuned to that and nearby frequencies, and so the distribution of activity produced by the test stimulus is now skewed towards neurons representing higher frequencies.

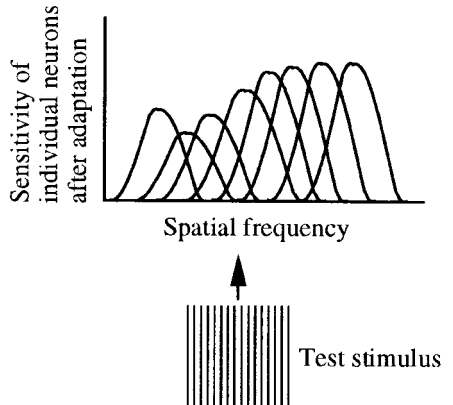
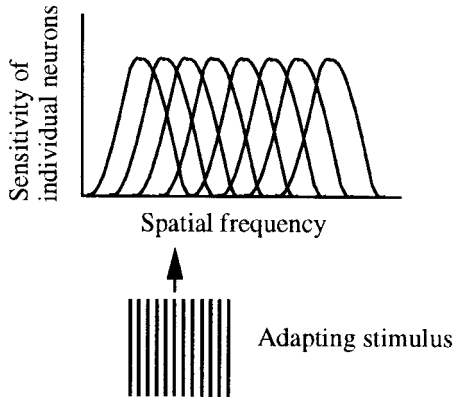
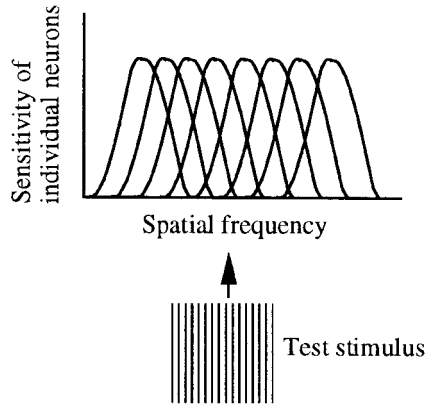
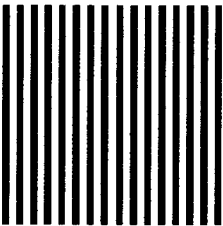
Adapting stimuli



Test stimuli



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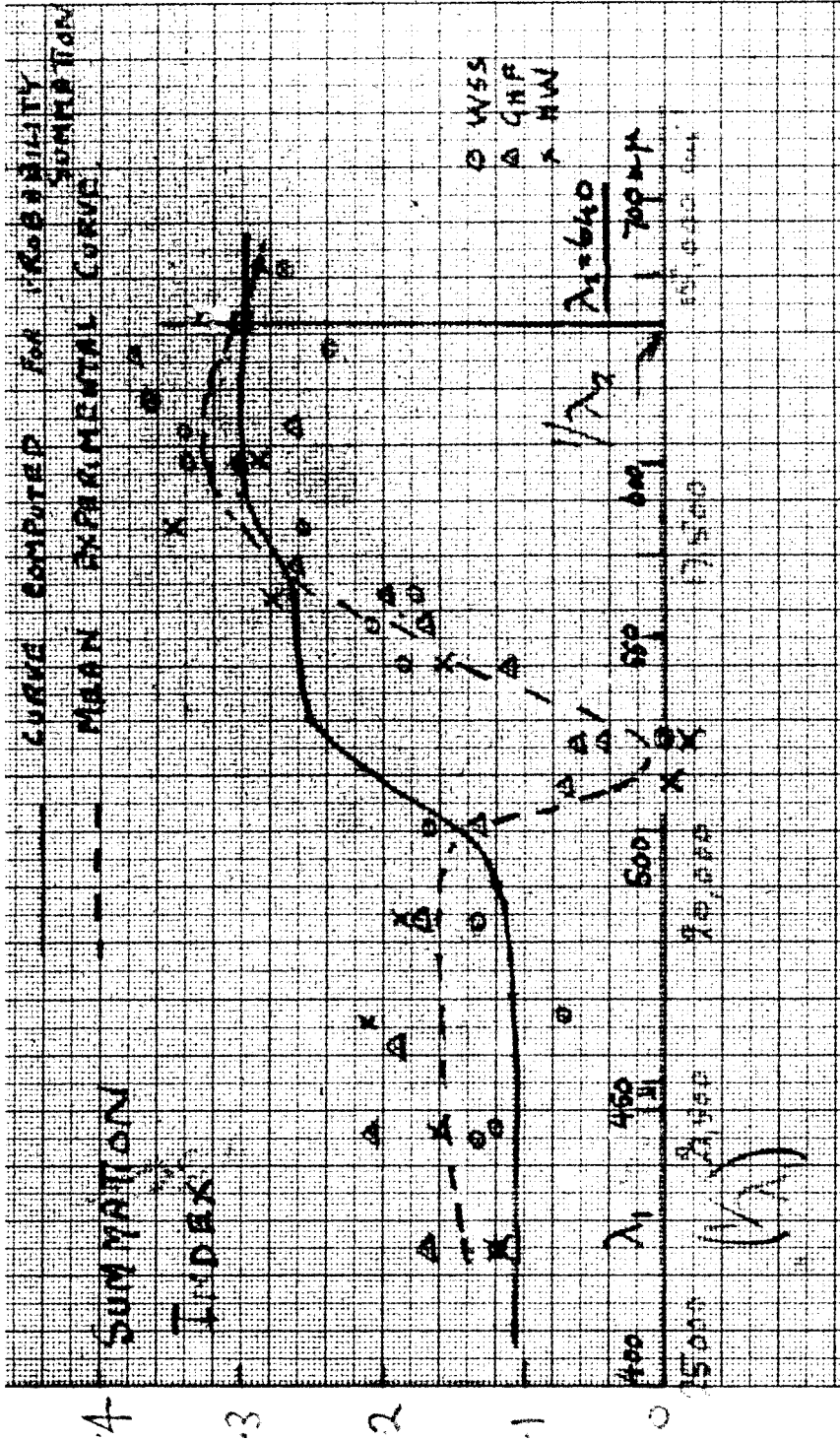


