Reprinted from *Normal and Defective Colour Vision*
edited by J. D. Mollon, J. Pokorny and K. Knoblauch,
Oxford University Press, 2003.

INTRODUCTION: THOMAS YOUNG AND THE TRICHROMATIC THEORY OF COLOUR VISION

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> As this paper contains nothing which deserves the name, either of experiment or discovery, and as it is in fact destitute of every species of merit, we should have allowed it to pass among the multitude of those articles which must always find admittance into the collections of a Society, which is pledged to publish two or three volumes every year...

These critical words came from a distinguished pen, that of Henry Brougham (1778–1868), later Baron Brougham and Vaux. While still a teenager, Brougham had published optical and mathematical papers in the *Philosophical Transactions* of the Royal Society; and he was later to become Lord Chancellor, the chief law officer of the United Kingdom. He is remembered as a campaigner for abolition of the slave trade, as the counsel for Queen Caroline in the divorce proceedings against her, and as the co-founder of University College London. But in the history of optics he is also remembered for the essay whose opening lines are quoted above (Brougham 1803).

The object of Brougham's scorn was a Bakerian Lecture delivered in two parts to the Royal Society of London on November 12 and 19, 1801, and published in the *Philosophical Transactions* for 1802. It was in this Lecture that Thomas Young developed the wave theory of light, introduced the generalized Principle of Interference, and proposed the trichromatic theory of colour vision in its recognizably modern form.

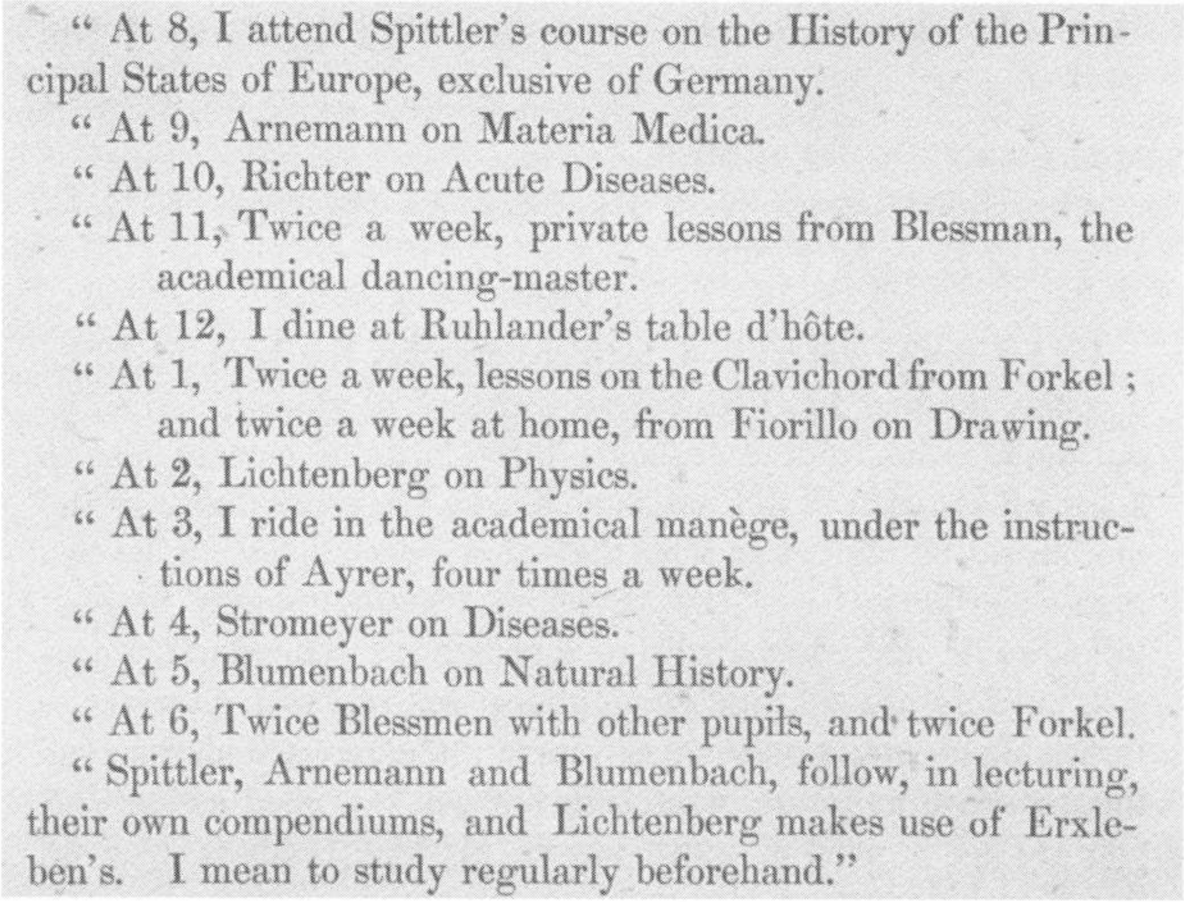
Born at Milverton in Somerset in 1773, Thomas Young was the eldest son of a banker and mercer. The family were Quakers. Young could read by the age of two—if we believe his own account—and had read twice through the bible by the age of four (Peacock 1855). At the age of 17, he read Newton's *Principia* and *Opticks*, but—by the standard of Henry Brougham—he was relatively old when he published his first scientific paper. This paper, on the mechanism of visual accommodation, appeared in the *Philosophical Transactions* when Young was 20 (Young 1793) and secured his election to the Royal Society the following year. His uncle, Richard Brocklesby, was a prosperous London physician and intended Young as his successor. Young began his studies at St. Bartholomew's Hospital in London, and then moved to Edinburgh for the academic year 1794–5. It was here that

