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# SIGHT AND THE PHYSIOLOGY OF THE RETINA

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The psychologist, in making observations on the discrimination of form, colour, light flicker etc., has a natural interest in what physiology can tell him about the means employed by the eye to accomplish such acts. Some general principles are well known. One could enumerate facts such as the greater density and smaller diameter of the receptors in the fovea which facilitate perception of fine structure, the general relation between impulse frequency and stimulus intensity (ADRIAN) enabling different levels of brightness to be perceived. These are examples of well-known correlations. Others might be mentioned to emphasize that physiology and psychology are interdependent sciences with problems which the one can help to clarify for the other. As a matter of fact the venerable science of psychophysics was claimed by both physiologists and psychologists as part of their domain. The old physiology of vision was largely a psychology of vision bent on establishing direct contact between the sensory experiences and certain measurable physical quantities such as wave-length, stimulus intensity etc. The neglect of the intermediate links, in retina, optic nerve, brain cells etc. was simply a consequence of the lack of appropriate methods of analysis. In making this statement I do not intend to underestimate the value of the early work on visual purple, retina and optic nerve. My intention is merely to explain why the development of these particular aspects of the problem had to wait for the necessary advancement of technique that began in the early twenties.

Elsewhere (GRANIT, 1947, 1950) I have given an account of the work with electrophysiological methods on the retina and the optic nerve. This field has not been developed in as close contact with psychology as the classical science of psychophysics. Many of the

problems raised by the physiology of the retina do not directly concern our visual experiences. But there are others which are connected with vision in the sense that they give a clue to the understanding of our sensory experiences. The physiologist can never hope to do more than to find properties of the retinal response by means of which the higher centres can differentiate one kind of information from another. The means, at the disposal of the retina, for transmitting a message are of the simplest kind: variations in the spike frequencies of impulses (ADRIAN). How can this wonderful world of form and colour be interpreted by the higher centres on the basis of information transmitted by such a simple mechanism? Or to put this question more precisely: what features of the impulse machinery can throw light on the performance of the eye as a sensory organ built for the purpose of discrimination?

In considering this question one is first struck by a number of observations which can be immediately translated into visual equivalents. Thus the distribution of spectral sensitivity of the dark adapted eye corresponds well with the photochemical absorption curve of visual purple. This curve can be measured by studying the impulse activity too. The day-light or photopic distribution of sensitivity is still lacking its photochemical equivalent but the psychophysical data agree with those obtained by measuring the impulses in the optic nerve.

When ADRIAN first studied the impulse frequency of the whole optic nerve as a function of time of exposure he pointed out that the frequency rose and fell much as the light sensation rises and falls, according to the well-known measurements by BROCA and SULZER.

There is a body of old data concerning the fact that for a visual impression time, intensity and area of the seen object, within limits, are interchangeable quantities. Both electroretinography, as well as work on the impulse activity has established these correlation for the end organ.

The examples chosen may serve to illustrate observations on the retina which lead on to more or less obvious parallels with earlier psychophysical observations. One could say that electrophysiology has filled in a missing link between stimulus and sensation. One might even add that such results were to be expected. This, at

least, has been my personal feeling when I have seen them published from time to time or myself have made observations of a similar nature. This does not in any sense detract from their intrinsic value. The electrophysiological situation can often be better analyzed than the psychophysical one and thus add new aspects to the understanding of the real basis for the phenomena observed.

Yet, in spite of all this, one's curiosity is aroused in a different fashion when one happens to strike electrophysiological facts for which there are no obvious correlations with psychophysics. In a sense they represent a greater challenge to the imagination and experimental initiative of both physiologists and psychologists. A number of such facts will now be considered.

One of the strangest phenomena within this second category is the so-called off-effect, seen already by the old electrophysiologists and then demonstrated by ADRIAN in the impulse activity of the optic nerve and subsequently studied by HARTLINE and myself from different points of view. It is easy enough to point to psychophysical observations on after-images and contrast but the plain fact remains that we do not yet understand in what way this discharge of impulses at cessation of illumination has to be incorporated in our psychophysical fabric of thought. We know, however, that the off-discharge is wiped away by some kind of inhibition by renewed illumination (GRANIT and THERMAN) thus clearing the field for on-activity. This inhibition is one of the elementary facts of retinal electrophysiology and, again, we do not know what it corresponds to in psychophysics. Why this ignorance? Clearly because retinology, owing to modern methods, has gone a bit too far for psychophysics. The psychologist, in his turn, is now faced with the necessity of doing something to recover the lead.

