

THE VERTEBRATE AND THE (INSECT) COMPOUND EYE IN EVOLUTIONARY PERSPECTIVE

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BOTH the vertebrate and the compound eye¹ are neuronal networks (with their accessory optical apparatuses) which endow the animal with the machinery to process visual information relevant for their behavior. However, the evolutionary gap separating the arthropod and the vertebrate line is enormous. Thus, if there are any convergences in the solutions given by both systems of information processing, these are of great interest for the understanding of animal vision and the nervous system at large. No discussion of these specific matters can be found in the literature since 1915. I think that recent investigations have produced enough new information to warrant some reconsideration.

For heuristic purposes, it seems convenient to consider separately the optical apparatus and the neuronal arrangement in both types of eye. The optical apparatuses are obviously different in both cases (Fig. 1), and what remains to be elucidated are the underlying causes for this difference. The neuronal arrangements are obviously very similar (Fig. 4) and what must be explained is the degree and significance of this similarity.

Accordingly, the purpose of this paper can be rephrased explicitly in the following terms: (i) To consider the selective pressures which led to an evolutionary stability of the two types of optical arrangements; and, (ii) To consider what is the degree and significance of the apparent similarity of wiring pattern in the vertebrate retina and the optic lobe of the compound eye.

THE OPTICAL ARRANGEMENT

The function of the optical apparatus is to channel to the receptors the light distribution present in the environment. In the vertebrate eye, this is done by the formation of an inverted image on the retina, which contains a closely packed array of photoreceptors. Thus, the details of the light pattern can be mapped into a pattern of receptor excitation with an accuracy limited only by the density of photoreceptors (Fig. 1). The accurate excitation patterns can in turn be the subject of processing according to the information that is relevant to the animal. In the primate fovea, the density of receptors reaches its maximum, and consequently this is the locus of our best visual resolution.

In the compound eye, the organization is based on ommatidia with separate optical

¹ The term compound eye will herein be a synonym of insect eye. Compound eye will also mean closed-rhabdom apposition eye. (In a few instances this is not the case, *Diptera* and some *Hemiptera*, and the possible significance of this is discussed later.) Superposition eyes are considered specialized cases of closed-rhabdom apposition eyes, for reasons given elsewhere (VARELA, 1970a). Although most of the facts used here are taken from the class *Insecta*, and the conclusions therefore restricted to that class, it is obvious that some extension is valid for the rest of the *Arthropods*.

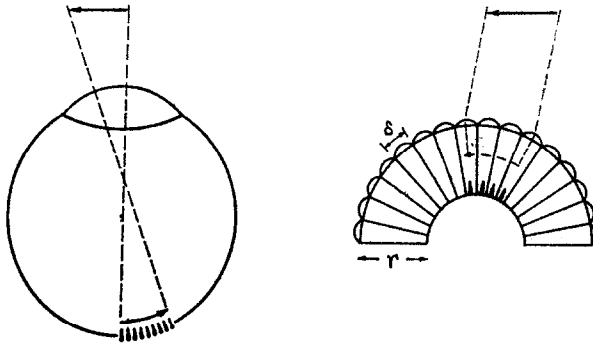


FIG. 1. Optical arrangement of the simple (left) and compound eye (right) are contrasted in this figure. Image analysis in the simple eye is limited only by the size of the receptors themselves. In the compound eyes, the receptors are organized in groups (ommatidia): thus, image analysis is more gross since the limit size of the "grain" is several cells, rather than one (δ).

apparatuses and groups of (about eight) receptors under each lens. At first glance, one does not see any reason why the ommatidia cannot be reduced more and more in size until their discrimination is as fine as in the simple eye. However, the optical apparatus imposes some limitation in size due to diffraction (BARLOW, 1952; FEYMMAN, LEIGHTON and SANDS, 1963). Let us examine this further. What is the optimum size for an ommatidium? Clearly if δ is the facet diameter and r is the radius of the eye, we can derive a number to define ommatidial packing, θ_1 ,

$$\theta_1 = \delta/r.$$

As the facet diameter decreases, the effect of diffraction increases and masks the effects of reducing the size of the ommatidia. This defines an angle, θ_2 , below which the resolution losses due to diffraction become significant. According to the usual optics,

$$\theta_2 = 1.22 \lambda/\delta,$$

where λ is the wavelength of light. To find an optimum size, we must consider the sum ($\theta_1 + \theta_2$) and look for its minimum. Thus,

$$\frac{\partial}{\partial \delta} (\theta_1 + \theta_2) = \frac{1}{r} - 1.22 \frac{\lambda}{\delta^2} = 0.$$

Whence

$$\delta = (1.22 r \lambda)^{\frac{1}{2}}.$$

For the bee we find $r = 1.2$ mm, and by using green light ($\lambda = 546 \mu$), we obtain $\delta = 29 \mu$. The actual average size for the bee's ommatidia is 32μ . Thus the eye has reached its optimum in resolution, and it is therefore reasonable to assume that there has been a strong selective pressure in this direction.