Figure i.1 Thomas Young (1773–1829).

he first crossed the path of Henry Brougham, for it is known that they both attended one of Joseph Black's last courses of chemical lectures (Cantor 1971).

The origins of the trichromatic theory

Young spent the academic year 1795–6 at the Georg-August University of Göttingen, which lay within the Hannoverian realms of George III. It was in Göttingen that Young probably first gave detailed thought to the nature of colour, as a result of contact with the physicist and aphorist, G. C. Lichtenberg. Although Young found most of the Göttingen professors rather distant and formal, he mentions in a letter to his uncle that 'Arnemann, in whose house I live, and Lichtenberg the lecturer on Natural Philosophy, are the most sociable' (Peacock 1855). Lichtenberg was an anglophile and a Fellow of the Royal Society, and brief entries in his diaries do record visits by Young ('Dr. Young bey mir') (Lee 2001). We know from Young's own account that he attended Lichtenberg's lectures on physics at 2.00 o'clock each afternoon (see Figure i.2). And we know from a transcript of Lichtenberg's lectures, taken down by a student and later published (Gamauf 1811), that Lichtenberg discussed in some detail the colour triangle of Tobias Mayer, the Göttingen astronomer. Mayer had died in 1762 and Lichtenberg had taken on the task of editing



“ At 8, I attend Spittler's course on the History of the Principal States of Europe, exclusive of Germany.

“ At 9, Arnemann on Materia Medica.

“ At 10, Richter on Acute Diseases.

“ At 11, Twice a week, private lessons from Blessman, the academical dancing-master.

“ At 12, I dine at Ruhlander's table d'hôte.

“ At 1, Twice a week, lessons on the Clavichord from Forkel; and twice a week at home, from Fiorillo on Drawing.

“ At 2, Lichtenberg on Physics.

“ At 3, I ride in the academical manège, under the instructions of Ayrer, four times a week.

“ At 4, Stromeyer on Diseases.

“ At 5, Blumenbach on Natural History.

“ At 6, Twice Blessmen with other pupils, and twice Forkel.

“ Spittler, Arnemann and Blumenbach, follow, in lecturing, their own compendiums, and Lichtenberg makes use of Erxleben's. I mean to study regularly beforehand.”

Figure i.2 Thomas Young's own account of his working day as a student in Göttingen in the academical year 1795–6. Reproduced from Peacock (1855).

his unpublished papers, which included the essay *On the Relationship of Colours* (Forbes 1971; Mayer 1775). Mayer had supposed that there were only three primary colours—red, yellow and blue—and that all other colours could be produced by mixing the primaries. The three primaries formed the apices of his colour-mixing triangle, and along each side there were twelve discriminably different mixtures.

Yet Newton's prismatic experiments had suggested that the physical variable underlying hue was a continuous one. In his lectures, Lichtenberg himself took a conventionally Newtonian position when discussing the dispersion of white light by a prism, but he also discussed the extensive eighteenth-century evidence that all colours could be constructed by mixing three ‘primary’ colours. The trichromacy of colour mixture had in fact been widely discussed before Mayer (e.g. Anonymous 1708; Castel 1740; Le Blon 1725) It was this accumulated evidence for trichromacy that led many commentators to suppose the Newton was wrong and that there were three physically distinct types of light. They were misled by a category error: they supposed that the trichromacy of colour mixture was a property of physics (Mollon 2003).

What most colour theorists lacked in the eighteenth century was the concept of a tuned transducer, that is, a retinal resonator responding to only part of the visible spectrum. Rather it was assumed, by Newton and by many subsequent writers, that the vibrations occasioned in the retina by rays of light were conveyed unchanged along the optic nerve to the sensorium, where they aroused sensations of hue. Without the concept of a tuned retinal transducer, it was not obvious that trichromacy was a property of our visual system rather than a fact of physics. An intermediate stage of understanding is represented by the shadowy figure of George Palmer (1740–95). A London dealer in coloured glass, Palmer was both a physical and a physiological trichromatist: he postulated three types of 'particle' or 'fibre' in the retina and three corresponding kinds of light (Mollon 1993; Palmer 1777). Colour blindness arose, said Palmer, when one or two of the three types of 'molecule' was constitutionally inactive or constitutionally over-active. His explanation of colour blindness first appeared in a scientific magazine edited by Lichtenberg's brother (Voigt 1781).

