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Correlations between the neurobiology of colour vision and the psycholinguistics of colour naming

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Dedicated to Prof. Roman Jakobson, Cambridge, Mass.

Summary. Neurobiological experiments demonstrate that colour sensation is perceived by the brain by processes which, in principle, follow the opponent colour pairs scheme proposed by Hering in 1874. Tests on colour naming in various European, Asian and Central American languages have shown that the opponent scheme is also reflected in psycholinguistics. The linguistic evolution of colour terms proposed by Berlin and Kay (1969) is correlated directly with the ontogenetic development of language in children as elucidated by Jakobson (1941). Colour vision is therefore a suitable field for interdisciplinary investigations of brain processes and linguistics.

Introduction

In 1672, Isaac Newton[1] published his observations concerning the refractive separation of sunlight by a prism into the various parts of the visible spectrum. He also demonstrated that a recombination of the spectral colours gave the sensation of colourless ('white') light. Some 130 years later, Johann Wolfgang Goethe[2] strongly opposed Newton's theory and even questioned his experimental data. According to Goethe, it is inconceivable that white is a combination of all spectral colours. Even today, most people would probably agree intuitively with Goethe - without, however, questioning the validity of Newton's data!

It is the purpose of this review to summarize the neurophysiological data on colour vision which explain the psychophysical basis of Goethe's opposition to Newton, and, in particular, to demonstrate that the biology of colour vision is reflected in, what might be called 'psychic response functions of the human brain'. These responses are, in a very literal sense, answers obtained in evaluations of colour naming, i.e. linguistic investigations.

This problem belongs therefore to the area of interdisciplinary work, correlating problems in brain research with linguistics. In recent years, it has become more and more evident that languages have, in spite of their diversity, universal structural features which reflect parts of the brain's basic information content. The elucidation of the functional organization of the brain should permit an understanding of the structure of languages and their use by man. Conversely, linguistic investigations indicate potential mechanisms of the way in which the brain functions.

It is, however, necessary to add a word of caution here. Results from linguistic investigations can *corroborate* mechanisms in neurobiology; they may even initiate additional biological experiments, but they cannot be used as the *sole* basis for a *new* theory in biology.

Young-Helmholtz' tristimulus theory versus Hering's opponent colour scheme

In continuation of Newton's work, Thomas Young[3], a medical doctor, discovered early in the 19th century that, with a *limited* number of principal colours, *all* conceivable colours can be obtained by mixing. Although Young suggested that this number is probably 3, the situation only became clear later from the work of Maxwell and particularly von Helmholtz[4].

The tristimulus or trichromatic theory is supported strongly in technology: colour printing, colour photography and colour television are based on it. It is also the basis of the colorimetric system introduced by the International Commission on Illumination (I.C.E.) in 1931[5]. Substantial support for the original physiological work of Helmholtz came in the nineteen-fourties and -fifties; it culminated in 1964 in 2 investigations on retinal photoreceptors. Using microspectrophotometry on individual cone cells, Marks, Dobelle and MacNichol[6] recorded the spectra of 10 primate cones, and Brown and Wald[7] recorded those of 4 human cones. The latter investigators found peak sensitivities at about 435 nm, 535 nm and 560–570 nm, corresponding to the receptors that have often been called blue-, green- and red-sensitive cones, respectively.

In the classical tristimulus theory it was assumed that each cone is associated with its own specific nerve fibre which is correlated with 1 of the 3 fundamental colour sensations, namely blue (or violet), green and red. Yellow was assumed to arise from combined red and green excitations, white from excitation of all types, and black from no excitation.

As the tristimulus theory explained much of the data on colour vision fairly well, another theory, namely Hering's opponent colour scheme[8], was almost forgotten in the mid-nineteen-fifties. Hering, a German physiologist, proposed in 1874 that there are 3 *pairs* of *opponent* physiological processes for vision, the members of each pair being antagonistic. The 3 pairs correspond to black/white, red/green and blue/yellow sensations; each member of a pair thus 'opposing' the other member. Hering's postulate of positive *and* negative responses (called 'assimilation' and 'dissimilation') of the same nerve cell was, at that time and for many decades, not accepted in physiology. Even in 1934 Hecht[9] wrote: 'Hering's ideas of assimilation and dissimilation mean nothing in the modern physiology of sense organs and of nerves.'

