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THE CONCEPT 'RECEPTIVE FIELD'

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PROFESSOR EBERHARDT DODT asked me to provide an Introduction to this meeting and gave me a free hand in the choice of a subject. I was very touched by his courtesy and kind loyalty in remembrance and felt that something had to be done to express my appreciation of his proposition.

The title of my Introduction ought to have been given a subtitle: how it strikes an ex-vision man when he takes a look at the labours of his successors. In general, of course, he is willing to admire the imagination and technical skill with which the subject has been developed. Progress has indeed been striking. When ultimately I seized on the concept 'receptive field' for a few remarks, this was because I have been wondering whether it has not seen its most prolific days and now could be allowed a period of rest for recovery and renewed uptake at some later date. I mean that on the whole other approaches to visual problems lately have seemed to me more rewarding.

SOME RETINAL ASPECTS

Essentially 'receptive fields' form an organized retinal matrix of excitation and inhibition modifying the responses of single ganglion cells so that both an increase or a decrease of light within the overlapping pick-up areas of a number of such cells leads to a discharge of impulses. It is tempting to regard the pick-up area of each ganglion cell as a spatial unit. The dimensions of such pick-up areas or receptive fields and their overlap with one another strikes one as having been somewhat neglected. Not until very recently (IKEDA & WRIGHT, 1972; HAMMOND, 1973) has it, for instance, become clear, that the centre of a concentric centre-surround field not only has a surround of opposite properties but that the latter also has a surround repeating the centre-properties, both in the retina and in the geniculate body of the cat. And for some time we have known of the McIlwain-effect which influences firing ganglion cells in these structures at a distance of the order of 30 to 50°, the stimulus being movement of an object at those distances.

Movement is of course a most essential parameter of visual stimulation and movement creates overlap of fields. The eyes move incessantly, the head moves, the body is in motion, objects move against a steady background etc. Then, at the next projection, the outcome of all this unavoidable scanning of the sur-

rounding world is thrown upon *non-movable foci* for re-interpretation in order to be dispatched to further sites for re-interpretation. The visual centres or areas have now in the papers of COWAN and of ZEKI reached a minimal number of nine'. Since in higher mammals on- and off-centre fields with opposite surrounds are stated wholly to dominate their retinae, something of this pattern will be reflected onwards until finally it is lost in the cascading synaptic organizations and interactions. Why this particular field-pattern should be the most suitable first stage for whatever information in the end is extracted at all those nine stations seems to be an essential question of coding principles. My guess is that the answer lies hidden within the polyganglionic matrix rather than within their individual receptive fields as such.

Let me put those problems a little differently: what is being explained by the existence of a retinal organization emerging in the shape of receptive fields? The responses to light and darkness and their antagonism were known long before the organizational features of the receptive fields through KUFFLER'S paper of 1953 rose to prominence. These facts were familiar in terms of single ganglion cell or fibre responses. They explained characteristic properties of seeing as an act. I do believe that the two types of concentric fields in the retinae of higher mammals represent a significant discovery and they serve, of course, as a kind of necessary *point d'appui* of the measuring technique. But what have they added to our understanding of vision, by which I mean seeing as an act? Relatively little, I should say. However, I cannot lay claim to have followed the literature well enough to equate my own ignorance with the knowledge of the up-to-date specialists in the field. It seems to me convincing to assume that concentric fields, in order to survive in the evolution, must have betoken a significant biological asset for the organism. What is this asset? This, briefly, is my question re-formulated. It is difficult merely to consider functions which the retinae of frogs and rabbits can handle without much need for this sort of an organization.

Speaking of frogs and rabbits, it is clear that there the concept of 'receptive field' has been turned into something very different. This the experimenters have done by thinking of the field as the detector of a 'cue'. Some of these cues represent quite advanced postulates of frog psychology. Now, sensory physiology is, and always has been a science in quest of cues. A classical example is the spectral distribution of sensitivity of rhodopsin which serves as a cue for our own scotopic distribution of perceived thresholds of light. To look for 'cues' in receptive fields seems to me, therefore, a quite legitimate pursuit. The most obvious criticism of it is that the selection of the proper stimulus plays a role for the result. In slight exaggeration: if we were to stimulate with a spiral pattern we might discover spiral-pattern detectors without making any advance whatsoever towards our goal of getting hold of the principles of coding. An advantage of using retinae of frogs and rabbits, rather than the cortex of the cat would be the increased chance of finding explanations of 'cues' in terms of structure, as many retinae on the whole are better known than the cortices of cats and monkeys. A good example is BARLOW & LEVICKS'S (1965) analysis of the directional sensitivity to movement of the rabbit's ganglion cells. Their

work followed the classical approach of physiology: to define a function, refer it to a structure, and then provide a final hypothesis in terms of operations carried out by that structure. If the 'receptive field' is brought into the final hypothesis, the interpretation presupposes (I) that the function actually requires one particular type of receptive field and (II) a notion as to how the field does it. The concepts 'cue' and 'receptive field' are not interchangeable. On the whole it seems to me that the least important element of detector philosophy has been the specific concept of 'receptive field'.