However, in the compound eye, diffraction sets a more severe limit on acuity than in the vertebrate case. In the latter, the limit is the size of a cell; in the compound eye, it is the size of an ommatidium containing about eight cells. This limitation can conceivably be com-

compensated by more complex mechanisms such as head movements, field overlap, etc. But this is another level of complexity.

The question then arises: what are the selective pressures that produced the compound eye's optical apparatus, in spite of those limitations in acuity which are avoided in the vertebrate solution? Let us try to explore this by considering the following arguments:

(i) EAKIN (1965, 1968) has indicated that one can envision the evolution of photoreceptors along two main lines: rhabdomeric and ciliary (Fig. 2). They coincide roughly with the protostomic and deuterostomic lines of evolution. One essential difference between the two

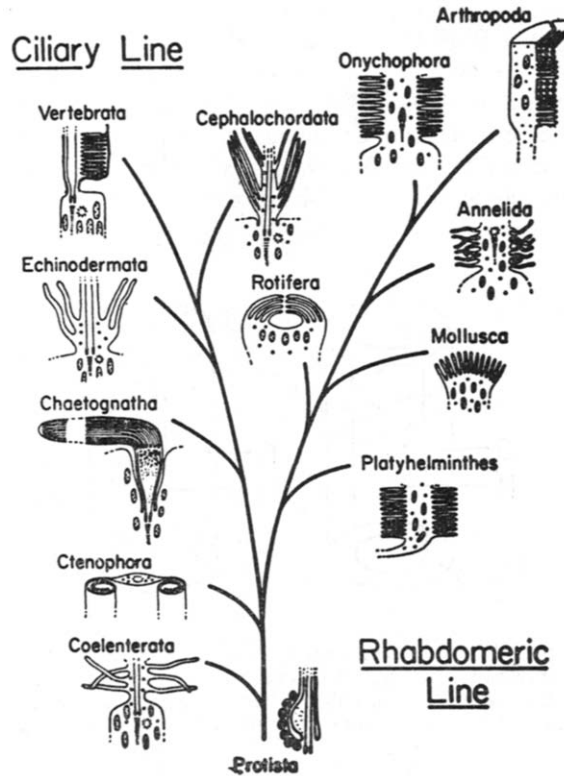


FIG. 2. Illustration of the rhabdomeric and ciliary lines of receptor evolution, according to EAKIN (1968). From common ancestors, there are two main lines of complexity: the ciliary line culminating with the vertebrate and the single-cell receptors, and the rhabdomeric line culminating in the Arthropods with the coalescent rhabdom formed by several receptors.

is that in the latter, the visual pigments are located in membranous structures apart from the main body of the cytoplasm, while in the rhabdomeric line the equivalent membranous structures *must* be surrounded by cytoplasm (Fig. 2). This, I suggest, is related to two primarily different forms of metabolic and trophic functions in relation to pigment recycling and synthesis. It could represent one of the many differences in biochemical endowment between protostomes and deuterostomes. In fact, it is known that in the cones there is active participation of the surrounding cells in the excitation cycle. It is very unlikely that this is the case in arthropod photoreceptors (GOLDSMITH, 1964; HORRIDGE, 1968; VARELA, 1970a).

(ii) Both vertebrate and invertebrate receptors seem to function as waveguides in light transmission (ENOCH, 1963; VARELA and WIITANEN, 1970). We must infer, therefore, that this condition represents an optimum in the performance of a photoreceptor, and that it has attached to it a strong selective value.

(iii) By taking (i) and (ii) into consideration we obtain the following picture. Natural selection acted upon the two types of primitive receptors, ciliary and rhabdomeric, selecting the formation of an optimum waveguide. In the ciliary case, this consisted in migration of the photoreceptor's cytoplasm so as to leave an outer segment as a cylinder of visual pigment, which, when surrounded by an external medium of lower refractive index, became a waveguide (Fig. 3). The rhabdomeric condition, however, was more resistant to change since migration of the cytoplasm from around the rhabdom would have involved a basic modification of its cellular physiology. Thus, it was perhaps a path of least resistance for natural selection to conjoin several receptors to form a central rhabdom (Fig. 3). This structure as a whole then functions as a waveguide analogous to the ciliary case. The difference is that the surrounding medium of lower refractive index are the cells themselves (VARELA and WIITANEN, 1970), consequently the whole structure is more bulky.