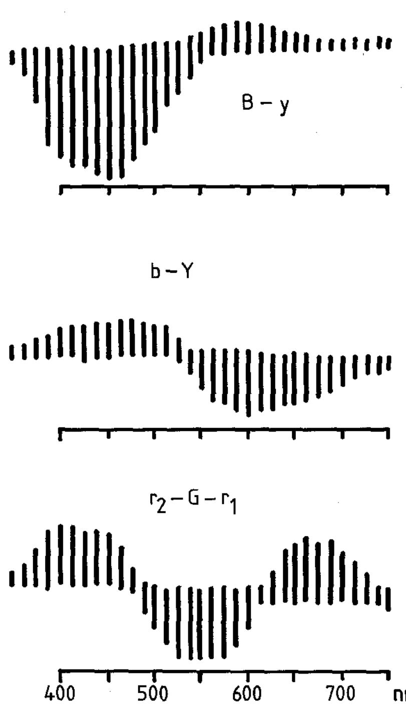


Fig. 1. Electropotentials of two yellow/blue and a red/green ganglion cells in a fish eye[11].

Later, however, physiologists discovered experimentally antagonisms in neural processes and this led to a renaissance of Hering's theory. Granit[10], for example, described his own work as a 'belated vindication of the essential truth of Hering's contention that there are 2 fundamental processes of opposite character in the retina'.

Direct experimental support for Hering's theory was found by Svaetichin[11] and de Valois[12] in the late fifties. Svaetichin found several types of ganglion cells (in the retinas of fish) which were excited by retinal stimuli of one group of wavelengths and were inhibited by stimuli of the complementary wavelength, both for red/green and for yellow/blue rays. In addition, cells were found whose excitation corresponded to the overall sensitivity of the eye, i.e. for achromatic ('white') light. Figure 1 gives examples of Svaetichin's measurements for yellow/blue and red/green sensitive cells.

De Valois et al. made direct recordings from cells in the lateral geniculate nucleus of macaque monkeys. They also found 3 groups of cells: a) excitators which, for stimuli of all wavelengths, respond with increased firing rates; b) inhibitors responding to all stimuli with a decrease in firing; c) opponent cells that respond to red/green or yellow/blue stimuli with increased and decreased firing, respectively. There are cells which are excited by red, and inhibited by green (+R–G cells), and the inverse type (+G–R) was also found. An analogous arrangement was found for yellow and blue (see figure 1 for fish eye cells).

It appears therefore that Hering's concepts were far ahead of the knowledge of neurophysiology at the time they were proposed. Electrophysiological investigations made after Svaetichin's and de Valois' pioneering studies showed, however, that the visual system is even more complex. This becomes evident, for example, from Hubel and Wiesel's work[13]. They demonstrated that, in the geniculate of monkeys, a wide variety of cells exist which have connections with rods and cones, or with cones only, and which handle spatial information, or colour information, or both of these together.

Already in the retina, the connections of the cells are complex. Each photoreceptor is connected to several bipolar cells in such a way that each receptor makes synapses with many secondary neurons and vice-versa. These bipolar cells connect in a similarly complex manner with the retinal ganglion cells whose axons finally form the optic nerve.

It is not the purpose of this review to summarize all the later work in the neurophysiology of colour vision, but to investigate whether the electrophysiological results obtained in the retina and the geniculate of animals are reflected in man's psychic reactions to colour as expressed in colour naming. Before discussion of the psycholinguistics of colour naming, however, Goethe's opposition to Newton's colour physics will be evaluated briefly. On the basis of Hering's opponent colour scheme, Goethe's view that white is not an additive mixture of chromatic colours becomes understandable. Achromatic stimuli are treated trichromatically only on the photoreceptor level of the retina. Later, in the ganglion cells of the retina and in the brain, achromatic information is treated separately, at least in principle, but not exclusively, as more recent investigations, e.g. by Wiesel and Hubel[13], have demonstrated.