FIG. 7. A hand-drawn slide by W.S. Stiles showing evidence for antagonistic interaction between cone signals. The task of the subject is to detect a compound flash presented on a bright green field. One component of the flash is red and of fixed wavelength (640 nm). The abscissa of the graph represents the wavelength of the other component of the flash. The ordinate of the graph is an index of the summation between the two components. Values near 0.3 (e.g. at right-hand side of the graph) correspond to complete summation of energy. The solid line represents the results expected if the two flashes are detected by independent channels and only probability summation occurs between them. When the variable flash has a wavelength near 520 nm, performance falls below even that expected from probability summation: an inhibitory interaction is occurring between the two stimuli.

channels of Hering. Figure 8 (colour plate) gives the modern view. One channel draws opposed inputs from the sparse short-wave cones, on the one hand, and the long- and middle-wave cones on the other (Derrington, Krauskopf, & Lennie, 1984; Mollon, 1989). This channel is phylogenetically very ancient, antedating the mammals. It has poor spatial resolution, and recent work by Dacey and Lee shows that it has its own morphological substrate—a special class of ganglion cells, the small bistratified cells, which project to the intercalated layers of the lateral geniculate (Dacey & Lee, 1994). The second channel arose only thirty million years ago, following duplication of a gene on the X-chromosome; it draws opposed inputs from the long- and middle-wave cones, and its anatomical substrate is the midget ganglion cell of the primate retina. I want to argue later that it evolved with frugivory in primates. Figure 9 shows a modern chromaticity diagram, due to MacLeod and Boynton (1979). The ordinate corresponds to the input of the older channel, the abscissa to the input of the phylogenetically newer channel. The curved line represents the spectrum locus—that is, the chromaticities of the monochromatic lights that constitute the visible spectrum. The wavelengths that appear pure yellow and pure blue to normal subjects are indicated. The line that connects these wavelengths is quite oblique and does not correspond to either axis. So pure blue and pure yellow are very far from producing the same ratio of excitation in the long-wave and middle-wave cones, and thus they cannot both correspond to the equilibrium state of a "red-green" channel that compares the signals of the long-wave and middle-wave cones. Colorimetrically, then, the channels

