Vision Res. Vol. 22, pp. 681 to 691, 1982
Printed in Great Britain

0042-6989/82/060681-11$03.00/0
Pergamon Press Ltd

THE "SILENT SUBSTITUTION" METHOD IN VISUAL RESEARCH

O. ESTÉVEZ and H. SPEKREIJSE

Laboratory of Medical Physics, University of Amsterdam, Herengracht 196, 1016 BS Amsterdam, and The Netherlands Ophthalmic Research Institute, P.O. Box 6411, 1005 EK Amsterdam, The Netherlands

Abstract—The "silent substitution" method, which has become well-known mostly through the work of Rushton and his collaborators, can be traced back to experiments performed by M. Ishihara under Exner's supervision at the beginning of the century. Rushton provided a theoretical framework for the method with the enunciation of his "principle of univariance". In this paper we show how the "silent substitution" concept can be further generalized to any arbitrary number of photoreceptor classes by making use of well-established concepts of colorimetry. With this approach, which we have called "spectral compensation", one also gains a better insight into the possibilities and shortcomings of the technique. To illustrate this, we apply our approach to examine a number of published studies where use has been made of "silent substitution", with particular emphasis on the work of W. A. H. Rushton.

INTRODUCTION—A SHORT HISTORICAL NOTE ON "SILENT SUBSTITUTION"

Several years ago we published a paper (Estévez and Spekreijse, 1974) in which the technique of "spectral compensation", as we called it at the time, was introduced.

Our method was meant to be used, both in psychophysics and electrophysiology, as a means of selectively stimulating one type of photoreceptor while keeping other photoreceptors from responding to the stimulus. We thought our technique to be a good alternative to the "chromatic adaptation" method which had become a favourite method for isolating photoreceptor types.

Our technique was based on a property of the visual receptors that Rushton and his collaborators had called the "principle of univariance":

"For each class of receptor the result of light depends upon the effective quantum catch, not upon what quanta are caught" [Mitchell and Rushton (1971a, b); see also Rushton *et al.* (1973a, b, c)].

At the time we thought that the idea underlying our method was a widely accepted concept and, therefore, we did not bother to search for its possible original source. As a matter of fact, Mitchell and Rushton themselves recognized: "The idea of univariance is not new. It is implicit in Young's specific formulation of '3 independent resonators' and equally in Helmholtz's much more general '3 fundamental sensations'."

There is no question, however, that it is largely due to Rushton that the "univariance" concept implicit in Young's and Helmholtz's formulations was made explicit and converted to a fundamental working tool of visual science. Not only did he repeatedly demonstrate the validity and usefulness of the "principle of univariance" in a series of studies concerned with normal and abnormal colour vision, but he also built a research methodology entirely based on, and to some extent inspired by, its validity.

In fact, the method that we called "spectral compensation" had been previously used by him (Donner and Rushton, 1959) for a very similar purpose and under the more appropriate name of "light substitution", although the term "silent substitution" introduced in the same paper has become the most widely accepted one. Rushton had attempted to use the "silent substitution" method as early as 1949 while working at Granit's laboratory, and also other researchers like Forbes and Burleigh (1952), Forbes *et al.* (1955), Biersdorf and Armington (1957), Bongard (1955) and Bongard and Smirnov (1957) had used the same idea before the 1959 article.

Who thought first of the "substitution" concept? In their paper, Donner and Rushton (1959) acknowledged Forbes *et al.* (1955), Bongard (1955) and Bongard and Smirnov (1957) for having used the method first, but the text of Donner and Rushton (1959) appears to indicate that they claim originality. This seems also to follow from the note Rushton added to his paper with Rodieck (Rodieck and Rushton, 1976): "Twenty seven years ago in Stockholm, Professor Granit encouraged me to take up the physiology of vision, and *my first attempt was to study exchange thresholds* (our italics) in the cat. My work was then too inadequate to publish, but the present paper with Dr. Rodieck makes me recall with gratitude the time when Professor Granit launched me into the rich sea of visual research."

In his 1955 paper Forbes mentions trying the "color shift" method—as he called it—in a preliminary experiment carried out in 1950 together with H. K. Hartline at Johns Hopkins University. In the same paper it is explicitly acknowledged that the method was proposed to Forbes by George Wald.

Armington was acquainted with the work of Forbes and he subsequently applied the method to the study of the human electroretinogram, which he published in 1957 (Biersdorf and Armington, 1957). However, he was also aware of Rushton's work and acknowledged him in the same paper (in a reference to a personal communication from Rushton).

It is curious that Granit, in the section "Light Substitution" of his chapter for Davson's *The Eye*, Vol. 2 (1962), does not mention Rushton's early attempts to use the method. The only reference he gives is Forbes's 1955 and 1958 papers.

Another omission of Granit and perhaps a more serious one in view of his intensive involvement in the field of electroretinography, concerns what—up to now—appears to be the earliest reference to the use of the silent substitution method: the work of Makoto Ishihara published in 1906!

Makoto Ishihara (1879–1938) graduated from Tokyo University (Physiology) and subsequently studied in Vienna under Prof. S. Exner. He later became Professor of Physiology at Kyushu University where his interest turned to the physiology of the heart.*

Under Exner, Ishihara conducted an extensive study of the ERG responses of the frog. Among many other experiments, he measured the responses to red and green coloured lights. He found that alternation of two lights that gave the same steady-state response (using a galvanometer) did not abolish the transient. In fact, he observed that the substitution of the two coloured stimuli would produce larger responses than the corresponding red to dark or green to dark transitions (Ishihara, M. 1906).

It appears that the idea of "silent substitution" has occurred to many of us more or less independently as a solution to the same problem. Actually, other methods currently used in visual research also involve the same concept. For instance, the minimum flicker setting achieved with the flicker method of heterochromatic photometry is meant to be a "silent substitution" for the "luminance channel". Another example is the appropriately named "double silent substitution" of Boynton *et al.* (1977): the substitution of one monochromatic light for another that has the same effect on the red and green cones in order to stimulate only blue cones. Finally, the widely used pseudo-isochromatic tests of S. Ishihara—not to be confused with M. Ishihara—are all based on the same principle: the dots forming the test figures are chosen (often empirically) to be a "blank"—or "silent" in spatial co-ordinates—for two of the three colour vision mechanisms.

This small survey of facts, concerning the history of the "silent substitution" concept, may serve those visual scientists who wish to acknowledge the first published reference concerning it. If that is the case, then there is no doubt that M. Ishihara deserves that honour. On the other hand, and without detracting from Ishihara's worth, we honestly believe that "In science the credit goes to the man who convinces the world, not to the man to whom the idea first occurs". (From: Sir William Osler, quoted in Mackay's *The Harvest of the Quiet Eye*, The Institute of Physics, London, 1977).