In very simple terms, it could be said that the conclusions of Newton are correct when the purely physical (optical) aspects of colour and the photochemistry in the cones are considered, whereas Goethe's opinion is valid when the situation is viewed at the level of the brain.

The transformation of a tristimulus process into a process of 3 opponent pairs is actually not only an intriguing problem for neurophysiologists, but also for information theory. It is interesting to note that it has long attracted the attention of scientists from various disciplines, e.g. Schrödinger[14] and others[15].

Psycholinguistics of colour naming

If the opponent colour scheme of Hering[8], as evaluated by the neurophysiological investigations of Svaetichin[11], de Valois[12] and others, is reflected in man's brain, psychophysical investigations should demonstrate a dominant role for black, white, red, green, yellow and blue, and, in psycholinguistics, terms for these colours should be of primary importance.

With respect to psychophysical investigations, this conclusion was first reached by Jameson and Hurvich[16] in 1955, i.e. at a time when convincing and direct physiological evidence for Hering's theory was not yet available. Jameson and Hurvich carried out colour-mixture experiments by matching stimuli in proper proportions, i.e. by a hue-cancellation technique. The results demonstrated clearly a correlation between the 2 opponent chromatic pairs red/green and yellow/blue. The wavelength maxima corresponded well to the dominant wavelengths of the so-called psychologically pure colours green, blue and yellow, and demonstrated that psychologically pure red is not a monochromatic red, but a mixture of red and a little yellow.

Can we go a step further, i.e. from psychophysical to a psychological response function, namely colour naming? The potential existence of such a correlation was mentioned by Hering, but no attention was paid to it for 98 years!

The study of Berlin and Kay[17] indicates that the Hering scheme might also be reflected in colour naming. From naming tests carried out with subjects in 20 languages, and with the help of a colour chart containing 329 colour samples, and additional evaluations of linguistic publications on colour terms in 78 other languages, Berlin and Kay concluded that the most simple colour lexicon contains words for black and white (or dark and light). If the colour lexicon contains 3 words, a word for red is added to black and white; the 4th word is an expression for green *or* yellow *or* 'grue' (=blue and green). Languages with 5 colour terms have words for black, white, red, green (including blue) *and* yellow; those with 6 words include a term for blue; next an expression for brown is added; and finally in an irregular sequence, expressions follow for pink, violet, orange, grey and others.

Berlin and Kay were actually not the first to discover this sequence: Woodworth and Luckiesh[18] made similar observations over 50 years earlier, but little attention was paid to them. This is obviously a case similar to the discovery of deoxyribonucleic acid by Avery, MacLeod and McCarty[19], where Stent[20] has demonstrated that the time was not ripe in 1944 but only in 1955 when Watson and Crick[21] published their investigations.

Berlin and Kay's monograph soon became one of the most frequently cited references in anthropological linguistics, although it was heavily critizised for some technical deficiencies.

Berlin and Kay's hypothesis indicates that correlations between sensation and perception of colour vision in man might exist, as the first 6 colour terms in their evolutionary scheme are related to the 3 pairs of basic physiological processes of the opponent colour theory. Yet, neither Berlin and Kay, nor reviewers of their work, realized this potential correlation. In a review[22] it was even emphasized that 'it is important to determine whether salience (of colour terms) can be reduced to some neuroanatomical or psychological basis'.

In 1972, we published a note[23] concerning the possible relation of colour term salience to Hering's opponent scheme. In order to test this hypothesis on a more reliable basis, we developed a colour naming test which we carried out with science students in German, French, English, Hebrew and Japanese[24]. It was later repeated with arts students in German and Hebrew[25], and in a slightly different form with illiterate, monolingual Indians in Central America speaking Misquito and Quechi (Kekchi)[26]. First, the subjects were asked to write down colour terms considered to be 'absolutely necessary' for a minimum colour lexicon; next, they were shown and asked to name a set of 117 colour samples made up of 20 hues of the Munsell system on 3–4 levels of brightness and 3–4 levels of saturation. Each sample had to be named within 20 sec.