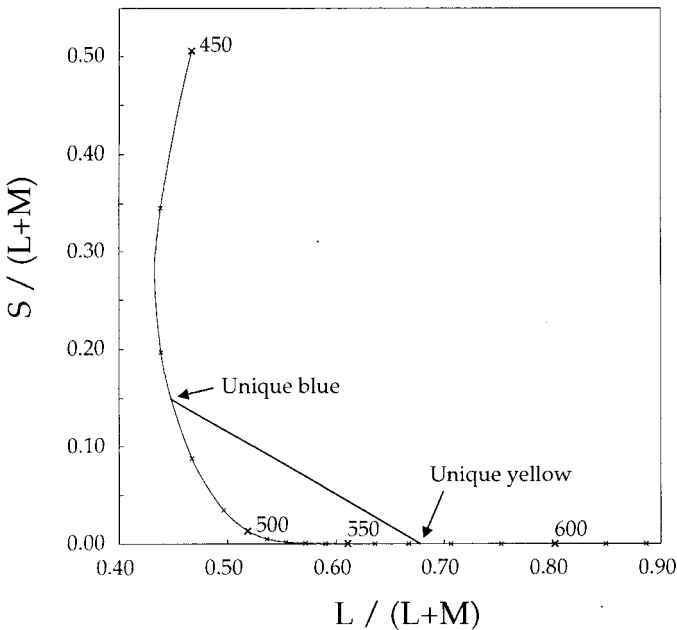


FIG. 9. The MacLeod-Boynton chromaticity diagram, which represents all colours in terms of the signals of the two channels thought to be present in the early visual system. In such a diagram, the line connecting unique yellow and unique blue is oblique, whereas it would have to be vertical if it corresponded to the equilibrium state of a channel that differenced the long-wave and middle-wave cones.

demonstrated physiologically in the early visual system simply do not correspond to the processes postulated by Hering. In fact, no one has found a site in the visual system where colour appears to be represented according to Opponent Colour theory—that is, a site where the cells might be held to secrete redness and greenness or yellowness and blueness. Cells are found in the cortex that respond to restricted regions of chromaticity space, but they are by no means confined to the loci of pure hues. Thirty years ago we thought we understood the existence of four unique hues, hues that are phenomenally unmixed. Today this is perhaps the major unsolved problem of colour vision (Mollon & Jordan, 1997). If we understood it, we should probably be much closer to understanding the general relationship between neural activity and qualia.

Pigment Polymorphisms and Perceptual Worlds

By contrast, the last fifty years have seen a complete transformation in our understanding of the photopigment molecules on which all vision depends. Fifty years ago, when the Experimental Psychology Group was founded, there was agreement neither on the number of retinal cone types nor on their spectral positions. From microspectrophotometry of individual cones, and from suction-electrode recording, we now have a much firmer knowledge of the spectral sensitivities of the cones (Dartnall, Bowmaker, & Mollon, 1983; Schnapf, Kraft, & Baylor, 1987).

But what has transformed our knowledge of the visual pigments is the sequencing of the corresponding genes by Jeremy Nathans and his colleagues (Nathans, Piantanida, Eddy, Shows, & Hogness, 1986a; Nathans, Thomas, & Hogness, 1986b). Figure 10 (colour plate) shows, on the left, the multiply enfolded outer segment of a cone; to the right is represented a visual pigment molecule embedded in the cell membrane. By inference from the DNA sequences, we know that these molecules consist of seven helices that span the membrane and form a palisade. What makes this small corner of neuroscience of wider interest is that the visual pigments are members of the much larger class of G-protein-coupled receptors or heptahelicals, which include the dopaminergic and serotonergic receptors (Watson & Arkininstall, 1994; Mollon, 1997).

Indicated in Figure 10 are the amino acids that control most of the difference in wavelength sensitivity between the human long- and middle-wave pigments. Let me concentrate for a moment on just one of these, number 180 in the sequence of amino acids that make up the protein part of the photopigment. This part of the molecule is coded for by the third exon of the gene.² In the case of the long-wave gene, there exists a polymorphism of one of the triplet of bases that encodes the 180th amino acid; in other words, within the normal population there is a non-pathological variation at this site. So about 62% of men express a gene that codes for serine at position 180, and 38% of men express a gene that codes for alanine (Winderickx et al., 1992). Now this difference of a single base shifts the spectral position of the pigment by several nanometers (Asenjo, Rim,

² The coding regions of photopigment genes—the regions that specify the amino-acid sequence of the protein—are interrupted by stretches of DNA that do not code for amino acids. The latter, non-coding regions are called introns, and the coding regions are called exons.

& Oprian, 1994; Merbs & Nathans, 1992): the serine variant peaks at a longer wavelength and so is relatively more sensitive in the red part of the spectrum. So if you and I differ by one base pair in our genome, we will pass out our lives in slightly different perceptual worlds: a mixture of red and green that matches a certain orange for me will be an unacceptable match for you and vice versa. The polymorphism at site 180 is not the only one: several polymorphisms are known for both the long- and the middle-wave pigments. So in fact there are many slightly different forms of colour vision among "colour-normal" men. And in the case of women, there will be an even greater richness of perceptual worlds: owing to X-chromosome inactivation (Lyon, 1972), each cone cell in a woman's retina may express either her father's or her mother's X-chromosome.