W. A. H. Rushton is, without any doubt, not only "the man who convinced the world", but also the one who, through his own work, definitely established "univariance" and "light substitution" as permanent research tools of the visual scientist.

UNIVARIANCE AND SILENT SUBSTITUTION

Rushton's principle of univariance essentially means this: the response r of a photoreceptor is a scalar, i.e. a one-dimensional variable $r(\lambda, I)$ of the wavelength λ and the (photon) flux I of the stimulus light. The specific nature of the "response" r, as well as its particular dependence on wavelength and flux is irrelevant. From univariance, it then follows that any two different stimulus lights can be made to produce the same r by allowing the flux of only one of them to change, i.e. silent substitution is possible.

The close relation of univariance with silent substitution can easily lead to confusing the two concepts. Note, however, that univariance is a sufficient condition for silent substitution to be possible, but it is not a necessary one. It is quite plausible that in a given experiment a set of stimuli could be found that would appear to be interchangeable to a multi-variant mechanism, at least as judged by some aspects of the response (e.g. maximum amplitude, or average discharge frequency). These stimuli would allow one to perform, under these conditions, "silent" substitution. In general then, from the fact that one can perform silent substitution in a given experimental condition, one can not prove that the underlying mechanism is univariant [see, for a discussion of this particular point, Sirovich and Abramov (1977)].

In cases in which univariance holds, one can then use the silent substitution paradigm to define a "spectral sensitivity" function $S(\lambda)$ of the univariant mechanism (Scheibner *et al.*, 1975) as: $S(\lambda) = I_0/I(\lambda)$, where I_0 is the flux of a reference stimulus of constant spectral composition (not necessarily monochromatic); and $I(\lambda)$ is the flux of the test stimulus of wavelength λ that produces the same response as I_0.

The attentive reader may have noticed that this is, in fact, the general definition of "spectral sensitivity". What we want to emphasize here is that, in such determinations, silent substitution is explicitly or impli-

*Although this survey is not intended to be exhaustive, we have not been able to find any reference to the use of "silent substitution" earlier than Ishihara's. The information on M. Ishihara's life was provided to us by Prof. Tsuneo Tomita through the agency of Prof. Tarow Indow. We thank both of them for their kindness. Prof. C. R. Cavonius helped us with the translation of the relevant parts of Ishihara's paper.

citly used; for instance, if a spectral sensitivity has been obtained by a constant criterion procedure,* any two stimuli producing the *same* criterion response would, if alternated, cause no detectable change in the *observed* responses, i.e. would silently substitute.

Again, while univariance allows silent substitution, and through silent substitution a spectral sensitivity may be determined, this spectral sensitivity can, in principle, be dependent on the characteristics of the reference stimulus used. The simplest, and best known, case is where the log stimulus–response function changes shape with wavelength, hence the shape of a spectral sensitivity function is dependent on the intensity of the reference (or the magnitude of the criterion response).

However, the principle of univariance—as enunciated by Mitchell and Rushton (1971a, b)—effectively rules out a mechanism with wavelength-dependent stimulus/response functions as being univariant. This follows from the—implicit—assumptions behind the concept "effective quantum catch". As explained below, by "effective quantum catch" Rushton meant that part of the quantum flux that actually produces pigment bleaching, so that "the result of light" on a receptor—its response—would be a function only of the amount of bleaching of its own pigment.

In its original form, the principle was stated in very simple terms because Rushton was clearly thinking only of this interaction of light with the visual pigments as the basis of univariance. In a later paper (Rushton *et al.*, 1973a) he changed the original "the result of light" (in a receptor) to "the intrinsic response of a receptor" and also explained the meaning of the terms "intrinsic" and "effective".

By "effective" quantum catch one is to understand that fraction of the quantum flux that leads to bleaching, and thus to a visual response—this excludes, for example, those quanta caught in a receptor by passive pigments or transition photoproducts. By "intrinsic" one is to understand the change produced in a receptor by its quantum catch, i.e. bleaching its photopigment.

Rushton *et al.* (1973a) found it necessary to make a distinction between receptor (membrane) responses and "intrinsic" responses because, they reported, it appears that in intracellular recordings of cones the responses may show the influence of the stimulus in other classes of cones [they refer to the work of Fuortes *et al.* (1973)].

It is, so far, fairly well established that different types of receptors converge—and interact—as early as the first synaptic connection to the horizontal or the bipolar cells. This means that univariance might in general not hold even as early as the output of the receptors (Svaetichin, 1953; MacNicol and Svaetichin, 1958; Kaneko, 1973). Also, at least in some retinas, there are indications that receptor cells seem to be directly coupled, so that even their membrane responses would not obey univariance either (Baylor *et al.*, 1971; Raviola and Gilula, 1973).

There is, at present, no reason to believe that univariance would not hold with reasonable approximation at the pigment level, thus restricting the sense of "intrinsic" response of a receptor to "pigment bleaching". In point of fact, within the range where the laws of colorimetry hold (Grassmann's laws) one can be reasonably sure that, up to a certain point in the transformation of light to a visual stimulus, the principle of univariance must hold. In what follows we shall try to demonstrate how the Grassmann's laws, themselves at the root of "univariance", provide a basis to develop the theoretical concepts and applications related to "silent substitution".

COLORIMETRY AND SILENT SUBSTITUTION

In order to understand how the "silent substitution" method can be derived very simply from the existing colorimetric concepts, we will review here some of the fundamental facts of colorimetry.

In the simplest case that is studied under laboratory conditions, that of two homogeneous fields seen side by side in a dark environment, one can easily demonstrate that many pairs of different spectral distributions of light can be found that cannot be distinguished from each other. All these spectral distributions are visually "colour matched" to each other and are said to be "colour metamers" or, simply, "metamers".

The laws of basic colorimetry are actually the rules of "metamerism". Since metamerism itself is but an expression of the limited ability of the visual system to make spectral matches, understanding its rules is equivalent to an understanding of the basic processes that underly colour perception.

The most important single property of colour vision revealed by metamerism is the linearity of the colour matching process as expressed in the following facts (Grassmann's laws):

(a) The stability of colour matches. Within wide limits, increasing or decreasing in the same proportion the intensities of two metameric lights A and B does not affect the visual match, these lights continue to be metamers.

(b) The additivity of colour matches. If another metameric pair C and D is found, the mixture of A and C is metameric with the mixture of B and D.

(c) The commutativity of colour matches. C and D may be interchanged, so that the mixture of A and D is metameric with the mixture of B and C.