In summary, as the eighteenth century closed, there was accumulated evidence for the trichromacy of colour mixture, but this evidence seemed to be at odds with the Newtonian theory of light. It was to be Thomas Young who released colour science from the category error that held it back. And it was almost certainly in Göttingen in 1795–6 that he was first exposed to the issues in detail.

Acoustics and the principle of interference

It was not, however, the theory of light that primarily occupied Thomas Young in the period that immediately followed his return from Germany to Emmanuel College in Cambridge. He was to come to colour theory by an indirect route. In order to graduate as Doctor of Physic in Göttingen, he submitted a dissertation on the preservative powers of the human body, but he was also required to deliver a lecture on some topic relevant to medical studies. He chose to lecture on the human voice and a fragment of this lecture was printed at the end of his dissertation. He included a proposed universal alphabet of forty-seven letters, which were designed to express, by their combination, every sound that could be produced by the human vocal organs and thus any human language. Wanting to develop this work, he soon realized that he was limited by his understanding of the nature of sound. He gives an account in a later pamphlet defending his optical papers against the criticisms published by Brougham in the *Edinburgh Review*:

> 'When I began the outline of an essay on the human voice, I found myself at a loss for a perfect conception of what sound was, and during the three years that I passed at Emmanuel College, Cambridge, I collected all the information relating to it that I could procure from books, and I made a variety of original experiments on sounds of all kinds, and on the motions of fluids in general. In the course of these enquiries, I learned to my surprise, how much further our neighbours on the continent were advanced in the investigation of the motions of sounding bodies and of elastic fluids, than any of our countrymen; and in making some experiments on the production of sounds I was so forcibly impressed with the resemblance of the phenomena that I saw, to those of the colours of thin plates, with which I was already acquainted, that I began to suspect the existence of a closer analogy between them than I could before have easily believed.' (Young 1804)

The reason that Young did not start immediately in medical practice in 1797 was that new rules of the Royal College of Physicians required him to spend two consecutive years at one university (Gurney 1831). So this is how he came to enter Emmanuel College, Cambridge, as a Fellow-Commoner, that is, a gentleman entitled to dine with the Fellows although still *in statu pupillari.* One of his contemporaries at the college recorded that he was known in Emmanuel as 'Phaenomenon Young' and wrote:

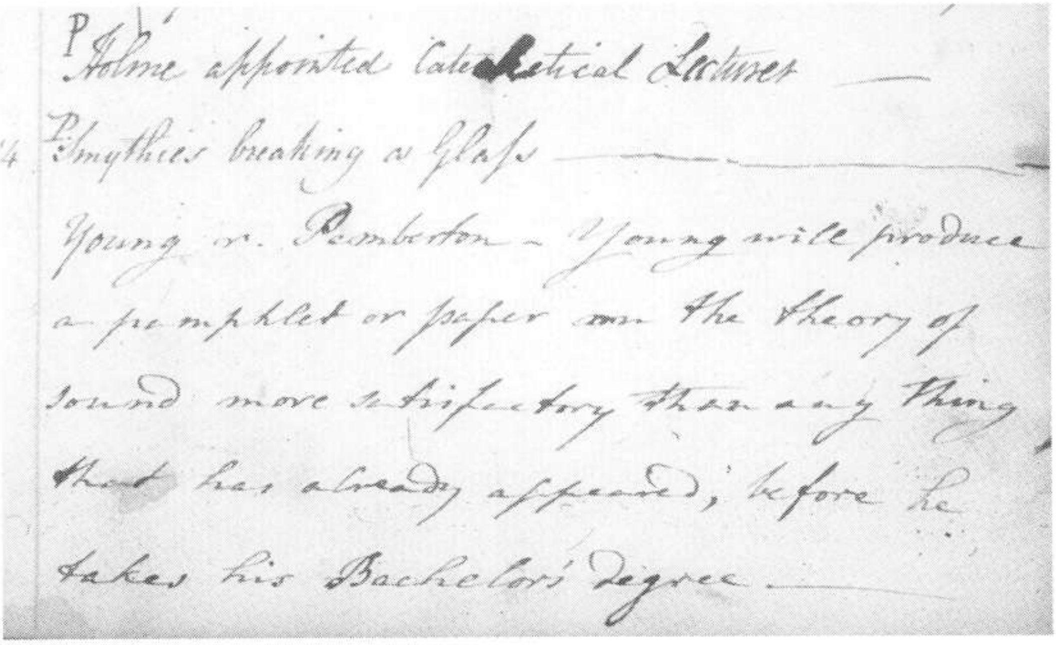
> '...his room had all the appearance of belonging to an idle man. I once found him blowing smoke through long tubes, and I afterwards saw a representation of the effect in the Transactions of the Royal Society to illustrate one of his papers upon sound; but he was not in the habit of making experiments.' (Peacock 1855)