Now this is the first case where we understand well the molecular basis of a perceptual variation in the normal population. But it is turning out that most of our brain proteins are polymorphic, and I believe that we shall soon know about many such polymorphisms that determine our perceptual, cognitive, and emotional worlds. Consider just one of the many thousands of brain proteins, the D4 dopaminergic receptor molecule, which is a close cousin of the visual pigments and has a heptahelical structure resembling that of Figure 10 (Van Tol et al., 1991). This molecule is encoded by a polymorphic gene on chromosome 11p. Within the normal population are found variations in the length of the third intracellular loop of the molecule (Van Tol et al., 1992): a sequence of 16 amino acids in the loop is repeated one to seven times. It is known that *in vitro* the variants differ in their affinity for clozapine, an atypical neuroleptic, and more recently it has been reported that this normal polymorphism accounts for a small but significant fraction of the variance in the personality dimension of Novelty Seeking (Benjamin et al., 1996; Ebstein et al., 1996). Anyone who follows molecular psychiatry, where associations between polymorphisms and disease prove notoriously difficult to replicate, will be cautious about particular links between genetic polymorphism and cognitive variation. Nevertheless, psychologists must accept, and should interest themselves in, the endless polymorphisms of brain proteins that are now known. Therein must lie much of the biodiversity of our mental lives.

The Ecology of Colour Vision

I'd like to return now to J.J. Gibson and to indulge myself for a moment by discussing work from my own group. In 1975 I gave a talk in the Psychology Department at Cornell, in which I discussed the eighteenth-century confusion as to whether trichromacy was a property of the physical world or of human physiology. The talk was titled, rather ambitiously, "Did trichromacy cause the French Revolution?" Gibson was in the audience, and I had hoped to meet the great man afterwards, but his comment on the talk was to disappear quickly. However, before I left I was handed a copy of the colloquium notice, on which he had scribbled his comment: "The nature of the world and the physiology of the visual system are not separable but complementary." It has taken twenty years for me to grasp that he was right and to become a paid-up visual ecologist.

The work I should like briefly to describe was carried out in primary uninhabited tropical rain forest in a little-known part of the European Community, French Guiana. It is the thesis work of Benedict Regan, and the project is a collaboration with the French

ecologist Pierre Charles-Dominique and his colleagues. We should like to argue seriously that the phylogenetically recent subsystem of colour vision, which has high spatial resolution, evolved with frugivory in primates. What has become clear from ecological work in the last decade is that in both the Old World and the New there is a subset of trees that is disseminated only by monkeys (Charles-Dominique, 1993; Gautier-Hion et al., 1985; Julliot, 1992). These trees constitute a significant component of the rain forest. The fruits of such trees typically weigh between 5 and 50 g, are yellow or orange in colour, and often have a hard outer coat. The fruit presents a signal that is visible at a distance to a trichromatic disseminator, and in return for nutritious pulp the monkey either spits out the seed at a distance or defecates it later, together with fertilizer. It is instructive that the one task that particularly handicaps human dichromats is picking fruit (Nicholl, 1818; Steward & Cole, 1989): one needs colour vision, not to detect equiluminant edges (which are very rare in the natural world), but to discover targets against a background that is varying randomly in luminance and form, as in the case of fruit amongst foliage (Mollon, 1989).