Evaluation of the 1st part of the test showed that in all languages the terms for white, black, red, green, yellow and blue were listed as 'absolutely necessary'. In the 2nd part of the test, the frequency of occurrence of colour terms and the certainty of determination, a figure derived from the ratio of the sum of all names given to a sample to the total number of subjects, also demonstrated that for samples of high saturation ('pure hues'), a correlation with the principal hues red, green, yellow and blue exists (no achromatic samples were included in this part of the test). Figure 2 shows the frequency of occurrence and the certainty of determination for the German language for the highest level of saturation (chroma 10 in the Munsell notation). The positions of psychologically pure green, yellow and blue are indicated with an arrow (not given for red because psychologically pure red is, as mentioned, a mixture).

This relatively good correlation disappears, however, as soon as we compare hues on a lower level of saturation. Obviously, the higher relative content of polychromatic ('white') light of these samples disguises the simple correlation between opponent colour perception and colour naming.

Colour naming is also disguised by cultural influences. The most striking example of cultural components in colour naming in our tests was found for the Japanese language. It is likely that characteristic differences between Japanese and European languages and Hebrew - lower certainty of determination and preference for black and white relation to chromatic colours - can be traced to the Japanese way of life and to Japanese cultural influences. These differences are at present under investigation. Similarly, the differences in colour test performance between science and arts students are statistically significant[24]; it is likely that they are based on the different educational and cultural background of these students[25].

On the other hand, the lack of a specific term for blue in the language of the Quechi Indians[26] (they use the same word for blue and green) did not influence the test performance of these subjects significantly. The Whorf hypothesis, which states that experience of man is based on categorizations in language, is therefore unlikely to be applicable to colour perception. The biological basis, i.e. the opponent scheme, also seems to be fundamental to colour perception in Quechi Indians.

In spite of the effects which may disguise the opponent colour scheme in colour naming tests, in all evaluations, without exception, the certainty of determination is highest at dominant wavelengths around 550 nm. This is the region of the visible spectrum where the cones have the highest overall sensitivity.

An interesting case is languages which have colour terms only for black and white. Berlin and Kay mention several languages of this type which, however, they did not study in detail. Yet, their findings coincide with newer, more elaborate investigations made by Berlin and Berlin[27] with Aguaruna, a people in the rain forest of North-Central Peru, by Branstetter[28] with Polynesian languages and by Heider[29] with Dani people in New Guinea. In all these languages, the results are similar; they can be exemplified by the test made by Heider. The Dani have 2 basic colour terms: mili (dark) and mola (light). 2 sets of 40 and 160 colour samples of 20 hues on 4 and 8 brightness levels and on a low and the highest possible saturation level were named by 40 Dani subjects. An interesting correlation (not recognized by Heider) was found when we plotted the percentage of Dani who called a certain hue 'mili' against the photopic luminosity, i.e. the sensitivity of the cones at the respective wave-

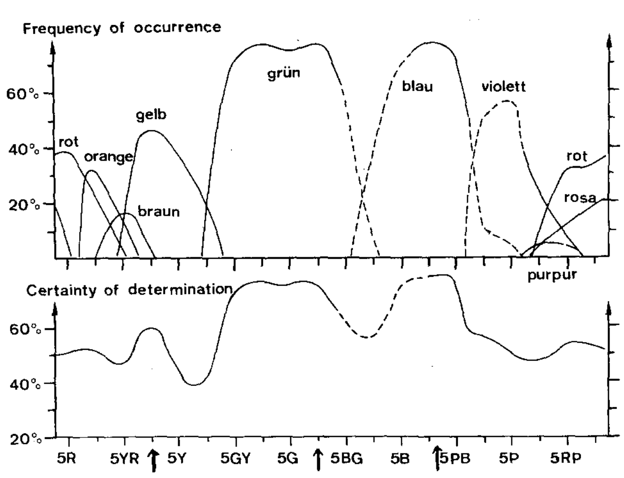


Fig. 2. Frequency of occurrence of colour terms and certainty of determination of colour samples in German (relatively pure hues, chroma = 10), after Zollinger[24].