The second question (how it does it) would nowadays be discussed in terms of 'coding', my term 'cue' probably being regarded as old-fashioned. The problem itself remains the old one: what is the fraction of experience recorded by a given cell and how does it do it. Present-day techniques have allowed us to raise such questions in terms of single ganglion cells or fibres, but what, if the really significant visual cues already at the retinal level happened to be basically tied to multicellular ganglionic activity, a minimal number of overlapping receptive fields?

All functional features need not necessarily in the first instance be thought of in terms of cues. The retina shares with the motoneurons of the spinal cord and the pyramidal cells of the motor cortex the differentiation into phasic and tonic ganglion cells, the X and Y cells of ENROTH-CUGELL & ROBSON (1966). These parallels extend to conduction velocities in that the tonic X-cells have slower conduction rates than the phasic Y-cells (CLELAND, DUBIN & LEVICK, 1971; FUKADA, 1971). To be sure, the receptive fields are reported to be different in the two types of cell but this does not explain their X or Y character. The phasic cells are likely to be specialized for temporal changes such as the perception of velocity of movement.

THE GENICULO-STRIATE PATH

It is a striking and well-known fact that the centre-surround antagonism of concentric type not only is preserved at the geniculate level but actually is improved upon (HUBEL & WIESEL, 1961). At the retinal level there is no off-effect in the state of dark adaptation. This is not true for the dorsal lateral geniculate. Many other lines of evidence suggests that a new deal takes place at that level. I refer to work by JUNG, CREUTZFELDT, BAUMGARTNER, MAFFEI, FIORENTINI. The anatomists tell us that there is both convergence and divergence of optic nerve fibres on the geniculate and we have long been familiar with the presence of interneurons in that nucleus. Interpretations are available for the redistribution of on- and off-centre retinal cells to produce their geniculate namesakes. Inhibition is known in two versions, as surround inhibition, also called synergistic inhibition, which partly may be of the recurrent type, and as reciprocal inhibition (JUNG, CREUTZFELDT). The geniculate body can be influenced from the cortex and from the reticular formation. Apart from the binocular rearrangement of fibres, nothing is really understood of the *raison d'être* of all these complications. All the more remarkable does it seem that at the geniculate level of the geniculo-striate path, which is the one serving discrimination by contrast,

the on/off-off/on concentric arrangement is preserved and improved upon. This suggests that such an organization is the optimal one for ensuring that small shifts in the level of illumination or retinal location produce the maximum of information obtainable from the polyganglionic retinal response to the scanning process.

Such considerations lead one to think that CAMPBELL and his many co-workers (ENROTH-CUGELL, KULIKOWSKY, MAFFEI, ROBSON and others) in their exciting work on spatial frequency-detectors and contrast may have hit upon 'des Pudels Kern', the real purpose of the concentric excitation-inhibition fields that I have been discussing. On the spatial-frequency hypothesis there would be a large number of narrow-band spatial filters tuned to different frequencies (cycles in grating per degree), each with its own contrast sensitivity. The optimal frequencies of the band-pass filters are inversely related to field diameter. In much of this work gratings of constant luminance, but variable spatial frequency, have been used, contrast being defined as $L_{\max} - L_{\min}$ divided by $L_{\max} + L_{\min}$, mean luminance being the latter sum divided by 2. Contrast sensitivity is the inverse value of contrast required for a constant criterion response. By application of FOURIER analysis the spatial-frequency hypothesis has been extended to square-wave patterns by CAMPBELL & ROBSON (1968) and by MAFFEI & FIORENTINI (1972). CAMPBELL & ROBSON have shown that the contrast sensitivity of the square-wave pattern is determined by the amplitude of its fundamental sine component and MAFFEI & FIORENTINI have synthesized a square-wave pattern from sine-wave components injected into different eyes, the way yellow is synthesized by green into one eye and red into the other.

The old sensory physiologists used to think of the eye as a synthetic and the ear as an analytic organ because a trained ear could pick up the components of a periodic sound while the eye had to be satisfied with the blended compound. But if the eye operates by a sine-wave recorder of form in spatial contrast, then their mistake was to stare their eyes out at colour instead of considering form as the more essential purpose of visual perception.

With these notions we have reached the cortex by the geniculo-striate passage and there HUBEL & WIESEL's discovery of cortical cells sensitive to orientation and direction of movement looms large. Neither response is developed at the level of the geniculate body (speaking now of cats and monkeys). The spatial-frequency hypothesis throws new light on all these problems of 'detectors'. If it be accepted, there is available a detector without the psychological definitions inspired by the frog retina, yet capable of a great deal, and there is more to come. The spatial-frequency idea is still at an early stage of development; yet some of its psychophysical consequences have already been worked out in experiments and the theory is accessible to a mathematical treatment. Single cell detector studies are at a disadvantage in both these respects, whatever the accuracy of the analysis of the structure of their receptive fields, in which much also depends upon the technical approach; witness the differences of opinion between HUBEL & WIESEL, SPINELLI & BARRETT (1969) and BISHOP with his colleagues (1971).