I'll consider here just one species of monkey, the red howler monkey, *Alouatta seniculus*, which has recently been shown to be a normal trichromat, like a macaque (Jacobs, Neitz, Deegan, & Neitz, 1996). By monitoring what this species eats over a period of three months, we believe that we have accounted for at least 80% of its diet during this period. The quantitative question we ask is how well the photopigments of the monkey are matched to the chromatic signals offered by the fruit. We measured reflection spectra of fruit known to be eaten on the same day by *Alouatta*, and we also measured the reflection spectra of the background foliage, the noise against which the fruit signals must be discriminated. Figure 11 (colour plate) shows typical reflection spectra for fruits and foliage. In modelling our data, we not only consider the actual positions of the long- and middle-wave photopigments, but we also let the computer try out all possible positions of these two pigments. For every possible pairing of pigments, we calculate the quantum catches of the different cones for each of several hundred samples of fruit and foliage. We plot the data in chromaticity diagrams like those of Figure 12. These diagrams are analogous to the MacLeod-Boynton diagram (Figure 9) and can be constructed for any putative set of cone pigments. The ordinate of the diagram represents the signal in the older subsystem of colour vision—that is, the ratio of the signal in the short-wave cones to the other two. The abscissa represents the signal in the phylogenetically recent subsystem—that is, the ratio of the quantum catches in the long- and middle-wave cones. The solid points show the foliage chromaticities, the open circles show fruit. Figure 12b is constructed for the set of photopigments thought actually to be present in the red howler monkey. The thing to notice is that the foliage in this diagram lies along a vertical line (in technical terms, a tritan confusion line, as the colours that lie along it would be indiscriminable to a tritanope): almost all the variance is in the signal of the older subsystem. As fruits ripen, they emerge from the foliage distribution and move orthogonally. So, with this set of pigments, the signal-to-noise ratio in the new subsystem is optimized, because all the foliage variation projects onto one narrow band of the abscissa. Now consider Figure 12a, which is for a hypothetical set of pigments more evenly spaced in the spectrum. Here the foliage distribution is tilted, and the abscissa signal exhibits more variance. Figure 13 (colour plate) summarizes a large number of such diagrams, showing

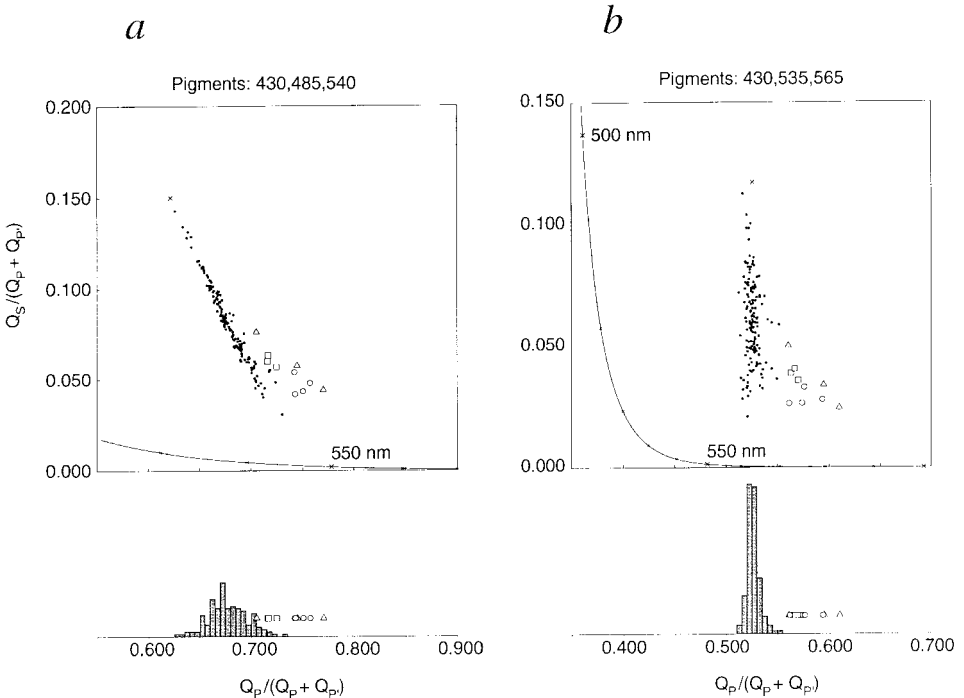


FIG. 12. Chromaticity diagrams analogous to that of MacLeod and Boynton (1979) but for different sets of photopigments. The abscissa represents $Q_P / (Q_P + Q_P)$, where Q_P and Q_P are the quantum catches in the two pigments with peak sensitivities in the middle- to long-wave region. The ordinate represents the signal of the phylogenetically older sub-system of colour vision, expressed as $Q_S / (Q_P + Q_P)$, where Q_S is the quantum catch of the short-wave cones. The continuous line shows part of the spectrum locus, with wavelengths indicated. The small solid circles show the chromaticities of foliage, and the open symbols show those of the three fruits most commonly observed to be eaten by howler monkeys at the field site: *Bagassa guianensis* (triangles), *Chrysophyllum lucentifolium* (circles), and *Vouacapoua americana* (squares). Diagram (a) is for a triplet of pigments with peak sensitivities at 430, 485, and 540 nm, a set never observed in a primate, whereas Diagram (b) is for a set close to those present in howler monkeys.

how the signal-to-noise ratio (the distance on this axis between a given fruit and the mean foliage, over the standard deviation of the foliage distribution) varies with the spectral positions of the middle- and long-wave pigments. One ordinate represents the peak wavelength of one putative photopigment, the other ordinate the second. The lighter the colour, the higher the signal-to-noise ratio. It is clear that widely spaced photopigments (such as those that subserve the phylogenetically older subsystem) do not well support the discrimination of fruit from foliage. The cross in the figure corresponds to the spectral positions of the actual pigments thought to be present in howler monkeys. We conclude that the asymmetric placing of the actual primate pigments is well matched to the discrimination of fruit signals. We do not, of course, know whether the monkey's trichromacy or the fruit signals came first, or whether the two co-evolved.