Because of these observations—Grassmann's laws—we know that the visual mechanism where

*Usually "constant criterion" is applied to amplitude only. Note, however, that this is not sufficient since any change in the response (i.e. latency, waveshape, etc.) caused by changing wavelength means that the system distinguishes between stimuli.

colour matches are performed must be in essence linear. It is, in fact, this linearity that we make use of in the "silent substitution" technique.

Thanks to the linearity and trichromacy of (foveal) colour vision a method to quantify "colour" can be given: the amount r, g and b of the three primaries used to obtain the match, called "tristimulus values" or, simply, tristimulus, define the colour of $Q(\lambda)$. By convention, and due to linearity, if one of the primaries was mixed with $Q(\lambda)$, then its amount is given with a minus sign. This is the basis of the colorimetric method.

Once a set of primaries has been chosen, e.g. the primary basis R, G, and B, the colorimetric method can be taken a step further if the spectral distribution $Q(\lambda)$ is known: since the tristimulus values of colour mixtures are the sum of the tristimulus values of the individual components (because of the additivity property), we can compute the tristimulus of $Q(\lambda)$ by considering it as a mixture of monochromatic lights and adding their tristimulus values.

To this end, it is convenient to have available the tristimulus of monochromatic bands of light, of constant energy, as a function of wavelength. These three functions, $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ are called the "colour-matching" functions (c.m.f. for brevity). In terms of the c.m.f. the tristimulus of $Q(\lambda)$ are:

$$q_r = \int Q(\lambda)\bar{r}(\lambda)\mathrm{d}\lambda,$$
$$q_g = \int Q(\lambda)\bar{g}(\lambda)\mathrm{d}\lambda,$$
$$q_b = \int Q(\lambda)\bar{b}(\lambda)\mathrm{d}\lambda.$$

The laws of colorimetry can be simply related to the physiological processes underlying colour vision provided that, (a) trivariance is interpreted as the expression of three independent mechanism S_1, S_2, S_3 and (b) each of these mechanisms performs a linear operation on the spectral distribution of the stimulus light. Given our present knowledge about receptor photopigments, a field that Rushton's contributions considerably enlarged, we can safely assume that the three mechanisms S_1, S_2, S_3 are the three cone pigments and that their linearity is that implicit in the principle of univariance: the effective stimulus for each colour mechanism is (proportional to) the total effective quantum catch in its corresponding pigment.

In colorimetric terms, if two lights with physically different spectral distributions $P(\lambda)$ and $Q(\lambda)$ are metamers, then these two lights have the same tristimulus values, i.e.

$$\int P(\lambda)\bar{r}(\lambda)\mathrm{d}\lambda = \int Q(\lambda)\bar{r}(\lambda)\mathrm{d}\lambda$$
$$\int P(\lambda)\bar{g}(\lambda)\mathrm{d}\lambda = \int Q(\lambda)\bar{g}(\lambda)\mathrm{d}\lambda$$
$$\int P(\lambda)\bar{b}(\lambda)\mathrm{d}\lambda = \int Q(\lambda)\bar{b}(\lambda)\mathrm{d}\lambda. \quad (1)$$

On the basis of the ideas presented above, the match of $P(\lambda)$ and $Q(\lambda)$ must be achieved when the equivalent quantum catch of the three colour mechanisms S_1, S_2 and S_3, the physiological tristimulus, are the same for the two lights, i.e.

$$\int P(\lambda)S_1(\lambda)\mathrm{d}\lambda = \int Q(\lambda)S_1(\lambda)\mathrm{d}\lambda$$
$$\int P(\lambda)S_2(\lambda)\mathrm{d}\lambda = \int Q(\lambda)S_2(\lambda)\mathrm{d}\lambda$$
$$\int P(\lambda)S_3(\lambda)\mathrm{d}\lambda = \int Q(\lambda)S_3(\lambda)\mathrm{d}\lambda. \quad (2)$$

[where $S_1(\lambda)$, $S_2(\lambda)$ and $S_3(\lambda)$ represent the quantum spectral sensitivities of the corresponding photopigments].

Let us consider now the relation between these internal physiological tristimulus values and the external tristimulus value as measured in a visual colorimeter. For this purpose, we can imagine that the colour-matching functions of a normal trichromatic observer are being measured; the three primaries R, G and B have been chosen to be monochromatic bands of light of equal quantum flux. Now, when the subject is presented with a unit of primary R, this will produce an effective quantum catch in the three photoreceptors: S_{1R}, S_{2R} and S_{3R}. Of course, if instead of one unit R we take r units, the corresponding values will be rS_{1R}, etc. and similarly for primaries G and B. Now, because additivity holds, the mixtures of r, g, b amounts of the primaries R, G and B will be equivalent in receptor S_1 to a single stimulus

$$S_1 = rS_{1R} + gS_{1G} + bS_{1B} \quad (3)$$

and similarly for S_2 and S_3.

If we are asking our subject to make matches to monochromatic lights $u(\lambda)$ of equal quantum flux, we can write his match equations as

$$u(\lambda) = \bar{r}(\lambda)\mathrm{R} + \bar{g}(\lambda)\mathrm{G} + \bar{b}(\lambda)\mathrm{B}, \quad (4)$$

where $\bar{r}(\lambda)$, $\bar{g}(\lambda)$, $\bar{b}(\lambda)$ will be his colour-matching functions (for an equal quantum spectrum). Since each unit quantum flux monochromatic light $u(\lambda)$ will produce in S_1 an effective stimulus $S_1(\lambda)$, as given in (3) above, the corresponding physiological tristimulus match equation can be written

$$S_1(\lambda) = S_{1R}\bar{r}(\lambda) + S_{1G}\bar{g}(\lambda) + S_{1B}\bar{b}(\lambda)$$
$$S_2(\lambda) = S_{2R}\bar{r}(\lambda) + S_{2G}\bar{g}(\lambda) + S_{2B}\bar{b}(\lambda)$$
$$S_3(\lambda) = S_{3R}\bar{r}(\lambda) + S_{3G}\bar{g}(\lambda) + S_{3B}\bar{b}(\lambda). \quad (5)$$

The functions $S_1(\lambda)$, $S_2(\lambda)$ and $S_3(\lambda)$ are, except for a constant factor, equal to the quantum spectral sensitivities of the three photoreceptors, since they correspond to the quantum catches produced in each by units of quantum flux of monochromatic lights. The above relation then states that each of these spectral sensitivities is a linear combination of the colour-matching functions of the normal trichromatic observer.

INDEPENDENT STIMULATION OF THE COLOUR MECHANISMS: SILENT SUBSTITUTION BY THE "SPECTRAL COMPENSATION" METHOD

We observe now that when two lights with physically different spectral distributions form a complete visual match (metamers), they are exactly equal for the three cone pigments and, therefore, completely interchangeable for the visual system. If one of these two lights was substituted for the other, the visual system would not be able to detect the change.