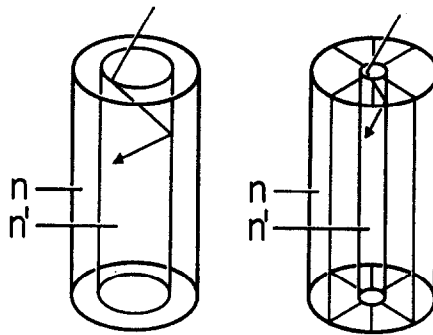


FIG. 3. Waveguide nature of the ciliary (left) and rhabdomeric (right) receptors. In order to function as such, the refractive index of the membranous structures (n) has to be lower than that of the surrounding structures (n'). This can be accomplished easily in the single receptor ciliary receptors, but rhabdomeric receptors have to coalesce to form a composite structure.

In passing, I would like to suggest that this might provide a rationale for the inversion of the retina in the vertebrate eye. In fact, if we are right in assuming the existence of a selective pressure for the displacement of the photoreceptor's cytoplasm, surrounding auxiliary cells became a must for the dynamics of excitation. Such is the function of the cell layers beneath the receptors. Since this structure needs to be in active contact with the metabolic flux of the organism, it would become too obstructive to light if located between the receptors and the light entrance. Bipolars and ganglion cells, being predominantly fibers, are much less obstructive. Thence, the advantage of inverting the retina.

(iv) Another factor that may have entered was polarized light perception. A rhabdomeric receptor is asymmetric, with cytoplasm on one side and straight tubules containing visual pigments on the other. This structure is preadapted to polarized perception: the tubules constitute a natural analyzer. Formation of waveguides by conjoining several receptors allowed this ability to be used, because the tubules could be organized geometrically with

respect to one another within one ommatidium. In fact, in most invertebrate eyes so far studied, polarized light plays an important role in behavior, and is directly related to the geometry of the tubules within one ommatidium (VARELA, 1970a). In ciliary receptors, on the other hand, since every receptor remains in isolation, it is more difficult to optimize a system necessitating a very accurate angular pattern of the membranes between two or more receptors.

(v) From (iii) and (iv) it seems reasonable to conclude that a rhabdomeric group of receptors forming an ommatidium has several selective values which make of it an evolutionary stable structure. The next problem is the development of an optical apparatus for such a structure. A pinhole camera eye functions only if the ratio of retinal surface to rhabdom surface is near unity, i.e. if the photosensitive part of the receptors are closely packed. Otherwise, the camera mechanism would focus a large amount of light onto non-sensitive structure, and thus would be very inefficient in the use of energy and very inaccurate in the mapping of a light distribution. However, this is exactly the situation in a rhabdomeric retina where the rhabdoms must be separated by at least two rows of receptor cell cytoplasm. In the bee, for example, only 15 per cent of the retinal surface is rhabdomeric. It is clear for cases like this, that an eye with separate optical elements which focus the light exclusively into the rhabdoms of each ommatidium is much more convenient and efficient, in spite of the optical limitations.²

(vi) In (iii) we said that rhabdomeric receptors have a resistance to the migration of the receptor cytoplasm, due to their metabolic constitution. This resistance, however, has proven not to be insurmountable. In fact, in the Molluscs, especially the Cephalopods, we have a rhabdomeric retina. However, in these animals, the cytoplasm seems to be reduced to a minimum and the rhabdomeric surface increased maximally. This is partly accomplished by making every cell participate in two rhabdoms (YOUNG, 1962; YAMAMOTO, TASAKI, SUGAWARA and ANTONOSAKI, 1965). In *Loligo*, for example, the percentage of retinal surface is increased to over 70 per cent. As is well-known, these animals have a pinhole camera eye, and in fact extremely good visual performance. This shows that the rhabdomeric retina can be retained and with it the ability for polarized light perception, but coadapted to an optimal optical apparatus, a camera.

(vii) This raises the question: why didn't the Arthropods also surmount the evolutionary obstacle between rhabdomeric receptors and camera optics? We consider this in conjunction with the observation that regardless of the type of retina, all *large* animals that use vision widely seem to have a camera eye (down to the size of small insectivores) while, in contrast, all *small* animals that possess some visual abilities seem to have a compound eye (up to the size of fossil Odonata). This second group only comprises Arthropods, since they are the only group which use vision extensively and are limited in size (see next section).