As a matter of fact inhibition sets in simultaneously with, or even before, excitation, and every response to light represents a balance between excitation and inhibition. Possibly »glare» means that inhibition has suppressed excitation. Inhibition is, of course, as essential for finely adjusted activity as excitation. Indeed, we can hardly, as neurologists, conceive of any central mechanism of discrimination without thinking of it in terms of inhibition and excitation cooperating towards a common goal. Our primary model of

thinking has long been the nervous machinery governing the incredibly finely regulated somatic motor activity and long ago SHERINGTON showed how this was achieved by excitation and inhibition in close collaboration. The retina is provided with its own nervous centre consisting of bipolars, horizontal cells, amacrine and ganglion cells with widely branching dendritic networks just below the receptors. Surely this nervous centre has not been placed in this locus merely to make it more difficult for the physiologist.

One of the more pressing tasks for the psychology of the special senses is to study the eye as an on/off-system adjusting its activity by means of excitation and inhibition. The psychologist will have to take to retinology in order to learn how to adjust his experiments in order to be able to elucidate these questions. Perhaps the best case hitherto made for inhibition in psychophysical experimentation is the so called  $\alpha$ -adaptation of SCHOUTEN.

The development of the electrophysiology of the retina into a method of studying the activity of single optic nerve fibres, which was begun with HARTLINE and GRAHAMS work on the *Limulus* eye in 1932, has multiplied the number of facts unexplicable by present-day psychophysics, particularly since that work expanded to the vertebrate retina.

The main facts will be found in the two summaries referred to, together with all the other references of this paper.

It is clear that psychophysicists will have to take to microstimulation too, if they want to utilize the information made available by modern retinology. A beginning has been made by WRIGHT, THOMSON, HARTRIDGE and WILLMER (see, for instance, HARTRIDGES summary *Recent Advances in the Physiology of Vision*, Churchill, London 1950) and enough has been found to justify this method of approach and make one hope for more work of this kind.

One of the essential new facts in the electrophysiology of the elementary retinal structures, which are small nervous centres joined to a ganglion cell ending up in a nerve fibre, is the incredible amount of differentiation of which these individual centres are capable. Some fibres merely respond to onset of illumination, others merely to cessation of illumination, the majority, however, are on/off-elements combining these two properties (HARTLINE). This again

suggests that the on/off-system is the most important one in the vertebrate retina.

At this point it is necessary, once again, to remember that in recording from these elementary centres, each of which has a ganglion cell as its final common path, one does not obtain the pure receptor response but a frequency pattern which is modified by the interaction between excitation and inhibition in the internuncial neurones mentioned. For this reason the off/on-ratio which is the ratio of off-sensitivity to on-sensitivity varies with wave-length and stimulus intensity. Assume that we are determining the threshold response of a single fibre in the optic nerve of a well dark adapted cat. There is first no response to sub-threshold intensities. Then, upon increasing stimulus strength the on-discharge, which is the response to onset of illumination, turns up. A further increase in stimulus intensity makes the cell respond also to cessation of illumination. This is the off-discharge. Again, in another cell, the off-response may turn up first and the on-response require stronger stimuli. Sensitivities are inverse values of the energy necessary for a response. The off/on-ratio, under these particular circumstances, relates the off- and on-sensitivities. At the threshold of the dark adapted eye, it varies as much as a 100,000-fold. The cells concerned in the cat's eye are the large so-called diffuse ganglion cells (RUSHTON) and thus selected specimens. Smaller cells probably introduce more variability.

We conclude that already at the threshold the off/on-ratio adds a new variable to the threshold itself. This factor is capable of modifying the impulse pattern discharged by optic nerve fibres to the brain, thereby giving »individuality» or »local sign» to the impulses, or spikes, as they are commonly called.

Consider next the case of one of the retinal elements being subjected to stronger and stronger stimuli. For the sake of comparison we can first imagine, what, under similar circumstances, would happen in the nerve from another sense organ such as, say, the muscle spindle. In this case the spike frequency would go on increasing with stimulus intensity to an upper limit. Not so with the spikes from an on/off-element which reach the brain through an intermediate centre attached directly to the organ itself. At certain

intensity levels the on-discharge would predominate, at others the off-discharge. A large number of on/off-elements would, at high intensities, merely give an off-response because their on-component of discharge would be wholly suppressed by inhibition. In other words, the off/on-ratio would vary in a complicated fashion with stimulus intensity. This, too, will add variability to the pattern, and this variability would be further modulated by the wave-length of the stimulus, the off-effects tending to be particularly well marked in the long wave-lengths and, again, to come somewhat more to the fore at the opposite end of the spectrum.

Because of these circumstances the original intensity-frequency relation, characterizing simpler sense organs, does not hold for the retina except as an average for a great number of individual fibres. This average response is greatly modulated before it reaches the individual fibres working as final common paths for the system. Pattern thus adds itself to frequency.

It is possible to prove by direct experimentation that stimuli from different wave-lengths interact in a complicated fashion upon the same element. One can throw a red and a green light singly, and together at half their energies, onto the same region of a dark adapted retina, after having adjusted the energies for equal stimulation of visual purple. Each stimulus will alone give its own pattern of off/on-ratio. Together they need not give intermediate or summed values but either of the two, generally the red, will succeed in impressing, upon the cell its particular off/on-ratio.