The paper referred to in this passage must be Young's 'Outlines of experiments and inquiries respecting sound and light', published in the *Philosophical Transactions* for 1800. In this paper he applies the principle of interference to acoustics but does not yet generalize it to optics. He devotes most of the text to acoustics but in §10 he does suggest an analogy between the colours of thin plates and the resonance of organ pipes. He does not yet have the critical insight—that the colours of thin plates are the product of constructive and destructive interference—for it is only in the following section of the paper ('Of the coalescence of musical sounds') that he uses the yet-unnamed principle of interference to explain the beating that is heard when two tones are of very similar but not identical frequency.

The *Parlour Book* of Emmanuel College records a wager dated 14 March 1799 between Young and Pemberton that 'Young will produce a pamphlet or paper on sound more satisfactory than anything that has already appeared, before he takes his Bachelor's degree' (Figure i.3). An Audit of Wagers in the *Parlour Book* for 1802 records that Young was held to have lost the bet.

Yet the Principle of Interference was to prove perhaps the single most important concept in the physics of the subsequent two centuries. According to college tradition at Emmanuel, Young first observed interference patterns in the ripples produced by a pair of swans on the rectangular pond in the college paddock (Bendall *et al.* 1999). It is a pleasant legend, but I have not found any nineteenth-century reference to it. However, in defending his theory of light against Brougham's criticisms, Young does certainly use a lake as his model:

> 'Suppose a number of equal waves of water to move upon the surface of a stagnant lake, with a certain constant velocity, and to enter a narrow channel leading out of the lake. Suppose then another similar cause to have excited another equal series of waves, which arrive at the same channel, with the same velocity, and at the same time as the first. Neither series of waves will destroy the other, but their effects will be combined: if they enter the channel in such a manner that the elevations of one series coincide with those of the other, they must together produce a series of greater joint elevations; but if the elevations of one series are so situated as to correspond to the depressions of the other, they must exactly fill up those depressions, and the surface of the water must remain smooth; at least I can discover no alternative, either from theory or from experiment.' (Young 1804)



P Holme appointed Catechetical Lecturer
4 P Smythies breaking a Glass
Young v. Pemberton – Young will produce
a pamphlet or paper on the theory of
sound more satisfactory than any thing
that has already appeared, before he
takes his Bachelors' degree

Figure i.3 A wager between Young and Pemberton recorded in the Parlour Book of Emmanuel College, Cambridge. The preceding entries record an appointment celebrated and a clumsiness fined.

The Bakerian Lecture of 1801

By Young's own account, it was not until May, 1801 that he realized that interference could be used to explain the colours of thin plates—the colours of soap bubbles and oil films, and the coloured rings observed by Newton when a convex lens was pressed against a glass plate (Newton 1730). Young set out the hypothesis in the Bakerian Lecture that was to draw Brougham's attack. The lecture was read in two parts to the Royal Society, on 12 and 19 November 1801, and published the following spring (Young 1802a). He supposed that light consisted of waves in an all pervading ether. Different wavelengths corresponded to different hues, the shortest wavelengths appearing violet, the longest red. In his initial model of 1802, the undulations were longitudinal—along the line of the ray—rather than transverse, as Fresnel was later to show them to be.

Young proposed that the colours of thin films depended on constructive and destructive interference between light reflected at the first surface and light reflected at the second: when the peak of one wave coincides with the trough of another, the two will cancel, but when the path length of the second ray is such that the peaks coincide for a given wavelength, then the hue corresponding to that wavelength will be seen (Young 1802a).

The principle of interference, in its generalized form, was first actually published in the *Syllabus* for the Royal Institution Lectures that Young gave in the winter of 1801–2 (Young 1802c). There he writes (page 117):

> 'But the general law, by which all these appearances are governed, may be very easily deduced from the interference of two coincident undulations, which either cooperate, or destroy each other, in the same manner as two musical notes produce an alternate intension and remission, in the beating of an imperfect unison.'