At first glance, there seems to be no reason why we could not reduce a simple eye to the dimensions of, say, a bee. It would imply a focal distance of about 1 mm (approximately the

² From this perspective, the open-rhabdom eye of Diptera and some Hemiptera represent interesting cases since each receptor functions as an independent wave guide. In this, they resemble vertebrates. However, they still have the limitations of separate optical elements. The fact that this arrangement appears rather rarely, and only in advanced orders of insects, points to the fact that we are dealing with a case of further evolution on the compound eye. It represents, I believe, a special adaptation to increase ommatidium receptive surface. In fact, the eye surface that looks into one region in space and converges into the same 2nd order neuron is six-times larger than in the closed-rhabdom case (TRUJILLO-CENÓZ, 1966). However, since we do not yet know the fate of this form of information gathering, we cannot properly evaluate its significance.

size of the compound eye), or about a 15-fold reduction in our eye. As far as I can see, there is no limiting factor in the optics for such a reduction. Let me point out a few things which do *not* constitute a limit. (a) Focal distance reduction: it can be approximated with the thick lens formula $f = (n-1) r_1 r_2 / D$, where the radii of curvatures are divided by a constant factor D including lens thickness. Clearly, a 15-fold reduction can be obtained by an approximately four-fold reduction in each curvature. This does not seem very difficult to accomplish, given the much larger variations of curvature existing in lenses of compound eyes. (b) Diffraction at the pupil: in our hypothetical eye we would have a pupil measuring hundreds of microns, and thus well above the size of the wavelength. (c) Angular resolution: this factor depends both on focal distance and pupil size, $\delta = f \lambda / d$. A commensurable reduction in f and d would leave δ unchanged. (d) Spherical aberrations: these depend critically on the curvature, $q = r_1 + r_2 / r_1 - r_2$. Since both radii can be changed proportionally [see (a)], the aberrations are unmodified.

Faut de mieux, let me make two suggestions for this fascinating problem.

(a) It is possible that Arthropods and Molluscs did not inherit exactly the same type of receptor, and thus the difficulties encountered by Molluscs in modifying their receptors were much less than in the Arthropod case. EAKIN (1968) points out that some observations in *Onchidium* and *Pecten* might be interpreted in this direction. The Molluscs might constitute a third line of evolution, combining features of the other two. Certainly a good deal of experimental work can be undertaken in this direction.

(b) It is possible that a small camera eye in Arthropods is *optically* possible, but not feasible, as a result of other factors: presence of cuticle, moulting, etc.

THE NEURONAL ARRANGEMENT

The extent to which the wiring diagram of the cells in the vertebrate retina and the (insect) optic lobe³ are similar, is evident in Fig. 4, if one does not take into account the two chiasmata and the special morphology of cell types, as it is indicated with parallel numbering in Fig. 4. This was already suggested by CAJAL and SÁNCHEZ (1915), and by others even before them (LENHOSEK, 1894). As a first approximation it is striking.

However, when we look at the more detailed pattern of connections, it becomes evident that the degree of convergence in the connections (i.e. number of axon inputs per cell) is significantly different. In fact, in Vertebrates every receptor connects to several type 2 cells, and, in turn, these are connected to several type 4 cells, so that it is not possible to distinguish a rigid pattern of connections (POLYAK, 1946). In Insects however, the mode of connections is highly regular and limited: each set of ommatidial receptors have target neurons precisely defined, in a pattern which is repeated throughout the eye. As a consequence, a type 2 cell in a typical compound eye "looks" only at the activity of a local group of receptors, e.g. one in the bee, six in the fly (VARELA, 1970b; TRUJILLO-CENÓZ, 1966). In contrast, in a vertebrate retina there is a whole gradation of type 2 neurons which "look" at the activity of varying groups of receptors, from one to several dozens. Unfortunately, there are no data available on the lamina-medulla connections to allow a similar comparison between type 4 cells (i.e. ganglion cells).