I have briefly summarized this work of ours to illustrate a current trend in visual science—that of asking how perceptual systems are moulded, in phylogeny and in ontogeny, to fit the theatre in which the organism lives. We are all Gibsonians now.

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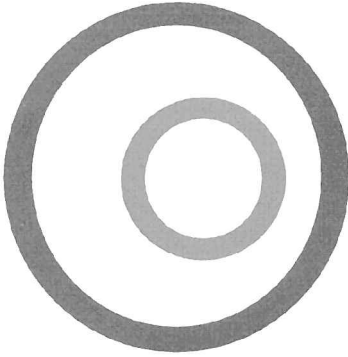
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Left eye



Right eye

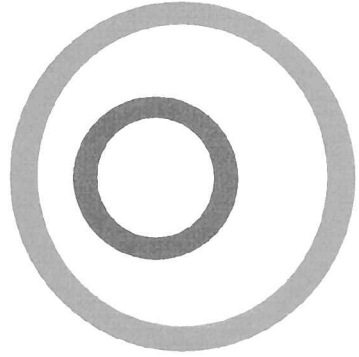


FIG. 5. A demonstration from Treisman (1962). When the stimuli are combined haploscopically, there is a stable depth difference between inner and outer rings, despite rivalry of colour.

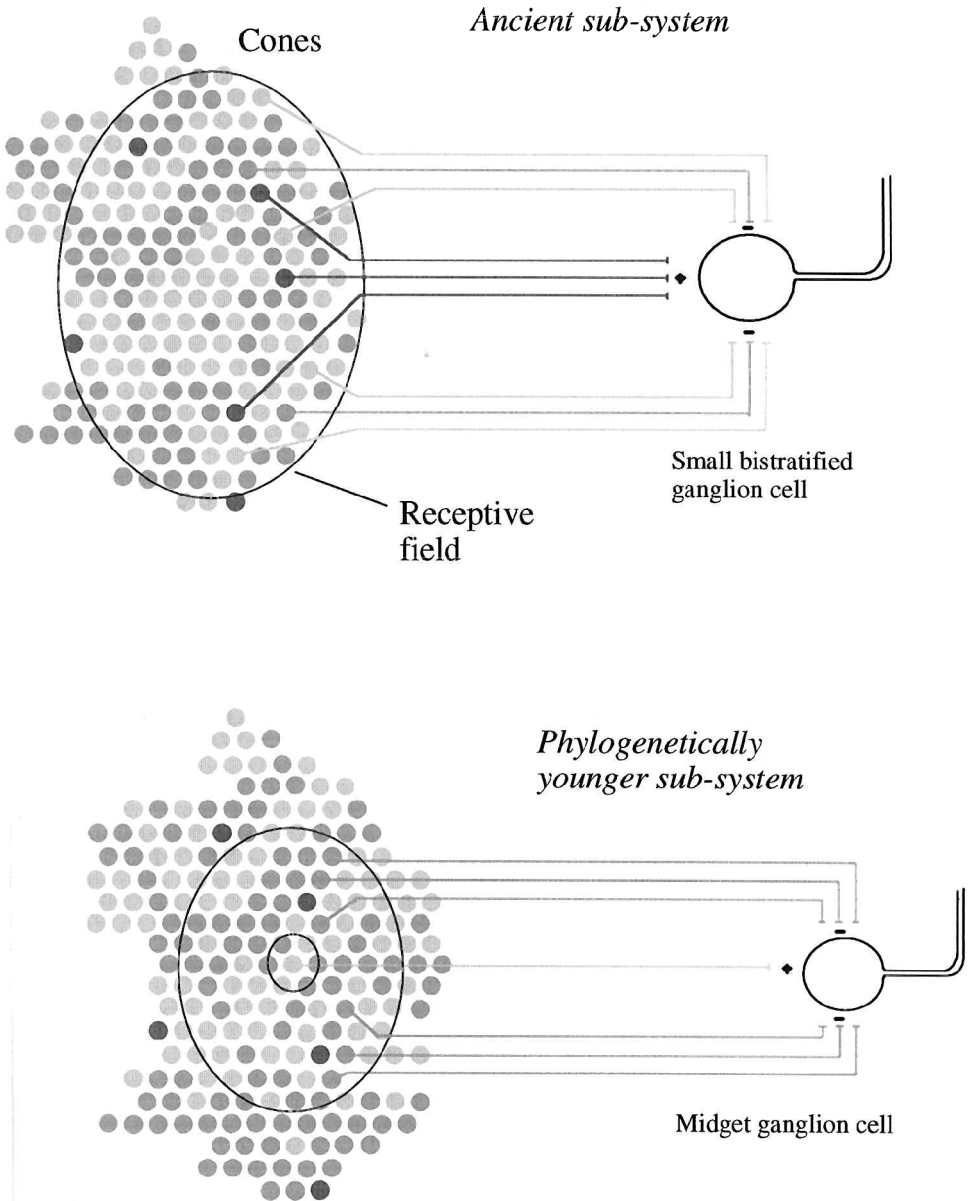


FIG. 8. The ancient and modern subsystems of colour vision. The phylogenetically older subsystem (above) draws excitatory inputs from the short-wave cones and inhibitory inputs from the long- and middle-wave cones in a small local region of the photoreceptor array. Short-, middle- and long-wave cones are represented by violet, green, and yellow discs, respectively, and the spatial distribution of the different types follows Mollon and