Enough has been said to illustrate what an exceedingly complicated message the individual fibres are transmitting to the brain. Some sort of »pattern» seems to be what the retina is trying to produce in order to aid differentiation.

Where, in this pattern, do the cues for wave-length detection come in? In considering this question, let us merely deal with light-adapted or photopic eyes so as to avoid the confusion with the specific spectral absorption band of visual purple used in night vision. I have several times pointed out that for colour work the large spike of the cat's eye has the disadvantage that information about its »coloured» components only can be obtained by indirect methods involving selective adaptation to certain wave-lengths or

electrical polarization of the retina. Direct methods can only be applied to other types of eyes.

Directly measured with a spectrum of equal energy, the spikes of the isolated ganglion cell in the cat's eye produce, after light-adaptation, a broad spectral sensitivity distribution with maximum in 5,600 Å corresponding to the average distribution of brightness in the spectrum, as seen by a similarly light-adapted human eye. This sensitivity distribution is called the photopic dominator. It is being assumed that this curve is complex, a kind of integration of individual response curves from the large number of receptors converging towards the ganglion cell recorded from. The basis for this assumption is the fact that, by adapting this system selectively to different wave-lengths, the average curve does not merely diminish in height, as a uniform system would do, but splits up into narrower colour bands with maxima in the red, the green and the blue regions of the spectrum. Similar effects may be achieved by electrical polarization of the retina. Speaking in psychophysical terms, it is likely that the synthetic photopic dominator mediates a general impression of brightness or »white» thus giving »white» a unique position in that it also is represented by a separate message to the brain.

The retina also delivers impulses conveying signals for »colour». In certain eyes specific regions of the spectrum are represented in the optic nerve by fibres which, studied by electrophysiological methods, behave as if their task were to inform the brain when wave-lengths from these regions are being activated. These specifically colour-sensitive fibres are called modulators. The modulators are confined to three regions of predilection, one in the red, one in the green and one in the blue part of the spectrum. In my recent summary (1950) I have discussed the nature of dominators and modulators. It is difficult to summarize this discussion here because more photochemistry and neurology are needed than can be taken up in the space available. The role of dominators and modulators in colour vision will ultimately have to be elucidated by psychologists experimenting with sensations. The experiments reviewed above have been wholly electrophysiological.

The three regions of predilection of the modulators have also been obtained by the indirect methods alluded to, selective adapta-

tion and electrical polarization, applied to the cat's eye. This animal may or may not perceive colour. But its retina has cones and a definite peripheral mechanism for colour reception, hidden, as it were, behind a veil of visual purple.

Recently two new methods for measuring specific colour sensitivity have been developed, one by DONNER, the other one by MOTOKAWA. DONNERS method is of particular interest for psychology. He studied the isolated large spikes of the cat's retina. As pointed out, above, their frequency of discharge first rises and then falls during illumination. DONNER was engaged in measuring the frequency-time differential, i.e. the rate of rise of impulse frequency as a function of time of exposure, and then noted that this function was influenced by the wave-length of the stimulus. The frequency-time differential rose quickly with red light, at a somewhat slower rate with green light and at the slowest rate with blue light.

DONNERS result points to a new mechanism of discrimination allowing different messages to be transmitted along the same cable, a kind of frequency modulation. This, according to him, is probably organized by the layers of cells behind the receptors. It must be of some significance in vision because the sensations of colour at short exposures are known to rise at different rates in a very similar way (PIERON). DONNER used his principle to determine colour sensitivity and again found the three specific regions of predilection. The reader is referred to his complete presentation of the method (*Acta Physiol. Scand. Suppl.* No. 72, 1950).

In a different way MOTOKAWAS very interesting work has emphasized time as an element in the discrimination of colours. He first noted that, after a brief period of illumination, the electrical sensitivity of his own eye, as measured by the phosphene elicited by a stimulating polarizing current, rose above its normal value. For this phenomenon, too, the rate of rise of electrical sensitivity proved to vary with the colour of the light in the period of illumination. MOTOKAWA used this phenomenon to determine colour sensitivity. His papers will be found in the last issues of *J. Neurophysiol.* for 1949. The many points of contact with the work on electrical polarization of the cat's eye (GERNANDT, GRANIT) and with DONNERS work on the spike frequency-time differential show

that retinology and psychophysics are coming together oddly enough, at a crossroad where a meeting seemed most unexpected. MOTOKAWA is applying his method to both man and animals.

On the whole it would seem as if the psychologists, by interesting themselves in the physiology of the retina, could learn a great deal about the sensory aspects of vision and the mode of organization of discrimination on the basis of general nervous mechanisms. May this brief essay serve to underline this view and bring it before the eyes of a different audience than the one apt to read the papers referred to.

#### BIBLIOGRAPHY

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