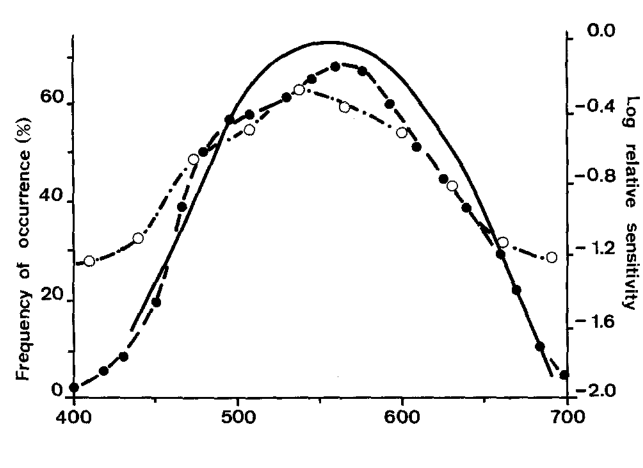


Fig. 3. Distribution of the Dani colour term mili (dark) for relatively pure colour samples (chroma > 8, ●-·-●) and for relatively impure samples (chroma = 2, ○---○). —— Photopic luminosity curve. Figure from v. Wattenwyl and Zollinger[30].

lengths[30]. We obtained a fairly good relationship for the series of samples of highest saturation (solid circles in figure 3). For samples of low saturation (open circles) the Dani do not differentiate as clearly between mili and mola. This is understandable as light reflected from colour samples with low saturation has a broader wavelength distribution or, in other words, the samples reflect more 'white' light.

This almost perfect correlation between a biological parameter and colour naming casts some doubt on the hypothesis of colour vision in man developed by Bornstein[31]. He showed that, with increasing proximity of societies to the Equator, colour terms applied to short wavelengths (green and blue), become more identified with one another. Bornstein claims that this effect is due to more intense yellow intraocular pigmentation which is biometerologically adaptive and which attenuates effective short wavelength radiation. If this hypothesis applies to the Dani, one might expect that the correlations at the short and the long wavelength of figure 3 would not be as symmetric as they are. However, the photopic luminosity curve is based on measurements with Caucasian observers only, whereas the linguistic data were obtained with Dani. Photopic luminosity measurements with Dani are not available, but they should be different if Bornstein's hypothesis is correct.

The smooth relationship between colour naming and the sensitivity of the cones contains a paradox. When the photopic luminosity *in*creases with change in wavelength, a sample is more frequently called mili (dark), and vice-versa for the part of the spectrum above 555 nm where luminosity decreases. If brightness is correlated with the mili/mola categorisation one would expect that the Dani would increasingly classifiy 'brighter' hues as mola (light) and not as mili (dark).

This paradox may be related to an area of colour vision research which has been relatively little investigated until recently, namely the distinction between brightness and luminance, i.e. the relation between a sensation experienced by the observer (brightness) and luminance as a purely physical quality. Guth[32] and Boynton[33] incorporated these factors into psychophysical investigations and demonstrated that they are highly colour- (i.e. wavelength-)dependent. Actually, these problems are also linked to Hering's classical work. Hering[34] believed that the brightness of a spectral light was not only determined by the response in the black/white opponent process, but also by a contribution from the 2 chromatic systems. According to Hering, these contributions were not simply additive; warm chromatic hues had a specific brightness and cool chromatic hues a specific darkness. This corresponds to the differentiation which the Dani make. Hues which they call preferentially mili (dark) are, for our feeling, cool, mola (light) hues are warm[35]. A more quantitative categorisation of cool and warm colour has, however, still to be made. From in vitro experiments, Wasserman[36] was able to show that there is a close relation between maximum brightness and psychologically unique green, yellow and blue, but as in our psycholinguistic tests, not with red!

Owing to the large influence of the colour term sequence described by Berlin and Kay, some investigations which can not easily be accomodated in their scheme have been neglected in the recent literature. For their correlation to Hering's opponent process, those languages in which - even on a restricted lexical level - complementary hues are named with the same words are very interesting. As summarized by McNeill[37], a word meaning both blue and yellow appears in a number of contemporary Slavic languages, e.g. in Servo-Croatian, in Russian, in Czech and in Polish. They are all derived from a Proto-Slavic term polvŭ. This phenomenon of categorizing blue and yellow together is also seen in other linguistic communities, e.g. in Ainu, the language of the indigenous people in Northern Japan, in Daza, a Nilo-Saharan language of East Nigeria and in the language of the Mechopdo Indians of Northern California. The Ainu have also a combined term for red and green. The Chinese and Japanese (Kanji) character for green consists of a combination of the characters for fresh and for red. In addition, it may be mentioned that flavus, used for yellowish hues in Latin, become bleu, blue and blau in French, English and German, respectively.