Let us see what happens if we restrict the metameric condition to only two of the three colour mechanisms, that is, assume we have two lights $M(\lambda)$ and $N(\lambda)$ such that

$$\begin{aligned} &\int M(\lambda)S_1(\lambda)\mathrm{d}\lambda = \int N(\lambda)S_1(\lambda)\mathrm{d}\lambda \\ &\text{and } \int M(\lambda)S_2(\lambda)\mathrm{d}\lambda = \int N(\lambda)S_2(\lambda)\mathrm{d}\lambda \\ &\text{but } \int M(\lambda)S_3(\lambda)\mathrm{d}\lambda \neq \int N(\lambda)S_3(\lambda)\mathrm{d}\lambda. \end{aligned} \tag{6}$$

The two lights $M(\lambda)$ and $N(\lambda)$, which we will call partial or dichromatic metamers, have a very important property, namely if one of these two lights is substituted for the other, the change will go unnoticed (i.e. it will be silent) for two of the three colour mechanisms. The same change will, however, be detected by the third mechanism.

This is the basic idea underlying what we called the "spectral compensation method": to find two stimuli that will be metameric for two of the three colour mechanisms (dichromatic metamers) in order to modulate the input to the third one.

The problem is, of course, that we need to have a means of finding, for every one of the colour mechanisms, the appropriate stimuli that will satisfy dichromatic metamerism. This is not so difficult as it would seem at first sight. In fact, we will now show that, if we know the spectral sensitivities $S_1(\lambda)$, $S_2(\lambda)$ and $S_3(\lambda)$, any three lights that satisfy the independence condition of a colorimetric primary basis, can be mixed and modulated in such a way that partial metamerism results.

We begin by writing in matrix notation the three linear relations [equation (3)] between the stimuli r, g and b and the total quantum catch produced in each of the cone pigments

$$\begin{bmatrix} S_1 \\ S_2 \\ S_3 \end{bmatrix} = \begin{bmatrix} S_{1R} & S_{1G} & S_{1B} \\ S_{2R} & S_{2G} & S_{2B} \\ S_{3R} & S_{3G} & S_{3B} \end{bmatrix} \begin{bmatrix} r \\ g \\ b \end{bmatrix}. \tag{7}$$

Since we are assuming that we know the three spectral sensitivity functions, and the primaries R, G, B are either monochromatic or their spectral distributions are known, the elements of the matrix can be found by simply computing the effect of each primary on every pigment, for instance

$$S_{1R} = \int R(\lambda)S_1(\lambda)\mathrm{d}\lambda \tag{8}$$

Let us write equation (7) in abbreviated form:

$$S = M \times C, \tag{9}$$

where S and C are the effective cone stimuli and colour mixture column vectors and M represents the transform matrix; if we call N the inverse matrix of M, then

$$C = N \times S. \tag{10}$$

We notice that, within the limits imposed by the transformation M, one can choose to stimulate the three cone systems in some ratio $x:y:z$ by finding the corresponding values of r, g, b solving equation (10).

Similarly, if the R, G and B lights were modulated by some value Δr, Δg and Δb, the corresponding changes in S are given by [using equation (9)]: $\Delta S = M \times \Delta C$.

We can impose the condition that ΔS_1 and ΔS_2 are to be 0 and ask what Δr, Δg and Δb should be. For this we solve equation (10), written in extended form as

$$\begin{bmatrix} \Delta r \\ \Delta g \\ \Delta b \end{bmatrix} = \begin{bmatrix} a_1 & a_2 & a_3 \\ b_1 & b_2 & b_3 \\ c_1 & c_2 & c_3 \end{bmatrix} \begin{bmatrix} 0 \\ 0 \\ \Delta S_3 \end{bmatrix}. \tag{11}$$

Clearly, making $\Delta r = a_3\Delta S_3$, $\Delta g = b_3\Delta S_3$ and $\Delta b = c_3\Delta S_3$ will result in the desired change, i.e. the stimulus formed by the mixture of r, g, b and the stimulus $r + \Delta r$, $g + \Delta g$, $b + \Delta b$ will be dichromatic metamers or silently substitute for the S_1 and S_2 cones, but will cause a stimulus ΔS_3 in cone class S_3. Notice that the solution is valid for any type of spatial or temporal modulation, as long as we can generate the necessary stimuli corresponding to Δr, Δg and Δb. Finally, notice that we are not restricted to modulating only one cone class: we can specify any desired solution ΔS_1, ΔS_2, ΔS_3 and solve for Δr, Δg and Δb exactly as above.

Given the state of present technology, one can easily realize the required trichromatic stimulus using a colour CRT monitor to generate almost any spatio-temporal input modulation to each of the cone systems, provided that the effective modulation of the systems need not be too great. All we need to do is, once the colour stimuli of the CRT have been calibrated, simply drive the monitor through a network that realizes the transform of equation (11).

The realization of (simultaneous) silent substitution by the "spectral compensation" method, as outlined above, is not only a simple solution to the problem of separately modulating the different colour mechanisms, but it is also a very powerful one. It is the only method* that allows, in principle, for simultaneous

*In principle, one could dissect a retina and prepare it so as to illuminate individual receptors with separate light stimuli. Such a preparation cannot yet be realized. The difficulty would be greater if we wanted to stimulate many receptors of a given type.

modulation of all three classes of cones (or even rods, if one extends the matrix to four dimensions and the stimuli accordingly) with totally different types of input.

A further advantage, and one that should be fully appreciated, is that the experimenter can specify his stimuli in a physiologically meaningful way: in terms of effective cone quantum input. This is more satisfactory than simply analysing data in terms of the physical features of the stimulus, such as colour and intensity used; the use of physical variables is, of course, necessary in a description of the experimental paradigm but, in order to analyse the results properly one would rather know what each cone class effectively received as its input.

The method also lends itself to simplifications, such as the one we originally used in our 1974 paper: if the blue stimulus is eliminated and the red and green lights are chosen in such a way that their effective input to the short-wavelength-sensitive cones remains negligible, the matrix reduces to two dimensions, with the corresponding simplification in the stimuli.

As we shall discuss below, every form of the "silent substitution" method can easily and readily be understood within the framework just outlined. The differences, when present, mostly concern the ways different researchers have followed in order to find the stimuli that will "silently substitute" in their own experimental paradigm and also, the particular purpose for which they used the method.