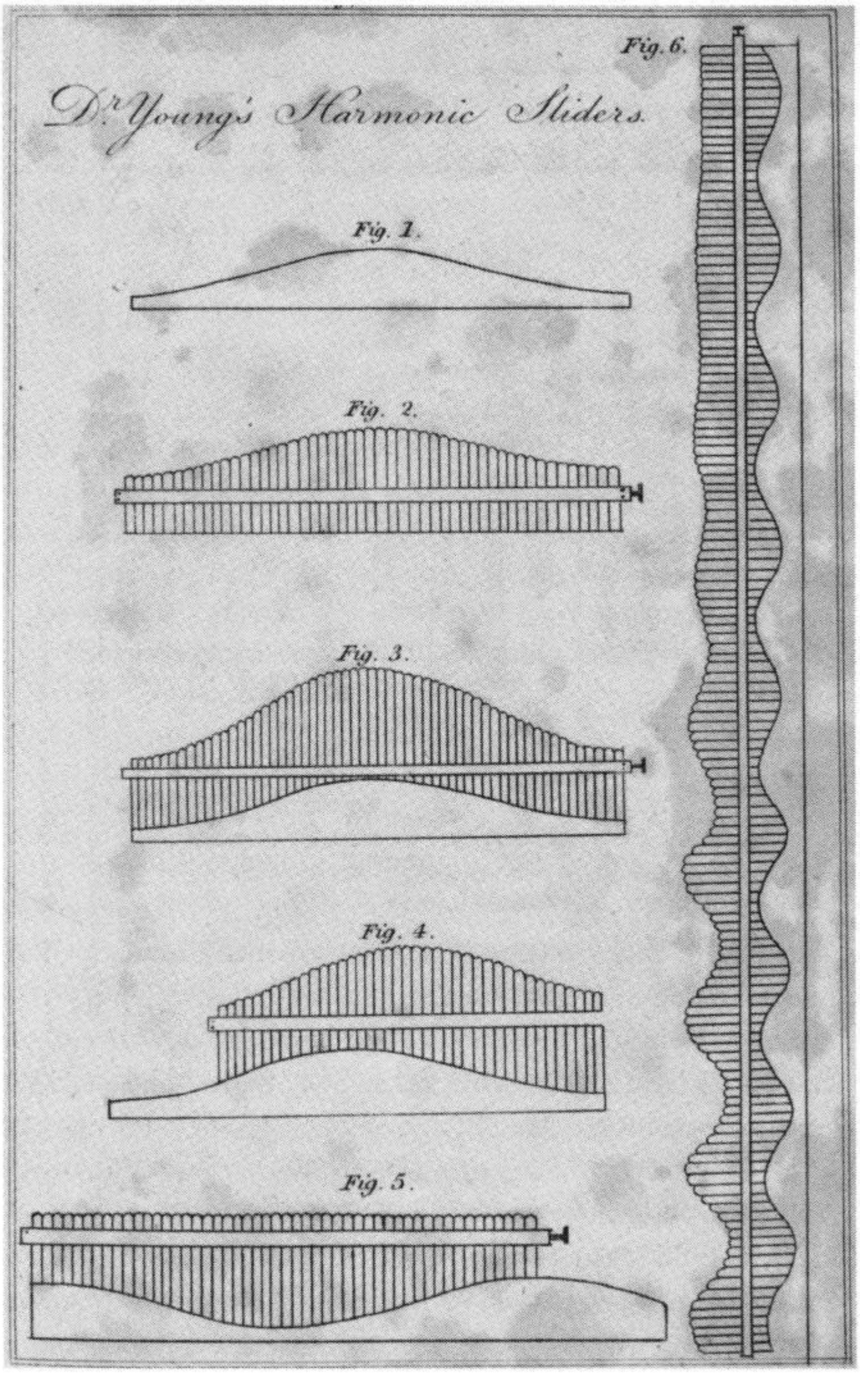


Figure i.4 Thomas Young's 'Harmonic sliders', designed to illustrate the interaction of optical or acoustic waves. A set of sliding rods of varying length (Fig. 2 in the diagram) can be placed on a shaped board representing a second wave (Fig. 1 in the diagram). In different phases (Figures 3–5 in the diagram), the two waveforms constructively or destructively interfere. Figure 6 in the diagram illustrates beating.

To illustrate the concept to his audience at the Royal Institution, Young developed the apparatus shown in Figure i.4: one of two component waves is formed by sliders of different length, the second by a shaped board. The former can be placed in different positions on the latter, to represent different phases (Young 1802b).

Colours.	Length of an Undulation in parts of an Inch, in Air.	Number of Undulations in an Inch.	Number of Undulations in a Second.	Wavelength nm
Extreme -	.0000266	37640	463 millions of millions	
Red - -	.0000256	39180	482	650
Intermediate	.0000246	40720	501	
Orange - -	.0000240	41610	512	609
Intermediate	.0000235	42510	523	
Yellow -	.0000227	44000	542	576
Intermediate	.0000219	45600	561 (= 2^{48} nearly)	
Green - -	.0000211	47460	584	536
Intermediate	.0000203	49320	607	
Blue - -	.0000196	51110	629	497
Intermediate	.0000189	52910	652	
Indigo - -	.0000185	54070	665	469
Intermediate	.0000181	55240	680	
Violet - -	.0000174	57490	707	444
Extreme - -	.0000167	59750	735	

Figure i.5 Young's estimates of the wavelengths and frequencies corresponding to particular hues (Young, 1802a). Values of wavelength in nanometers are added to the right.