Besides Berlin and Kay, various authors[38] classify colour terms linguistically in such a way that they group together terms for black, white, red, green, yellow and blue, but not others, as 'primary' or 'landmark' (etc.) colours; they make, however, no reference to potential correlations with the opponent scheme in physiology.

The primacy of a purely physiological component in colour perception was demonstrated elegantly by Bornstein et al.[39] in their investigation of infant's responses to the perception of hue. Their work corroborates well with Hering's scheme, because by several techniques it could be shown that 4-month-old infants responded preferentially to lights in the wavelength ranges of pure blue, green, yellow and red.

Colour and the development of language

In this section we shall discuss a striking correlation between, on the one hand, the step-by-step development of the phonemic system of languages, and, on the other hand, colour perception as elucidated by Hering's opponent scheme (and its more recent neurophysiological corroboration) as well as by the linguistic evolution of colour terms. This correlation can be found in a pioneering study of linguistic research, namely in Roman Jakobson's Kindersprache, Aphasie und allgemeine Lautgesetze (Child Language, Aphasic, and Phonological Universals), published for the first time in 1941. In this monograph Jakobson showed that the development of language in the child takes place in a regular sequence, a sequence which is reversed in patients with aphasia, i.e. persons who lose speech because of mental illness. This sequence is, as Jakobson writes, 'by its very nature closely related to those stratified phenomena which modern psychology uncovers in the different areas of the realm of the mind'.

For our present problem, it is extremely interesting to note that Jakobson recognizes close relationships between speech sounds and colour perception: 'Like visual sensations, speech sounds are, on the one hand, light or dark, and, on the other hand, chromatic or achromatic in different degrees. As the chromatism (abundance of sound) decreases, the opposition of lightness and darkness becomes more marked. Of all the vowels, *a* possesses the greatest chromatism and is the least affected by the opposition light ~ dark ...' Jakobson demonstrates that the vowels *u* and *i* show a 'minimally distinct chromatism' which turns out to be the basic process of dark (*u*) and light (*i*) to which chromatism is added as the 2nd dimension; it leads to *a* which Jakobson calls in later papers[41] the most 'compact' sound. Analogous relationships are observable for the consonants, although they are sounds 'without pronounced chromatism'; the dark quality of labials (e.g. *p*) opposes the light character of the dentals (t); *k* being a relatively chromatic consonant.

That sounds are psychologically related to the perception of colour was already realized before Jakobson, particularly by Köhler[42] and Stumpf[43]; the specific understanding of the development of sounds as parallels to colours is, however, due solely to Jakobson.

These relationships can be symbolized by triangles, the triangle of vowels having been used by Hellwag[44] as early as 1781 (figure 4).

In the context of our problems, the correlations between sounds and specific colours as analysed by Jakobson are most interesting. The vowel *a* as the most chromatic and compact sound is symbolized by red, as various analyses of psychological sensations demonstrated. The axis *u-i* is related to black and white. Blue is between red and black, it corresponds to *o*; *ae* and *e* are located on the *a-i* axis, their corresponding colours are rose and yellow.

Jakobson also realized from the analysis of child language that 'the less structured units in the development of the phonemic system are replaced by more and more structured units (and that) all laws of solidarity are explained by the stratification of more simple and undifferentiated oppositions by more refined and differentiated ones'. Later analogous investigations, e.g. in French by Chastaing[45] confirmed the essential results of Jakobson.

From what has been said in the previous sections of this review one realizes that, in a certain sense, Jakobson predicted the most important parts of the linguistic evolution of colour terms on the basis of analogies to sound developments! First are achromatic oppositions (white/black), followed by an opposition to the optimum chromaticity (red) and by a further refinement within that framework.