The reasons for this lack of convergence in the neurons of the optic lobe, have to be

³ Of course, in this analysis we are arbitrarily restricting ourselves to the first two neuronal stages in the optic lobe, which, in insects, are not spatially discontinuous with the rest of the brain, as in vertebrates. Further comparisons are very difficult to make, due to the scanty anatomical information.

traced to the very roots of the arthropod adaptations: the exoskeleton and its derivatives. This structure allows for a tremendous adaptive plasticity, as the number of arthropod species testifies, but it has serious intrinsic limitations. In particular, mechanical considerations lead to the conclusion that beyond a certain size of the skeleton, there is not enough space to accommodate the metabolic machinery necessary to provide energy for body movements.

Thus, Arthropods are intrinsically limited in size. Further, the absence of fine capillaries to transport nutrients deep into the organs imply that there is an additional limitation in organ size. For a nervous system these limitations are particularly crucial. A nervous

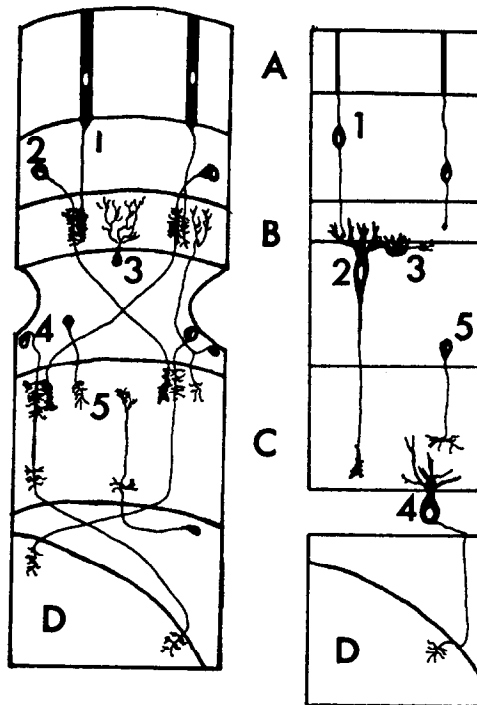


FIG. 4. Diagrammatic comparison between the cellular component of the vertebrate retina and the insect optic lobe. A basic pattern of wiring is apparent as we can be allowed some freedom the chiasmata and the special form of the invertebrate neuropile. To facilitate the comparison, the cell types have been numbered in both diagrams, and the stages have been labelled with letters. Based on CAJAL and SÁNCHEZ (1915).

system needs both convergence at some stages, and certain numbers of neurons performing several computations in parallel at others. As has been argued by VOWLES (1963), if there is a limit in size, too much convergence implies too few neurons of large size thus setting a severe limit to parallel processing. Consequently, it seems that a balance is struck, in insect nervous systems, between both demands: a limited convergence and a reasonable number of neurons of small size. This is probably the main reason why insect neurons are smaller and

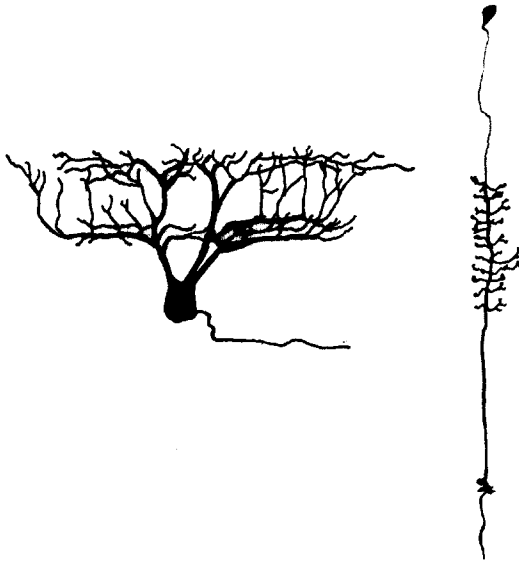


FIG. 5. Comparison between a ganglion cell of a frog retina and a similar cell in the bee's medulla (type 4 in Fig. 3). The size and extent of the contact surface is markedly different. The reason for this might be found in the limitation of size of invertebrates and the necessity that both convergence and parallel processing in any nervous system attain a balance between small cell size and a limited convergence capability. Cells redrawn from CAJAL (1893) and CAJAL and SÁNCHEZ (1915).

have less surface for synaptic contacts (the dendrites are thinner and the cell bodies do not participate in synapses (Fig. 5).⁴

In conclusion, I wish to emphasize that the present considerations should be understood as invitations for further work in a neglected but important area. Under no circumstances do they claim to be satisfactory or final. However, I do believe that they are experimentally accessible and sufficiently suggestive to warrant attention.⁵