In the following section, we will examine some of the most notable applications of "silent substitution" and the (in our opinion) most interesting and important results obtained with it. It will be shown that the method allows not only the determination of the spectral characteristics of the separate photoreceptor-systems, but also—and more importantly—the controlled study of the interaction between these systems. However, because this paper is written primarily to honour Rushton, we will especially emphasize those questions where he was particularly active and to whose solution he largely contributed.

ELECTROPHYSIOLOGICAL STUDIES WITH SILENT SUBSTITUTION

It is remarkable that all of the early work using silent substitution was done in electrophysiological studies. In fact, the birth of the concept can probably be attributed to the need some researchers felt for a means of assessing whether "colour" sensitivity could be demonstrated in animals and animal preparations.

Ishihara, for example, was attempting to find if there was indeed a sensitivity specific to changes of colour in the frog retina. He stated: "Wenn es eine spezifische Empfindung für Veränderungen gibt und dieselbe im elektromotorischen Verhalten des Bulbus und seines Nerven zum Ausdruck kommt, so war auch der Fall zu untersuchen, wo Lichter gleicher Intensität nach einander dieselbe Netzhautstelle treffen, diese Lichter aber doch verschieden waren. Die Verschiedenheit betraf natürlich ihre Farbe." (As there is a specific sensitivity to change, which can be observed in the electrical response of the eye and optic nerve, we would investigate what happens when lights that have the same intensity, but which differ in some other way, are presented in succession to the same part of the retina. The lights differ, of course, in colour.)

He found that ERG (corneal) responses of the excised frog eye could always be obtained by the exchange of red and green lights. This result was obtained irrespective whether these lights had been equated according to human heterochromatic photometry (Ishihara acknowledges Brücke for the photometric method) or, more importantly, whether the lights had been adjusted to produce the same ERG response measured with the galvanometer. Perhaps his most interesting observation was that the responses to red/green transitions were larger than either red to dark or green to dark, although he did not draw any conclusions from these facts.

The first paper of Rushton on silent substitution (Donner and Rushton, 1959) was also a study on the frog retinal-ganglion cell responses recorded with a Pt electrode. The question that Donner and Rushton investigated was whether different photoreceptor types (rods and cones) could contribute to the response of a single ganglion cell. To find out, they used the silent substitution paradigm in its most straightforward application: to determine spectral sensitivity functions of the ganglion cell discharges during different states of light adaptation.

Of historical interest is to note that the term "silent substitution" was first used in this paper: since the ganglion cell discharges were fed to a loudspeaker, the researchers could tell by ear that the substitution of two lights did not produce a noticeable change in discharge rate, e.g. the substitution was "silent".

In their study, Donner and Rushton chose to investigate only those cells for which silent substition was possible. They found that in fully light-adapted retinas the spectral sensitivity was that identified by Granit as "photopic dominator". Similarly, in the fully dark-adapted retina the same cell sensitivity function corresponded to rhodopsin.

During light adaptation silent substitution was possible up to mesopic levels but the spectral sensitivity functions changed in a way that reflected contributions from cones. At high mesopic levels, however, silent substitution was not possible until the retina was fully light adapted. At this point the sensitivity functions were clearly those of cones. From these results Donner and Rushton concluded that rods and cones could feed the same ganglion cells.

In their discussion they noted that the results obtained at both extremes of adaptation could be easily understood: a single receptor contribution implies that silent substitution should hold. Similarly,

they readily accepted the impossibility of obtaining silent substitution at intermediate levels where both types of receptors would be contributing. They were puzzled, however, by the fact that near the dark-adapted state changes in the sensitivity functions could occur without disturbing silent substitution. In view of the ideas presented above, we could theorize that at low levels the signals from cones added linearly to those of rods, hence silent substitution was possible, whereas at intermediate levels nonlinearities in the receptor–ganglion cell paths would preclude it.

In comparison with the work of Rushton, the studies of Forbes and collaborators were of a simpler kind, as was the case with Ishihara's. They only asked whether an ERG response (in turtle's retina) could be obtained to a pure "color shift". As Ishihara did, Forbes *et al.* adjusted the intensities of different coloured lights to produce responses as nearly equal as possible (with different colours they obtained different ERG waveshapes).

The main conclusion of their studies was that, in the fully light-adapted turtle retina, a pure "color shift" always produced a detectable transient response which... "can be taken as strong presumptive evidence of color-discriminating mechanism in the cones of the turtle". (They probably meant: in the retina of the turtle.)

A study more akin to that of Donner and Rushton was performed by Scheibner *et al.* in the optic tectum of the frog (Scheibner *et al.*, 1975). They investigated two specific types of ganglion cell discharges (classified according to their sensitivity to spatial features of the stimulus), and asked "whether or not the frog possesses a neurophysiological basis for a colour vision".

It was Scheibner *et al.* who made explicit reference to the relation between silent substitution and the measurement of spectral sensitivity functions. They did not, as did Donner and Rushton, exclude any cell from their study, but rather investigated whether silent substitution was possible over all or only part of the spectrum, and found the latter to be true in certain cases. Because of this, the functions they obtained were formed sometimes by two or three disconnected sections. In those cases they correctly identified the underlying mechanism as not being univariant. If a single connected spectral sensitivity function could be measured, i.e. if silent substitituon was possible over the full visual spectrum, they called the underlying mechanism "univariant". There is a theoretical problem here since, as we have discussed above, the fact that silent substitution can be performed need not imply that the underlying mechanism is univariant.

They were, nevertheless, aware of these problems, as they state: "If a visual mechanism is fed by only one photopigment, its response behaviour is necessarily an univariant one.... But the converse is not necessarily true: if an univariantly responding mechanism appears, it need not be subserved by only one photopigment." The only problem, then, with their analysis is their identification of an "univariantly responding mechanism" whenever silent substitution appears to be possible.

Although this is an important theoretical point, it is of no significance with respect to their most interesting results and conclusions, namely the finding of ganglion cells with disconnected sensitivity functions, which "necessarily means that more than one visual pigment contributes to the output of this neuron".

As we remarked concerning the conclusions of Donner and Rushton's study, we should also add here that if silent substitution is impossible we know not only that more than one receptor type is contributing to the response, but also that their outputs do not add linearly, for if that was the case, silent substitution would be possible.

From the results of the studies mentioned above, it appears quite well established that the ganglion cell signals convey information from several types of receptors, mixtures of cone signals and/or rods, and that these receptors interact non-linearly at some point either before or at the ganglion cell level.

In a very elegant and thorough study Rushton and Rodieck re-examined the contributions of the cat's rods and cones to ganglion cell discharges using the silent substitution method (Rodieck and Rushton, 1976).

They were the first to use, in electrophysiological experiments, one of the most powerful features of the silent substitution paradigm: the ability to present a stimulus to one receptor type while maintaining the others unmodulated. In this way, they were able to follow individual dark adaptation curves of rods and cones simultaneously as well as their adaptation curves following strong bleaching.

