

(4) There should be rapid "adaptation" to a tone of high frequency if the amplitude and frequency are kept constant. There would therefore be a "phasic response" or "on effect". Tympanal organs, however, are clearly very lightly damped systems compared with sub-genual organs and the possibility arises that sound around the optimal frequency would set up strong resonant vibrations of the accessory cells which would be strong enough to keep the scolopale units in continuous vibration, giving rise to a "tonic response". (It is known that substratum vibration of high intensity will sometimes provoke a tonic response in the sub-genual organ⁸.) It follows that the tonic response, although deriving from the same sensilla, would have a longer latency because of the time taken for the build-up of resonance.

(5) At a fixed frequency the rate of production of nerve impulses should be related to the square root of sound intensity, or to the amplitude of displacement of the tympanic membrane, because intensity is equal to ka^2f^2 , where k is a constant, a the amplitude and f the frequency. A limit will be imposed by the non-linear elasticity of the tympanic membrane.

(6) An after discharge should follow a very brief stimulus, and the length of the after discharge reflects the duration of the natural oscillation of the scolopale cells and, therefore, it is proportional to the square root of the sound intensity. It can easily be shown that $A/A' = t/t'$, where A and A' are initial amplitudes of natural vibration and t and t' the respective times required for the vibrations to die down to a given level. An after discharge might also follow the sudden cessation of a constant stimulus because the energy released would result in a free oscillation. This is a special case of (3).

(7) The latency of the response to a harmonic stimulus should vary inversely with (frequency)² if the amplitude is kept constant, or inversely with intensity if the frequency is kept constant. This is because the threshold acceleration in a harmonic stimulus will be attained earlier as its frequency or amplitude is increased.

It will be recognized that these are all typical characteristics of the responses of tympanal organs and are illustrated particularly well in orthopteran and lepidopteran tympanal organs, for example, in *Tettigonia viridissima* studied by Autrum and in the tympanal organ of the moth *Prodenia eridania* investigated by Roeder and his co-workers¹¹. It is significant in the latter case that touching the sensilla with a fine probe, which would damp any natural vibration, abolished the response to sound.

If the theory proposed here is accepted it is clear that the practice of referring to the tympanal organ as a displacement receptor as opposed to a pressure receptor, while correct, is misleading. It appears that the organ is a pressure gradient receptor⁵, that is, an acceleration receptor. Transients are seen as special cases of amplitude modulation as indeed they are accepted to be, and the importance of a short rise time in provoking responses in the tympanal organ is then clear, because the shorter the

rise time the greater the acceleration imparted to the tympanum. This is not to say that other features of modulation of a sound would not affect the perception of a transient there. Frequency modulations involving the order of change of acceleration we are considering are probably rare in nature and would be difficult to achieve without simultaneous changes in amplitude. Detection of changes in frequency would, however, be possible in some form if sensilla of graded sizes, and therefore differing natural frequencies, were present in a receptor. It is then possible that there is a "typical intensity" of a sound of a certain frequency, which results in the stimulation of a certain proportion of all sensilla, because the optimal and natural frequencies may be equated, and the higher the optimal frequency the lower the threshold at this frequency (see note 2). Sound of greater or lesser intensity would activate more or less sensilla. Evidence for a typical intensity is found in the work of Busnel and Loher¹², who found an increase in phonoresponses in *Chorthippus brunneus* to sounds up to a certain intensity, after which there was a falling off in the number of responses. At 85 dB with a time rise of 2 msec they found a maximum of 45 per cent positive responses, but only 9.5 per cent at 100 dB. The same sort of condition could arise with a shift in the frequency of a sound stimulus with constant amplitude, and this would explain very well certain unexpected findings. In the tettigoniid *Gampsocletis buergeri* Katsuki and Suga^{13,14} found an increase to a maximum in impulse frequency in central neurones and then a decline as the frequency of sound was increased at constant intensity. They found evidence for the existence of two groups of neurones. Those of one group were activated only by sound of higher frequencies, and were more sensitive to stimuli than those of the other group which were activated by sounds of lower frequencies. Horridge¹⁵, studying *Locusta migratoria*, *Schistocerca gregaria* and *Acheta domesticus*, also found evidence for two different groups of receptors, sensitive to higher and lower frequencies, and showed that the discrimination took place at the level of the sense organ.

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Origin of Eyes and Brains

by

R. L. GREGORY

Psychological Laboratory, Cambridge

The evolution of the mechanism of visual perception must entail the separate elaboration of eyes and brain. But which came first? Or is this a "hen and egg" problem?

ALL knowledge comes through the senses, and this suggests an intimate link between the evolutionary development of brains and eyes. Somehow brains and eyes are developed by the random steps which form the evolutionary ladder according to the dictates of survival value at each rung.

The restraints imposed on the development of perception by natural selection give some clue as to the way in which eyes and brains came into being. The fossil record is of no use in tracing the origins of these organs because the crucial steps have not been preserved. An attempt

may, however, be made to put existing "primitive" forms into sequence according to various criteria. I shall not attempt a detailed account but rather endeavour to outline how the principal forms of eye could have come about and consider the "hen and egg" problem: which came first—the eye or the brain?