By applying his interference hypothesis to Newton's measurements of the colours of thin films, Young was able to map particular hues to the underlying physical variable. Figure i.5 shows his table of the wavelengths that correspond to given colours (Young 1802a). On the right, I have re-expressed Young's values in nanometers. They closely resemble modern estimates. A good test of their accuracy is the value that Young gives for yellow, since this is the part of the spectrum where hue changes rapidly with wavelength and where therefore a physical error would easily reveal itself. His value converts to 576 nm and this is within a nanometer of modern estimates of the wavelength that appears neither reddish nor greenish to an average eye in a neutral state of adaptation (Ayama *et al.* 1987). His estimates for orange, green and violet are similarly close to modern ones. But what makes the accuracy so impressive is that Thomas Young was using not his own measurements but rather those made by Newton in the seventeenth century.

The value given in Figure i.5 for blue (497 nm) is a longer wavelength than would be given today for the blue that is neither reddish nor greenish. However, Newton's 'blew' was embedded in a spectrum that also included indigo. 'Blew' may have been close to cyan, resembling the primary colour term *golyboi* in modern Russian.

The trichromatic theory

In the broader domain of science, Young's Bakerian Lecture is most important for the principle of interference, for the explanation of the colours of thin films, and for the first quantification of the visible spectrum. Visual scientists, however, most often cite the Lecture for its statement of the trichromatic theory of vision. Having grasped that the physical variable corresponding to hue was wavelength and very unlikely to be anything other than a continuous variable, Young saw that the results of colour mixing must be determined by the physiology of the human visual system, by the presence in the retina of a limited number of types of resonator. Yet he introduces the theory only briefly, and as an aside:

> 'Now, as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance, to the three principal colours, red, yellow, and blue, of which the undulations are related in magnitude nearly as the numbers 8, 7, and 6; and that each of the particles is capable of being put in motion less or more forcibly, by undulations differing less or more from a perfect unison; for instance, the undulations of green light being nearly in the ratio of 6 1/2, will affect equally the particles in unison with yellow and blue, and produce the same effect as a light composed of those two species: and each sensitive filament of the nerve may consist of three portions, one for each principal colour...' (Young 1802a)

Notice that in this first account, Young does not refer explicitly to the trichromacy of colour mixture, and he remains hesitant about the number of types of resonator. His uncertainty at this period (1801–2) is clear from the manuscript notes of his Royal Institution Lectures (University College London Archives, *Ms. Add. 13./14, 13./15*): at one point he offers red, yellow and blue as the primitive colours, but at another point he derives all colours from '4 simple colours', red, green, blue and violet. And neither in the manuscript notes nor in the printed *Syllabus* does he clearly explain to his audience what he means by 'simple' or 'primitive' colours.

In his later account of 'Chromatics', written for *Encyclopaedia Britannica* (Young 1817), the trichromatic theory takes on a more sophisticated form. Young assumes the three distinct 'sensations' to be red, green and violet. The rays occupying intermediate places in the Newtonian spectrum excite mixed sensations. Thus monochromatic yellow light excites both the red and green sensations, while monochromatic blue light excites both the violet and the green sensations. By 'sensation' he means here the excitation of his 'sympathetic fibres' or resonators. So he explains that 'mixed excitations' of the fibres—whether produced by monochromatic lights or mixtures—may produce 'a simple idea only', as when excitation of the green and violet fibres leads to the sensation of a pure blue. This is a critical insight. Young realized that the peak sensitivities of the receptors do not necessarily correspond to the hues that are phenomenologically the purest. This insight was not always shared by those who later adopted his theory.

There is a second way in which Young's version of the trichromatic theory was more advanced than that of his successors. For he allowed that the perceived colour of a patch in a complex scene depends not just on the relative excitations of the three types of fibre in the part of the retina illuminated by that patch. It depends also on the context, on the spectral distributions of surfaces in the surrounding field. Already in his *Syllabus* of 1802 he recognizes the existence of colour constancy, the approximate stability of our perception of surface colour when we view a given surface in illuminants of different colour.

> 'Other causes, probably connected with some general laws of sensation, produce the imaginary colours of shadows, which have been elegantly investigated and explained by Count Rumford. When a general colour prevails over the whole field of vision, excepting a part comparatively small, the apparent colour of that part is nearly the same as if the light falling on the whole field had been white, and the rays of the prevalent colour only had been intercepted at one particular part, the other rays being suffered to proceed.' (Young 1802c).