To achieve this, they adjusted the intensities of an orange and a white (tungsten) light, so as to render them equal for the cat's rod receptors, thus obtaining a light mixture which only stimulated cones. Rushton liked to call this equality condition the isolept, from the Greek equal and take, or equal catch. Therefore, he called this stimulus the "rod isolept". Similarly, they adjusted these same lights to be equal for the cones—the "cone isolept"—so that their exchange would be a stimulus only for the rods. Once the rod and cone isolepts had been determined, it was an easy matter to follow rod and cone adaptation simultaneously by switching back and forth between the two. As they say in the introduction: "At the cone isolept the time course of early rod dark adaptation could thus be determined when the rod threshold to flashing spots lay well above that of cones."

Their results of cone and rod adaptation were in agreement with those previously obtained using more conventional adaptation techniques. However, the strength of the silent substitution paradigm is that by measuring these function simultaneously one can also determine their positions relative to each other. Rodieck and Rushton could conclude: "We have a new observation to contribute: for white lights, or

weakly coloured ones, the cat rod increment threshold curve leaves the Weber region in going to saturation at about the same point that the cone curve is entering its Weber region. Thus for the coding of contrast, cones take over just where rods leave off."

Another electrophysiological study in which the potential of the silent substitution paradigm has been exploited is that of Gielen (1980). He studied responses at the lateral geniculate nucleus of rhesus monkey while modulating the input to either red or green cones. Since many cells studied revealed a colour-coded center surround organization, he was able to separate the two contributions to the responses, thus revealing subtle but significant differences in their latencies. His study is also interesting in that it combined advanced system-analytical methods, such as the use of noise-modulated stimuli and cross-correlation techniques, with the silent substitution method to study the dynamic characteristics of the pathways fed by each of the cone classes. Of interest here is to mention that no significant difference between the dynamics of the red and green fed pathways was found. Thus, presumably, the underlying neural systems may have a comparable structure.

As far as we know, the full potential of the silent substitution method, i.e. modulating simultaneously different receptor types with different stimuli to study interactions, has only been performed by us in our studies of the human contrast evoked potentials (Estévez, 1977; Spekreijse *et al.*, 1977; Estévez and Dijkhuis, in preparation).

We have found that the EP responses obtained by stimulating either red or green receptors are in all senses comparable: the waveforms do not differ, the latency, the sensitivity to changes of temporal and spatail parameters of the stimuli are identical and, finally, the distribution over the scalp is the same (Estévez and Dijkhuis). From these results we have concluded that, in humans, the neural pathways fed by red and green receptors must have similar or identical structures. These conclusions agree with those of Gielen (1980) mentioned before. The use of simultaneous stimulation of red and green cones has given us a better insight in the characteristics of the conventional—white light—EP responses. For instance, using silent substitution we had previously found that each of the cone systems—blue, green or red cones—or even the rods, could give rise to a true contrast evoked potential (Estévez *et al.*, 1975). From those results we concluded that either, (a) each system comprises a cortical EP generating mechanism or, (b) one single cortical stage where contrast is processed can be accessed by all receptor types (Regan and Spekreijse, 1974). These alternatives were tested in a study with simultaneous presentation of contrast stimuli to both red and green receptors. We have concluded that, first, only one cortical EP mechanism is present and secondly, that these two cone systems actively compete to gain input to this cortical stage. This conclusion is supported by the following findings: if only one cone system is presented with a contrast pattern, the responses can be larger than the largest one obtained with white light—stimulating several mechanisms; if a low contrast non-modulated pattern is presented to one cone system the responses to contrast modulation of the other are much diminished or even suppressed; finally, when the contrast pattern is presented alternating to red and green cones, the EP resembles the characteristic responses to pattern reversal stimuli (Spekreijse *et al.*, 1977; Estévez and Dijkhuis, in preparation).

Except for the interactions at the level of contrast processing, we have, so far, not been able to find any sign of colour-coding per se. So far, the responses we obtain appear to be mainly determined by the contrast features of the stimuli to the red and green cones and not by the presence or absence of chromatic modulation.

PSYCHOPHYSICAL STUDIES WITH SILENT SUBSTITUTION

Rushton's theoretical and experimental ingenuity, and his ability to exploit a concept from every possible angle can be illustrated by the many ways in which he applied the concept of silent substitution. Of special significance in this context are the two articles of Mitchell and Rushton (1971a, b) and the three from Rushton *et al.* (1973a, c).

We have shown above that, if the sensitivities of the cones are known, we can easily find the appropriate silent substitution stimulus by computation. Rushton undertook, with success, to determine these cone sensitivities. It is remarkable that, to do this, he also applied in many imaginative ways the substitution concept itself.

The first article with Mitchell reported on measurements of the spectral sensitivity of the long wavelength cone pigments of protanopic and deuteranopic dichromats (Rushton liked to call the respective pigments "chlorolabe" and "erythrolabe"). The data were obtained by means of Rushton's fundus reflection densitometer: the intensities of different monochromatic lights were adjusted so as to obtain a constant amount of bleaching—essentially a silent substitution technique—in the foveal retinas of dichromats. Furthermore, the sensitivity functions of the same subjects were determined by means of subjective brightness matches. By these means the subjectively determined sensitivity function was shown to be in agreement with the objective densitometric measures.

In their second paper, Mitchell and Rushton applied an elegant technique, that combined silent substitution and colour matching, to demonstrate that chlorolabe is one of the pigments of normal and protanomalous trichromats and that erythrolabe is a pigment of normal and deuteranomalous trichromats.

Their method was as follows: after a protanopic

subject had adjusted the intensities of a red ($\lambda > 620$ nm) and a green (550 nm) light to be equal, these two lights were mixed in a variable ratio. The subjects had to change the hue of this field to match that of a monochromatic light (550–634 nm) by adjusting the ratio red/green, but this did not change the intensity "seen" by chlorolabe, since these lights were equal for the protanope. Once the hue was right, the intensity of the monochromatic light had to be adjusted to obtain complete equality of the two fields. Now, since at match the quantum catch in all pigments must be equal in both sides, the intensity of the monochromatic light had to be such that chlorolabe, if present, would receive equal flux from both sides. Therefore, if chlorolabe was one of the normal pigments, normal trichromats would make in this situation exactly the same intensity settings as the protanopes. This proved indeed to be the case.

When the instrument, called the Florida Analytical Anomaloscope, was adjusted by the protanope, it was said to work in its "prot mode". The experiments were also carried out in the "deut mode", in both normal and anomalous trichromats, with similar results: deuteranomalous and normal trichromats would set the intensities of the test monochromatic lights to the same values previously chosen by deuteranopes. This demonstrates that these trichromats had erythrolabe as one of their cone pigments.