"Simple" eyes have a single optical system serving many photoreceptors. "Compound" eyes, found in arthropods, have up to many thousand individual optical systems, each with its own photoreceptor. Both kinds of eye must have appropriate neural systems to handle the information they provide. There is then a "hen and egg" problem, for it is very difficult to imagine how an eye could develop unless there were some suitable neural system already present to handle its information. Why, however, should a visual "computer" arise before there was an eye to feed it with information? If there is an answer to this, there is then the question of why there should be the two great classes of eyes.

Animals live in a world of objects, some edible, others dangerous, some protecting, such as crevices in rock, and others irrelevant to their survival. Objects have many characteristics beyond shape and colour, which alone are represented by optical images. It is these other characteristics which are biologically important. One cannot be attacked and eaten by an image—hence the vicarious pleasures of the cinema—and neither can one feed on images. It follows that information given by eyes is only of indirect use to living creatures, and to make any use of visual information considerable computing is required. Other senses, especially touch and taste, do, however, give information of immediate value and thus it can be assumed with some confidence that these senses were the first to develop. Touch and the chemical senses directly monitor biologically vital features of the environment, and their information requires but a minimal "computer". It is therefore reasonable to suppose that vision is a lately acquired sense. How did it arise? How did a neural computer develop which was capable of reading significance into the non-biologically important optical images? The problem is especially acute because the significance of the images is not in the present state of affairs, but rather in what they presage of the immediate future. Touch and the chemical senses signal the state of the environment in immediate contact with their owner, but vision signals distant events, and may give warning of the future. The visual computer cannot be a simple reflex affair, which acts as soon as possible to a "stimulus". It must transform optical information into hypotheses of the nature of distant objects, which may be friend or foe, food or disaster. The eyes give time to compute; they allow brains to devise strategies more subtle than reflexes in response to stimuli.

Origin of the simple eye. The first eyes^{1,2} were merely regions of the outer skin which were sensitive to light, perhaps originally responding more to heat than to light. These first light-sensitive regions could have fed the original touch neural systems. Simple tropisms and immediate reflex action to photic stimuli could have been mediated by the touch neural system. It is not too difficult to imagine a gradual improvement in the sensitivity to light and that certain cells became specialized photoreceptors in regions where they would be most useful. The ends of the animal were favoured with the first true eyes—gradually deepening pits lined with specialized cells sensitive to light. The pits served to increase the contrast of shadows, reducing ambient light like the shafts dug in the ground by ancient astronomers to view stars in daytime. Plato describes how Thales fell down such a pit; obviously he should have covered his pit to prevent such accidents. It seems that the eye pits of primitive creatures did develop such protective covers—in the form of transparent windows—to prevent blockage by alien bodies, such as particles in suspension and grains of sand. It is usually held that these windows gradually thickened

towards their centres, for this would increase the intensity of light at the bottom of the eye pits. From such a process a lens would have evolved, and thus give true formation of images. With improvement in the resolution of the lens the acuity would increase to match it, transforming skin which was sensitive to touch into a true retina. The optical reversal of the lens must have imposed the biggest jolt since life began, for the ancient touch inputs were suddenly reversed, evidently requiring the dramatic reorganization of the nervous system which we see today in the crossings of the chiasma. Retinal information is different from the information gained from touch, for not only is the pattern reversed but also it refers to distant objects. The crossings of the chiasma probably served to relate the reversed retinal patterns to touch information from the body^{1,3}. Primate perceptual systems can compensate for systematic translations of their retinal images^{4,5}, but there is no evidence of this ability in creatures as advanced as even the amphibians⁶, and so explicit reconnexion seems to have been necessary at the early stages of perception. The retinal image is not only reversed: it shrinks as represented objects become more distant. It seems that this is compensated by scaling mechanisms, which give size constancy⁷, to maintain an effective connexion between the neural representations of touch and vision despite changing image size.

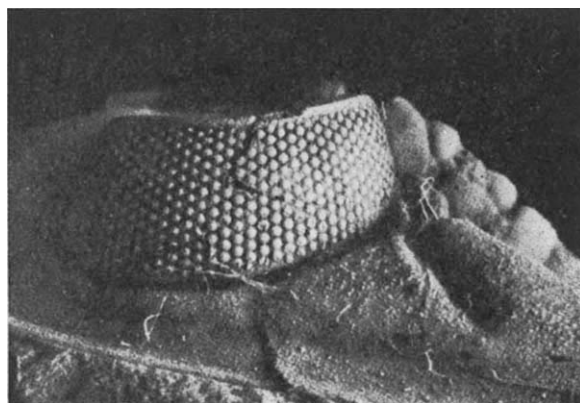


Fig. 1. An early compound eye of a trilobite from the Cambrian.