Young was not sympathetic, however, to the phenomenological approach of his contemporary, Goethe. Young's editor saw fit to suppress Young's review of the *Farbenlehre* from his collected works. A short quotation will give a feel for Young's style—and for his opinion :

> 'Our attention has been less directed to this work of Mr. von Goethe, by the hopes of acquiring from it anything like information, than by a curiosity to contemplate a striking example of the perversion of the human faculties, in an individual who has obtained enough of popularity among his countrymen, by his literary productions, to inspire him with a full confidence in his own powers, and who seems to have wasted those powers for the space of twenty years, by forcing them into a direction, in which he had originally mistaken his way, for want of profiting by the assistance of a judicious guide.' (Young 1814).

'. . .but he was not in the habit of making experiments'

Thomas Young published no original experiments on colour mixing or on the perception of colour. Although he did enter into the spirit of the Royal Institution and devised demonstrations to illustrate his lectures (*v.* Figure i.6), and although the two-slit experiment described in his published *Lectures* has proved one of the most influential experiments in modern physics, he was not at heart a committed experimentalist. His lifelong friend and first biographer, Hudson Gurney, records:

> 'In the winters of 1790 and 1791, having prepared himself by previous reading, he attended the lectures of Dr Higgins in chemistry, and began to make some simple experiments of his own on a small scale. But he was afterwards accustomed to say, that at no period of his life was he particularly fond of repeating experiments, or even of very frequently attempting to originate new ones; considering that, however necessary to the advancement of science, they demanded a great sacrifice of time, and that when the fact was once established, that time was better employed in considering the purposes to which it might be applied, or the principles which it might tend to elucidate.'

Similarly, his second biographer, George Peacock, quotes Young as saying: 'acute suggestion was...always more in the line of my ambition than experimental illustration' (Peacock 1855). Later in life, Young opposed any addition to the fund that Wollaston

Figure i.6 A satire by Gillray on the fashionable lectures at the Royal Institution. The engraving was published in May 1802 and almost certainly depicts Thomas Young as lecturer (centre). Young is experimenting on Sir J. C. Hippisley, applying gas to his mouth. To the right of Young, holding the bellows, is Humphry Davy, and standing on the right is Count Rumford.

had left to the Royal Society for the support of experimental science, declaring: 'For my part, it is my pride and pleasure, as far as I am able, to supersede the necessity of experiments, and more especially of expensive ones' (Mayer 1875). The criticisms of Young by Henry Brougham (see above) were taken by nineteenth-century commentators to be inspired purely by personal bitterness (Tyndall 1892)—in the *British Magazine* for 1800 Young had scathingly criticized a mathematical paper by 'a young gentleman of Edinburgh' (Brougham)—but in fact Brougham was also expressing the preference for inductive science and critical experiment that was favoured in the Scottish methodological tradition (Cantor 1971). To be fair to Young, it has to be allowed that the Bakerian lecture of 1801 contains one imaginative set of measurements (on the colours produced by striated surfaces); but for the most part it is theoretical, and in particular it postulates a luminferous ether, an unobservable that members of the Scottish school could not accept.

The trichromatic theory is a good example of the 'acute suggestion' that Young saw as his role. He never attempted to place the theory on a quantitative basis. In his *Lectures* he describes demonstrations in which colours are mixed on rotating discs, but such demonstrations were already antique in 1802. Young's contribution was to release colour science from the category error that had held back the understanding of physical optics in the eighteenth century. He realized that the trichromacy of colour mixture did not mean that there were only three physical kinds of light. Rather it meant that colours were represented by just three variables somewhere in our visual apparatus. James Clerk Maxwell was later to write:

> 'So far as I know, Thomas Young was the first who, starting from the well known fact that there are three primary colours, sought for the explanation of this fact, not in the nature of light, but in the constitution of man.' (Maxwell 1871).

The trichromatic theory after 200 years

It was Clerk Maxwell who first attempted to estimate quantitatively the spectral sensitivities of Young's retinal resonators, by identifying the sets of colours in the trichromat's colour space that were confused by a dichromat (Maxwell 1855). Yet general agreement on the spectral sensitivities, and even the number, of the receptors did not come until the second half of the Twentieth Century, when estimates by Maxwell's method were found to be consistent with direct measurements by reflection densitometry of the fundus of the eye, by microspectrophotometry of individual receptors, and by electrical records from isolated receptors sucked into a micropipette.

Today, it is known that there are four classes of photoreceptor in the normal retina: the rods, which subserve our vision at low light levels, and three kinds of cone, which subserve colour vision as well as the other functions of daytime vision. The rods are most sensitive near 500 nm, a wavelength that appears blue green. The peak sensitivities of the cones lie in the violet, the green, and the yellow-green regions of the spectrum (Figure i.7), and the three types are referred to as short-wave, medium-wave and long-wave respectively. The long- and middle-wave cones are more numerous than the short-wave cones (see Chapter 5).