It must be realized that the experimental paradigm is not only elegant, but also powerful: it assumes nothing about the subjects being tested. However, if the different subjects do make the same intensity settings, then it necessarily follows that they share the long-wavelength pigment with the corresponding dichromat.

The results of Mitchell and Rushton were further confirmed and augmented in the studies of Rushton *et al.* (1973a, b, c). In this series, Rushton *et al.* used silent substitution to keep one of the two pigments at the long-wavelength side from responding so that the other could be measured. The first experiment consisted of exchanging two different monochromatic lights in different proportions—superimposed on a background formed by a mixture of them—and determining, for each ratio, the intensity necessary to just perceive the exchange.

For protanopic and deuteranopic dichromats there was always a ratio at which no increase in intensity would reach perception: this coincided with the corresponding "isolept" for the two lights. At both sides of the isolept the settings followed a course consistent with Weber's law, but protanopes generated functions that were displaced relative to the deuteranope's according to their respective pigment sensitivities. The important finding of this study was that normal trichromats, tested in the same way, generated a function that coincided in every case with the lowest of the two threshold settings. This implies, as they observed, that normal subjects possess both the pigments of the deuteranope and the protanope and that, in that case, the thresholds are governed by the pigment that is most sensitive.

In their second and third papers they reported on the spectral sensitivities of the normal and anomalous pigments measured with the colour-matching technique in the Analytic Anomaloscope as explained above. However, this time they did not use only the "prot" and "deut" modes but also undertook to find the subject's own isolept settings and used them to measure the normal and anomalous pigments. To find the "isolepts" they applied the exchange technique in a recursive way: determining increment thresholds (Stiles, 1959) on each of the exchange lights and readjusting the exchange ratios to the values corresponding to equal increment sensitivity. Starting the experiment near one isolept and repeating the procedure a couple of times both "isolepts" could be found in normals and anomalous subjects.

Although the results with normal subjects essentially confirmed Mitchell and Rushton's study, this paper provided new support for Rushton's claim that two pigments of normal vision are chlorolabe of protanopes and erythrolabe of deuteranopes. Since this time the measurements were carried out using the normal subjects own "isolepts", any suspicion of introducing artifacts by use of dichromat's settings is dispelled. This holds also, more forcefully even, in the case of their anomalous subjects, for they shared only one of the dichromatic "isolepts". In their case it was absolutely necessary to determine the anomalous pigment isolept in order to use the colour matching procedure with the Analytic Anomaloscope. In fact, the second paper, where the method of finding the normal subject's own isolepts was introduced, was meant as a validation of the procedure before attempting using it with anomalous trichromats, just as the first paper's main purpose was to introduce and validate the method of exchange thresholds in normal and dichromatic subjects.

In all of the studies just discussed, Rushton's main aim was to identify the pigments present in the human retina and also to determine their spectral sensitivity functions. Even when he applied silent substitution to modulate only one cone system, he was concerned with measuring the spectral sensitivity of the other. When we rediscovered the idea of silent substitution our aim was rather to study the characteristics of the neural pathways fed by only one type of cone. We considered that, for this purpose, the existing data on spectral sensitivity functions were accurate enough to allow one to modulate each cone class in-near-isolation.

Although spatial modulation transfer functions (MTF) and temporal flicker characteristics had been measured previously by Green (1968, 1969) and Kelly (1973, 1974), using Stiles (1959) chromatic adaptation method, we felt that the adaptation technique was not completely satisfactory. Our main concern was that, as was well known from the results of De Lange (1958) for flicker and Robson (1966) for spatial MTFs,

the functions are strongly dependent on the mean level of adaptation. Using the chromatic adaptation method, one is forced to suppress the unwanted system by using intense adapting fields intensities, but this also must affect the measured system to some extent. What made the situation even worse was that this last level, as well as the effective modulation, had to be estimated by extrapolation.

With the "spectral compensation" method these problems were avoided, since, as we have shown before, both the absolute level and amount of modulation are under the experimenter's control. Furthermore, the values of effective modulation depth can be simply calculated from the "compensation" equations.

After our initial paper in 1974, where we examined De Lange functions obtained by modulating red and green cones, we subsequently reported on a number of aspects concerning chromatic sensitivity (Estévez and Cavonius, 1975), dichoptic modulation of two different cone systems (same paper), spatial MTFs of each of the three cone classes (Cavonius and Estévez, 1975a, b) and De Lange functions of dichromatic observers (Cavonius and Estévez, 1976).

Although the main aim of our studies was always the determination of dynamic characteristics of single cone fed pathways, like Rushton, we became preoccupied with the spectral sensitivities of the cones. For us, the reasons were of a practical, rather than theoretical nature: we felt that, in order to improve isolation, we had to have as accurate as possible data on the spectral sensitivities of the cones. Furthermore, since it was crucial in our experiments to show that our stimulus did indeed modulate only one cone class, we undertook to measure the spectral sensitivities of the systems responding to each of our calculated stimuli. The results of these investigations were reported partly in Cavonius and Estévez (1975b), using purely psychophysical methods and later, in Estévez *et al.* (1975) using both psychophysics and electrophysiology.

The most important, and surprising, result of these investigations was that the spectral sensitivity functions strongly resembled (although were not identical with) those called π-mechanisms by Stiles (1959). Since we also investigated, as Rushton did, the sensitivities of deuteranope and protanope dichromats with the same instrument and stimulus used with normal subjects, we could verify that dichromatic long-wavelength systems were in no way distinct from those measured in the normal subjects; a conclusion that Rushton had already reached.

As is the case with our electrophysiological results, the most important single conclusion from our work is that the two long-wavelength mechanisms appear to have a similar neural organization since, by modulating the input to each of the systems separately, one obtains identical De Lange functions and spatial MTFs, as well as identical changes in these functions with different adaptation levels.

It is perhaps worth stressing here that, when we have spoken of isolated cone systems, what we really meant was isolated modulation through one cone class, as we are aware that the neural pathways of different receptor types may soon converge in the retina (perhaps as early as the first bipolar cell). However, the silent substitution paradigm, especially when generalized as in our "spectral compensation" method, allows one to investigate just what sort of interactions the signals generated by the different receptor types may be undergoing in the complex neural transformation that finally lead to the perception of contrast and colour.

REFERENCES

Baylor D. A., Fuortes M. G. F. and O'Bryan P. M. (1971) Receptive fields of cones in the retina of the turtle. *J. Physiol.* **214**, 265–294.