With two gratings produced by beam-splitting CAMPBELL & KULIKOWSKI

(1966) showed that, if one used a vertical test grating and turned its companion over it at different angles for masking purposes, the perceived contrast sensitivity depended on the orientation of the masking companion. For identical (vertical) directions of the two gratings there was a masking effect, a kind of selective adaptation to orientation, that fell off exponentially as the angle between them was increased. At 12° on either side of the vertical test, the masking was reduced by a factor of 2. BLAKEMORE & CAMPBELL (1969) have studied psychophysically the adaptation produced by a superposed contrast-grating and found this process also to possess interocular transfer. It has even been possible to demonstrate such selective adaptations by recording a smoothed-out evoked potential in man (CAMPBELL & MAFFEI, 1970). The demonstration that contrast-sensitivity produced by spatial frequencies combines with sensitivity to orientation seems to me a singularly interesting finding.

I cannot here review the many experiments inspired by the spatial-frequency hypothesis. The ones I have mentioned suggest that if there is no selective adaptation to an assumed detector property, then it is likely not to be fundamental. There is, for instance, none to width of a bar. Lines, edges and bar widths, inasmuch as they are assumed to be represented by detector cells, may indicate apparent detectors and not real ones, 'real' taken in the sense of representing primary coding. The emphasis of many recent experiments is thrown on spatial-frequency detectors of different orientations and thus on multicellular events.

This section should really be concluded with some words on the results of ablation experiments but this would carry us too far for an introduction. Let me end by quoting from DOTY's summary (1973): 'Despite these problems of definition (sc. adequate tests) it is clear that processes in nonstriate cortex are able to sustain an unexpectedly high level of vision in the absence of the striate system in certain species'.

THE SUPERIOR COLLICULUS

The receptive fields of this structure are very large; up to 70° are stated to be very common in the cat, from 2 to 90° in the monkey, all according to SPRAGUE, BERLUCCHI & RIZOLATTI (1973). The particular geometry which according to HUBEL & WIESEL is such a marked feature of their so-called 'simple cells' (quite complex, according to BISHOP and his colleagues) is absent in the colliculus which as a structure long has been held to play a role in the regulation of eye movements. In agreement with this view, the most striking property of the colliculus is that it requires a moving stimulus and to this its cells are sensitive, sometimes with, sometimes without directionality. The explanatory significance of the concept 'receptive field' seems difficult to evaluate for a size variation from 2 to 90 degrees.

Directional sensitivity we have now seen represented in the ganglion cells of the rabbit's retina, in the striate cortex of cats and monkeys and in the colliculus. Relatively large, geometrically unorganized fields occur in the merely movement-sensitive cells of the rabbit's retina, both on/off- and on-fields of

about 3° are in addition directionally sensitive (BARLOW, HILL & LEVICK, 1964). The large fields respond to fast, the small ones to slow movement, as seems *eo ipso* reasonable. The BARLOW-LEVICK explanation may well be valid for directional sensitivity in all three cases (rabbit retina, cortex, colliculus), but very little of the receptive-field concept is reflected in its formulation based, as it is, on a lopsided distribution of inhibition.

I have given this much time to movement and direction of movement because these responses, as well as velocity, are likely to be fundamental cues with cellular representations of their own. What then about the stationary background against which eye movements occur? Exceedingly suggestive are the observations by WURTZ (1969 a, b) on the monkey. The animal was trained to make a 20° eye movement in the horizontal direction. In its striate cortex 188 units were studied. Of them 32% continued to give an excitatory response, a burst of spikes, when the eye moved rapidly over the stimulus which was a slit of light of optimal orientation for the cell in its stationary position. A group of units, 20% in number, were inhibited by movement although they, too, had been excited by a stationary stimulus. This seems quite unexpected. The largest group, 48% of the total, did not respond to movement although the units fired to a stationary or very slowly moving test. The latter property all units seemed to share. They were distinguished merely by their response to movement. Thus it seems that by different cells ample cues are being provided for both the stationary and the moving outer world.

SUMMARY

I indicated in the beginning of this talk that my reading of papers on vision is cursory rather than systematic and so I may well have formed a wrong opinion of what is what. I have tried to motivate my impression that the concept 'receptive field' has been overplayed, extremely useful though it has been at one stage of the analysis. Much of what we want to understand and have means of furthering cannot just now be profitably furthered by sticking to 'receptive fields' as a major object of research. They represent but one aspect of the search for the biological 'hardware' explaining 'cues' by principles of coding. But, as I said, I do not exclude the possibility that the concept 'receptive field' may turn up at some later date imbued with new relevance and with an explanatory value that at the moment is scant in relation to the labour devoted to analysing vision in terms of it.

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