This refinement is already indicated marginally in Jakobson's Kindersprache when, in a footnote, he mentions that a 'combination of parallel phonological oppositions' of 2 pairs of vowels or, in Czech, of 2 pairs of consonants[41] might be present:

a	*e*	*k*	*c*
u	*i*	*p*	*t*

The horizontal dimension is the grave-acute opposition, the perpendicular dimension the compactness.

One is inclined to assume a similar square relation for the 4 basic chromatic colours red, green, yellow and blue. However, Vallier[46] has convincingly demonstrated recently that the opponent pairs red/green and yellow/blue are not equivalent. The opposition red/green is a relation between a 'fundamental' colour (red) and its opponent colour green; it signifies the perception of *contrast* of chromaticity. Yellow and blue are, however, chromatically equivalent (but not achromatically, i.e. with respect to darkness); they signify the perception of the *chromatic opposition*. The

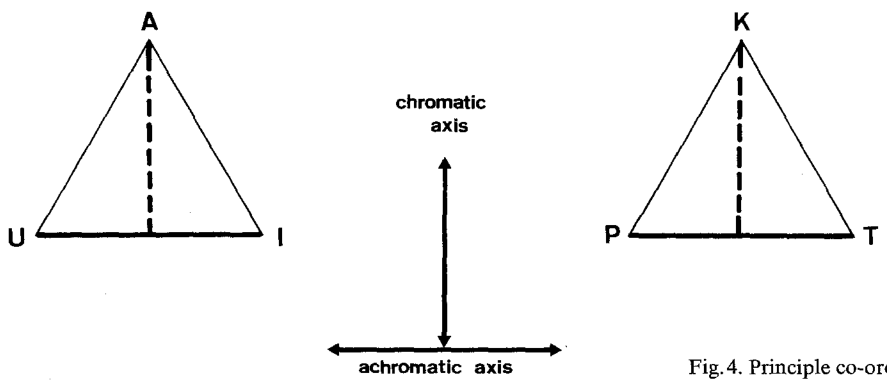


Fig. 4. Principle co-ordinates of sound systems, after Jakobson[40].

pair black/white signifies the perception of the *achromatic opposition.* The weak chromatic character of green can be demonstrated well by the development of the meaning of pallidus which means yellowish green in Latin, but pale in English, in Italian (pallido), and in French (pâle). The feeling that green is normally not a colour of high chromaticity also becomes evident from the expression 'giftiges Grün' (poisonous green) for a very brilliant green, i.e. for a hue considered to be unnatural.

The electrophysiological work of Svaetichin may also indicate that the opponent pair red/green is not equivalent to the yellow/blue pair. As seen in figure 1, there are 2 maxima in the wavelength dependent firing of the yellow/blue cells, but 3 maxima in the cone of red/green cells; the perception of green being the only basic hue requiring excitation in 2 regions of the spectrum. In addition, the nonequivalency of the 2 pairs of opponent colours can be seen from the positions of psychologically pure red, green, yellow and blue in the C.I.E. diagram (figure 5). The positions of yellow and blue (dominant wavelengths $\lambda_D = 583$ nm and 477 nm, respectively) are on an almost perfect straight line through the achromatic centre; this is, however, not the case for red and green ($\lambda_D = 494$ nm and 515 nm, respectively). This result coincides with Vallier's claim that yellow and blue but not red and green are 'perfect' chromatic oppositions. This may seem astonishing to the naive, technical colourist whose experience tells him that by mixing yellow and blue colours one obtains green, whereas mixtures of red and green result in grey. On the other hand, according to Miescher's analysis[47], Goethe[2] was already close to the cognitions that the red-green axis is not equivalent to the blue-yellow axis.