REFERENCES

- BARLOW, H. B. (1952). The size of ommatidia in apposition eyes. *J. exp. Biol.* **29**, 667.
 CAJAL, S. R. (1893). La retina des Vértèbrés. *Cellule* **9**, 121.
 CAJAL, S. R. and SÁNCHEZ D., (1915). Contribución al conocimiento de los centros nerviosos de los insectos. *Trab. Lab. Inst. Invest. Biol. Univ. Madrid*, **13**, 1-165.
 EAKIN, R. M. (1965). Evolution of photoreceptors. *Cold. Spring Harbor Symp. Quant. Biol.* **30**, 363.
 EAKIN, R. M. (1968). Evolution of photoreceptors, in *Evolutionary Biology* (edited by T. DOBZHANSKI) Vol. 2, pp. 194-235. Appleton-Century, New York.

⁴ The limit in the number of neurons that can be fitted inside an Arthropod body might be another reason for the existence of a compound eye. In fact, let us return briefly to point (vii) of the preceding discussion, and consider again the possibility that the bee might have a chamber eye of about 1 mm dia. (approximately the volume the compound eye occupies). Simple calculations will show that not less than 70,000 receptors of the size existent in bees can be fitted in the corresponding retinal surface. This contrasts with 2000 ommatidia (about 16,000 cells) present in the compound eye. It is possible that with a pinhole camera eye there would not be enough neurons in the optic lobe to process all the information that can be obtained from the numerous receptors.

⁵ This paper is a significantly modified version of part of a Ph.D. Thesis presented at Harvard University. I wish to thank Drs S. FRENK, H. MATURANA and C. MARTINOYA for their many insightful comments.

- ENOCH, J. M. (1963). Optical properties of retinal receptors. *J. opt. Soc. Am.* **53**, 71–85.
- FEYMAN, R. P., LEIGHTON, R. B. and SANDS, M. (1963). *The Feynman Lectures on Physics*, Vol. 1. Addison-Wesley, Reading.
- GOLDSMITH, T. H. (1964). The visual system of insects, in *The Physiology of Insects* (edited by M. ROCKSTEIN). Academic Press, New York.
- HORRIDGE, G. A. (1968). *Interneurons*. Freeman, San Francisco.
- LENHOSEK, N. VON (1894). Zur kenntnis der Netzhaut der Cephalopoden. *Z. wiss. Zool.* **58**, 636.
- POLYAK, S. (1946). *The Retina*. University of Chicago Press, Chicago.
- TRUJILLO-CENÓZ, O. (1966). Electron microscope observations of the peripheral and intermediate retina of *Depterans*, in *The Functional Organization of the Compound Eye* (edited by C. G. Bernhard). Pergamon Press, Oxford.
- VARELA, F. G. (1970a). Insect retinas: Visual processing in the compound eye, Ph.D. Thesis, Harvard University.
- VARELA, F. G. (1970b). The fine structure of the visual system of the honeybee—II. The lamina. *J. ultrastruct. Res.* **31**, 178–194.
- VARELA, F. G. and WIITANEN, W. (1970). Optic in the compound eye of the honeybee. *J. gen. Physiol.* **55**, 336–358.
- VOWLES, D. M. (1963). Neural mechanisms in insect behavior, in *Current Problems in Animal Behavior* (edited by W. H. THORPE and O. L. ZANGWILL). Cambridge Univ. Press, Cambridge.
- YAMAMOTO, T., TASAKI, K., SUGAWARA, A. and ANTONOSAKI, A. (1965). Fine structure of the octopus retina. *J. cell. Biol.* **25**, 345.
- YOUNG, J. Z. (1962). The retina of cephalopods and its degeneration after optic nerve section. *Phil. Trans. R. Soc.* **B245**, 1.

Abstract—This paper discusses, first, the selective pressures which led to the two basic types of animal eyes, compound vs. camera eyes. Secondly, it considers what is the significance of the apparent similarity of the wiring patterns in the vertebrate retina and in the optic lobe of the compound eye.

No discussion of these matters can be found in the literature since 1915. The present treatment, while it is admittedly only suggestive, is nevertheless open to experimental verification.

Resumen—Este trabajo discute primeramente las presiones selectivas que condujeron a los dos tipos básicos de ojos de animales, ojos compuestos vs. ojos de cámara. En segundo lugar se considera cuál es el significado de la aparente similaridad entre la manera de conectarse de la retina de los vertebrados y del lóbulo óptico del ojo compuesto.

Desde 1915 no se ha encontrado ninguna literatura sobre estos asuntos. El estudio presente, aunque es solamente sugestivo, está, sin embargo, abierto a verificación experimental.