Biersdorf W. R. and Armington J. C. (1957) Response of the human eye to sudden changes in the wavelength stimulation. *J. opt. Soc. Am.* **47**, 208–215.

Bongard M. M. (1955) Colorimetry in animals. *C.r. Acad. Sci. U.R.S.S.* **103**, 239–242.

Bongard M. M. and Smirnov M. S. (1957) Spectral sensitivity curves for the receptors connected to single fibres of the optic nerve of the frog. *Biofizika* **2**, 336–341.

Boynton R. M., Hayhoe M. M. and MacLeod D. I. A. (1977) The gap effect: chromatic and achromatic visual discrimination as affected by field separation. *Optica Acta* **24**, 159–177.

Cavonius C. R. and Estévez O. (1975a) Contrast sensitivity of individual colour mechanisms of human vision. *J. Physiol.* **248**, 649–662.

Cavonius C. R. and Estévez O. (1975b) Sensitivity of human color mechanisms to gratings and flicker. *J. opt. Soc. Am.* **65**, 966–968.

Cavonius C. R. and Estévez O. (1976) Flicker sensitivity of the long-wavelength mechanisms of normal and dichromat observers. *Mod. Probl. Ophthalm.* **17**, 36–40.

De Lange H. (1958) Research into the dynamic nature of the human fovea–cortex systems with intermittent and modulated light. *J. opt. Soc. Am.* **48**, 779–789.

Donner K. O. and Rushton W. A. H. (1959) Retinal stimulation by light substitution. *J. Physiol.* **149**, 288–302.

Estévez O. and Cavonius C. R. (1975) Flicker sensitivity of the human red and green color mechanisms. *Vision Res.* **15**, 879–881.

Estévez O. and Spekreijse H. (1974) A spectral compensation method for determining the flicker characteristics of the human color mechanisms. *Vision Res.* **14**, 823–830.

Estévez O., Spekreijse H., Van den Berg T. J. T. P. and Cavonius C. R. (1975) The spectral sensitivities of isolated human color mechanisms determined from contrast evoked potential measurements. *Vision Res.* **15**, 1205–1212.

Estévez O. (1977) EPs to contrast modulation. In *Spatial Contrast. Report of a Workshop* (Edited by Spekreijse H. and Van der Tweel L. H.), pp. 72–75. North-Holland, Amsterdam.

Forbes A. and Burleigh S. (1952) Retinal response to color shift. *Fedn Proc. Fedn Am. Socs exp. Biol.* **11**, 47.

Forbes A., Burleigh S. and Neyland M. (1955) Electric responses to color shift in frog and turtle retina. *J. Neurophysiol.* **18**, 517–535.

Fuortes M. G., Schwartz E. A. and Simon E. J. (1973) Colour-dependence of cone responses in the turtle retina. *J. Physiol.* **234**, 199–216.

Gielen C. C. A. M. (1980) Spatio-temporal and chromatic

properties of visual neurones in the Rhesus Monkey geniculate nucleus. Thesis, Katholieke Universiteit Nijmegen.

Granit R. (1962) The visual pathway. In *The Eye* (Edited by Davson H.), Vol. 2, Part III, pp. 535–763. Academic Press, New York.

Green D. G. (1968) The contrast sensitivity of the colour mechanisms of the human eye. *J. Physiol.* **196,** 415–429.

Green D. G. (1969) Sinusoidal flicker characteristics of the colour sensitive mechanisms of the human eye. *Vision Res.* **9,** 592–601.

Ishihara M. (1906) Versuch einer Deutung der photoelektrischen Schwankungen am Froschauge. *Pflügers Arch. ges. Physiol.* **124,** 569–618.

Kaneko A. (1973) Receptive field organization of bipolar and amacrine cells in the goldfish retina. *J. Physiol.* **235,** 133–153.

Kelly D. H. (1973) Lateral inhibition in human colour mechanisms. *J. Physiol.* **228,** 55–72.

Kelly D. H. (1974) Spatio-temporal frequency characteristics of color-vision mechanisms. *J. opt. Soc. Am.* **64,** 983–990.

MacNicol E. F., Jr and Svaetichin G. (1958) Electric responses from the isolated retina of fishes. *Am. J. Ophthalm.* **46,** 26–46.

Mitchell D. E. and Rushton W. A. H. (1971a) Visual pigments in dichromats. *Vision Res.* **11,** 1033–1043.

Mitchell D. E. and Rushton W. A. H. (1971b) The red/green pigments of normal vision. *Vision Res.* **11,** 1045–1056.

Osler, Sir William. Quoted in *The Harvest of a Quiet Eye*, Mackay A. L. (Edited by Ebison M.). Institute of Physics, London (1977).

Raviola E. and Gilula N. B. (1973) Gap junctions between photoreceptor cells in the vertebrate retina. *Proc. natn. Acad. Sci., U.S.A.* **70,** 1677–1681.

Regan D. and Spekreijse H. (1974) Evoked potential indications of colour blindness. *Vision Res.* **14,** 89–95.

Robson J. G. (1966) Spatial and temporal contrast-sensitivity functions of the visual system. *J. opt. Soc. Am.* **56,** 1141–1142.

Rodieck R. W. and Rushton W. A. H. (1976) Isolation of rod and cone contributions to cat ganglion cells by a method of light exchange. *J. Physiol.* **254,** 759–773.

Rushton W. A. H., Spitzer Powell D. and White K. D. (1973a) Exchange thresholds in dichromats. *Vision Res.* **13,** 1993–2002.

Rushton W. A. H., Spitzer Powell D. and White K. D. (1973b) The spectral sensitivity of "red" and "green" cones in the normal eye. *Vision Res.* **13,** 2003–2015.

Rushton W. A. H., Spitzer Powell D. and White K. D. (1973c) Pigments in anomalous trichromats. *Vision Res.* **13,** 2017–2031.

Scheibner H., Hunold W. and Bezaut M. (1975) Colour discrimination functions of the frog optic tectum (*Rana esculenta*). *Vision Res.* **15,** 1175–1180.

Sirovich L. and Abramov I. (1977) Photopigments and pseudo-pigments. *Vision Res.* **17,** 5–16.

Spekreijse H., Estévez O. and Reits D. (1977) Visual evoked potentials and the physiological analysis of visual processes in man. In *Visual Evoked Potentials in Man* (Edited by Desmedt J. E.), pp. 16–89. Clarendon Press, Oxford.

Stiles W. S. (1959) Color vision: the approach through increment threshold sensitivity. *Proc. natn. Acad. Sci. Wash.* **75,** 100–114.

Svaetichin G. (1953) The cone action potentials. *Acta physiol. scand.* **29,** Suppl. 106, 565–600.