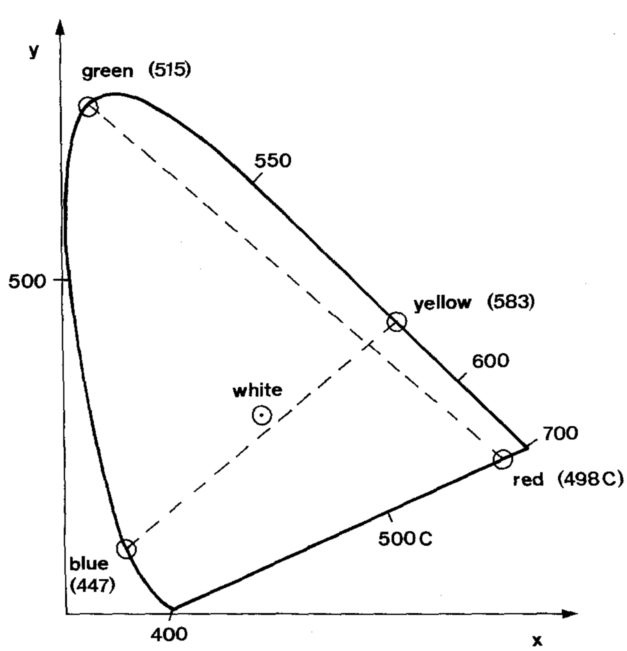


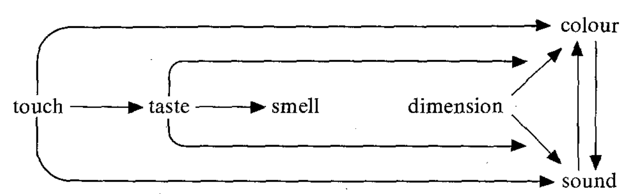
Fig. 5. Positions of psychologically pure red, green, yellow and blue in the C.I.E. colour diagram.

This discussion and figure 5 demonstrate that the 2 opponent pairs of psychologically pure colours red-green and blue-yellow are not pairs of complementary colours, even not compensatory colours in the definitions of (physical) colorimetry.

At least one experimental study of aphasic misnaming of colours with a large number of patients is known. Poeck and Stachowiak[48] found that misnaming is clearly less frequent for black, white, red, green, yellow and blue than for other hues.

In summary, Jakobson, on the basis of investigations of child language and aphasia, predicted results on colour naming 30 years before Berlin and Kay carried out their cross-cultural linguistic study. Jakobson approached the problem from a side which might be called the ontogenetic approach. It is interesting to refer here to a recent linguistic investigation on the phylogenetic evolution of the human senses. Williams[49] investigated the metaphorical use of adjectives which are related to the five senses. He found that adjectives belonging to a certain human sense are transferred metaphorically to the area of another sense almost without exception only in those directions given in scheme 1.

Scheme 1: Metaphorical transfers of sensory adjectives to other senses[a]



[a] The visual sense is referred to in 2 areas, colour and dimension (= spatial perception).

As the senses are arranged in this scheme, metaphorical shifts take place in general only from left to right. Examples which are interesting in the context of colour vision are warm (touch → colour), full (dimension → colour), austere (taste → colour), bright (colour → sound) and strident (sound → colour). Williams demonstrated that scheme 1 applies not only to English, but also to Japanese.

There is strong evidence that the directions of transfer shown in scheme 1 parallel the biological evolution of the senses, i.e. their phylogenetic development in animals and man[50]. The hindbrain of early vertebrates processes tactile, gustatory and vestibular experience, the midbrain of higher vertebrates is specialised in processing olfactory and visual stimuli. The acoustic sense probably developed parallel to the visual sense. This leads to a sequence of sense development from tactile to gustatory, olfactory and finally to acoustic and visual (or visual and acoustic). The fact that the visual and the acoustic senses cannot be put in a distinct sequence parallels their position in William's scheme of metaphorical transfers; this was also recognized by Vallier[51].

It is therefore striking, and probably not incidental, that the sequence of metaphorical transfers of sensory adjectives follows the phylogenetic development of the senses.

Summarizing this review, it can be said that sensation and perception of colour is indeed an area where correlations between the biological basis of colour vision and linguistic aspects of colour perception can be recognized, and even that linguistic principles, such as those developed by Jakobson in a study of the development of speech in children, found their correlate in neurobiology decades later. In a more general way, this becomes evident from 2 statements quoted by Jakobson in his essay 'Linguistics and Natural Sciences'[52]: in his book 'The Language of Modern Physics', E.H. Hutten in 1956 stated that 'science is a linguistic representation of experience', and the biologist A. Lwoff wrote in 1965 in 'Biological Order' that linguistics shares with biology the view that 'stability and variability reside in the same structure'.

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