Bowmaker (1992). The more recent subsystem (below) draws antagonistic inputs from the long- and middle-wave cones. Its receptive field is smaller and is spatially opponent.

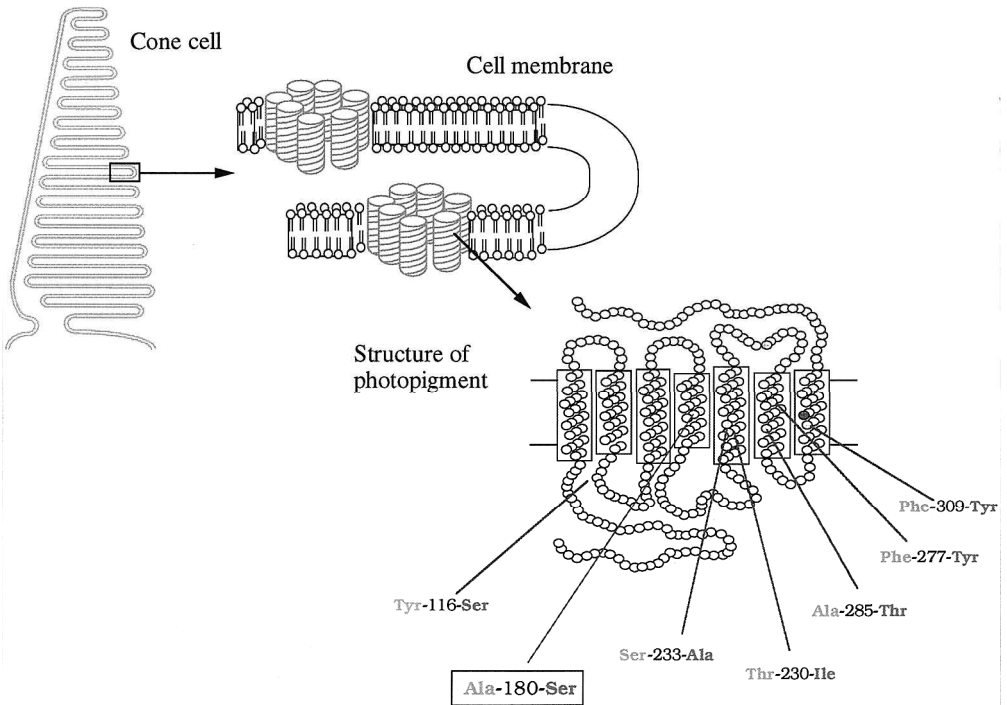


FIG. 10. The enfolded outer segment of a retinal cone cell (upper left) is packed with photopigment molecules. Each of these consists of seven helices, which span the membrane of the cell and are linked by loops outside the membrane. (Dopaminergic receptors have a very similar structure.) Identified at the bottom is the small number of amino acids that primarily determine the difference in wavelength sensitivity between long-wave and middle-wave pigments. The coloured lettering indicates the alternative amino acids at each position: in each case the amino acid shown in green is the alternative that shifts the peak sensitivity of the molecule to shorter wavelengths, that in red is the one that shifts sensitivity to longer wavelengths. One amino acid site (no. 180) is highlighted: this site is polymorphic in the case of the long-wave pigment and, to a lesser extent, in the case of the middle-wave pigment.