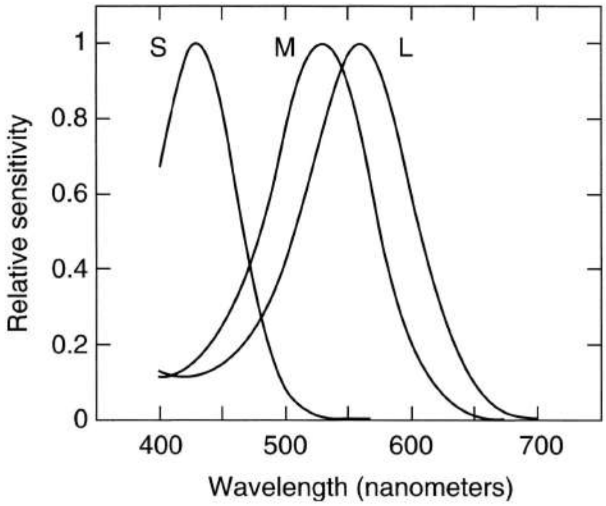


Figure i.7 Sensitivities of the three types of cone receptor in the normal eye. S= 'short-wave', M= 'middle-wave', L='long-wave'.

Each of the four classes of photoreceptor obeys the *Principle of Univariance* (Baylor *et al.* 1987; Rushton 1972): although the stimulus may vary in its radiance and in its wavelength, the response of the photoreceptor varies on only one dimension—the difference in electrical potential between the inside and the outside of the cell. Once an individual photon has been absorbed, all information about its wavelength—its electromagnetic frequency—is lost. What does vary with wavelength is the *probability* of a given photon being absorbed, and spectral sensitivity curves, such as those of Figure i.7, reflect this changing probability.

Each class of photoreceptor gains its characteristic light sensitivity from the photopigment molecules embedded in the enfolded membrane of the cell. Each photopigment is a member of the extended family of G-protein coupled receptors and has a heptahelical structure: the 'opsin', or protein part of the molecule, consists of seven helices, running between the inside and the outside of the cell membrane; and these form a splayed palisade that surrounds the chromophore, 11-*cis*-retinal (see Chapter 1). Variations in the amino acid sequence of the opsin lead to variations in the wavelength of peak sensitivity of the molecule. The short-wave cone opsin is encoded by a gene on chromosome 7, whereas the long- and middle-wave opsins are encoded by genes on the q arm of the X-chromosome (Nathans *et al.* 1986). Most of the common types of inherited colour deficiency are associated with alterations of this cluster of genes at Xq28 (see Chapters 31–33). The gene for the short-wave pigment is ancient and antedates the mammals, whereas the long- and middle-wave photopigments are thought to have diverged during the evolution of the primates, as the result of the duplication of an ancestral gene on the X-chromosome. The ecological factors that drove this divergence are the subject of current debate (see Mollon (2002) and Chapter 3).

The univariance of photoreceptors means that any individual cone, or individual class of cone, is colour blind. The long-wave cones, for example, will give the same signal to lights from any part of the visible spectrum, provided only that the radiances of the lights are adjusted to give the same rates of photon absorption in this class of cones. To find out what colour is present, the visual system must compare the rates at which photons are absorbed in different classes of cone. This is achieved already within the retina, by particular types of ganglion cell that draw inputs of different sign—excitatory or inhibitory—from different classes of cone. Such 'chromatically opponent' cells are typically excited by one part of the spectrum and inhibited by another (see Chapters 7–9).

There are several types of chromatically opponent cell in the retina, distinct in the signals they carry, in their morphology, and in their central projections. At least two minority types of cell oppose the short-wave cone signal to some combination of the signals of the other receptors (Dacey *et al.* 2003), and these ganglion cells project to the koniocellular layers of the lateral geniculate nucleus. The more numerous midget ganglion cells draw opposed inputs from the long- and middle-wave receptors; and these ganglion cells project to the parvocellular laminae of the lateral geniculate nucleus.

For much of its history, the trichromatic theory had the disadvantage of being tied to a simple form of Müller's 'Doctrine of Specific Nerve Energies': there were three types of receptor, these directly excited three types of nerve, and the latter secreted red, green, or blue sensations at some central site. When chromatically opponent cells were first reported in the primate visual system (De Valois 1965), it became the fashion to identify them with the red-green and yellow-blue antagonistic mechanisms postulated by Hering (1878) and to declare that the Young-Helmholtz theory held at the level of the receptors while the Opponent Process Theory held at a post-receptoral level. In fact, the chromatically opponent channels of the early visual system do not correspond in a simple way to the red-green and yellow-blue axes of phenomenological colour space: for example, at the wavelength of unique blue (c. 480 nm), the blue that looks neither reddish nor greenish, a neural channel that extracts the ratio of middle- and long-wave cone signals will not be in equilibrium but will be strongly polarized in the +M direction (Mollon & Estévez 1988). To this day, we do not understand how to incorporate phenomenological observations into our mechanistic theory of colour vision; but the trichromatic theory itself has been released from the ancient demand that it should account for how colours look.

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