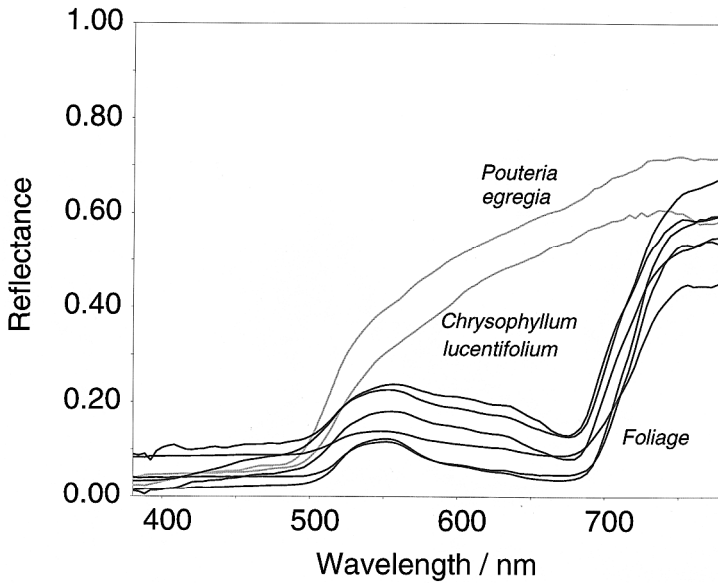


FIG. 11. Examples of reflectance spectra measured in French Guiana. The green curves represent foliage, and the yellow curves represent two fruits eaten by *Alouatta seniculus* at the field site. Measurements were made with a PhotoResearch 650 spectroradiometer. A white (barium oxide) reference plaque, measured immediately after the sample, was taken to represent 100% reflectance.

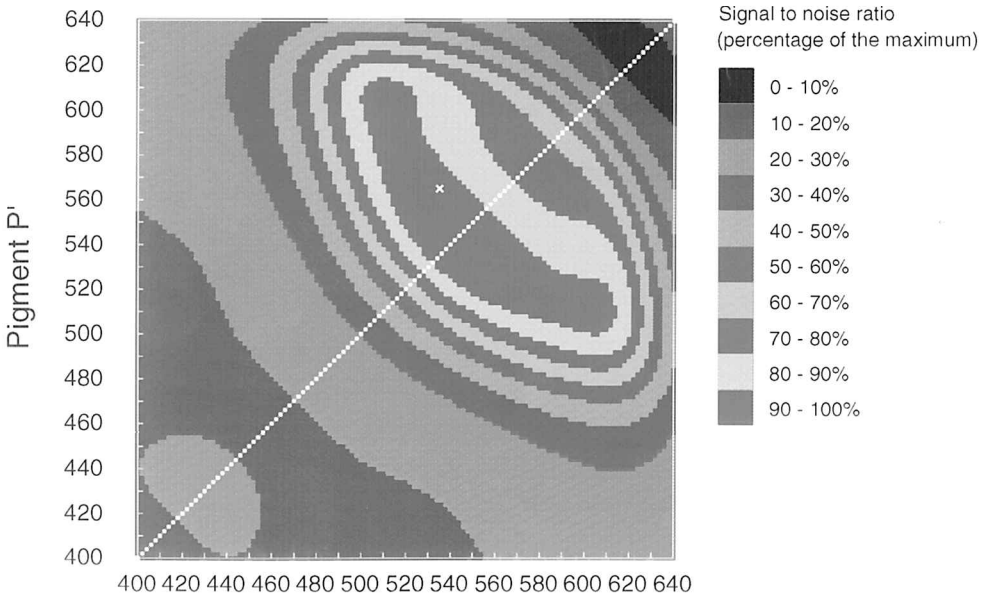


FIG. 13. Average signal-to-noise ratios for fruits eaten by *Alouatta seniculus* when different spectral positions are assumed for the pigments P (abscissa) and P' (ordinate). The lighter the hue, the higher the signal-to-noise ratio (see key). The figure is symmetrical about the diagonal line, which represents $P = P'$. The white cross indicates the pair of pigments believed to be present in the retina of *Alouatta*. The asymmetrical spectral positioning of primate photopigments appears to be nearly optimal for detecting fruits in foliage.