Origin of compound eyes. Each unit, or ommatidium, of a compound eye consists of three basic elements: the corneal lens, crystalline cone and the photoreceptor, or rhabdomere. Compound eyes are found in early fossils, in trilobites from the lower Cambrian rocks of about 600 million years ago (Fig. 1). They appear to be essentially the same as modern insect eyes, but because there are no earlier examples in the fossil record it is only possible to guess at the earlier stages, using living creatures as examples of what has occurred, however uncertain the order may be. There is a special difficulty with the compound eye: what could give rise to many separate and identical elements, each complete with lens and photoreceptor? It is difficult enough to imagine how the simple eye developed—but how could several hundred, all at once? A single element would seem quite pointless—or is it?

I have supposed that the simple eye took over existing touch neural mechanisms, and will later point out that there are basic reasons for supposing that touch information was essential for the first vision. There are two kinds of touch, which involve entirely different neural mechanisms. These are skin pattern touch and limb probe touch. Pattern touch involves the reception of patterns by contact with areas of skin, while probe touch is very different and

requires exploratory movements of a limb. Pattern touch gives information only of structures lying on the two dimensional surface of the skin, while probe touch gives information in three dimensions, within the reach of the limb. Pattern touch is mediated by many parallel neural channels simultaneously sending pattern information to the central nervous system; active touch is essentially single channel, signalling structure in three dimensions but spread out in time as the probe explores external space. The neural systems for the two kinds of touch must always have been very different; one requires many parallel channels, the other a single channel transmitting information of space traced in time.

If the first retinal images were accepted by the original nervous system responsible for pattern touch, could the compound eye be a multiplication of a single moving element, signalling down a single channel to explore space in a manner similar to probe touch?

An example exists of a living creature in which a single unit eye seems to work as a photic probe. Exner⁸ described a small copepod, *Copilia*, living in the bay of Naples. He described that it has a pair of strange eyes, like telescopes with two lenses; the second "eye piece" lens is deep in the body, and in "continual lively motion". We have examined living specimens, and it appears that these eyes could be single channel scanning probes^{9,10}.

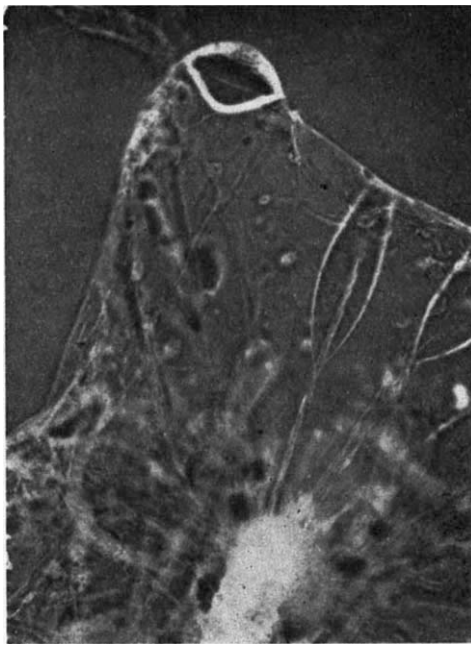


Fig. 2. Photograph of a single channel scanning eye of *Copilia quadrata*.

The female of *Copilia quadrata* is 4–5 mm long, 1 mm wide, and entirely transparent; there is no colouring except for an orange pigment which surrounds the single photoreceptors of each eye. Under the microscope the internal structure of *Copilia* is clearly visible, including that of the eyes and the optic nerve. The two eyes occur on opposite sides of the animal, which has an unusual shape for a copepod because it is very wide at its anterior. There are two large lenses placed far apart in front. Each eye has a large anterior lens and a second posterior smaller lens which is shaped like a pear. Almost half the total volume of the animal is taken up by the two eyes. Attached to the posterior lens, which is situated deep in

the body of the animal, is a long orange pigmented structure which extends back from it and curves inward, but does not touch its counterpart from the other eye. The posterior lens is situated at the image plane of the large anterior lens, and moves horizontally across the image plane of the first lens with a "saw-tooth" scan. The "scanning" rate varies from about one scan/2 sec to about five scans/sec. The movements are synchronized; the posterior lens and photoreceptor of each approach and recede together. In the resting position the optical units are separated from each other, near the tough transparent outer cuticle of the creature, from which position they rapidly approach each other and then slowly separate across the image planes of their respective anterior lenses.

The optic nerve arises from about half way down the pigmented photoreceptor, and enters the brain which is located at the centre of the creature. *Copilia* has very simple mouth parts and, because it is a filter-feeder, does not have to seek its "prey". It is almost certain that sexual reproduction occurs; obviously this requires recognition of the male. It is not known, however, what use *Copilia* makes of its eyes; however, it does seem clear that each eye is an optical unit, which works by temporal scanning somewhat like a simple television camera. Detailed examination reveals that the elements of the eye are extremely similar to corresponding elements of an ommatidium of a modern compound eye. The spacings between the anterior and posterior lenses, however, are quite different—distant in *Copilia* but almost touching in normal compound eyes. The lenses themselves and the single "rod" photoreceptors, however, are almost identical.

Copilia could be a surviving form with a prototype single channel scanning eye. The compound eye could have developed by multiplication of these units. It seems easier to suppose this than that a hundred or a thousand units sprang up together. Why should the prototype single element scanning eye not develop further, but rather multiply to form the compound eye? The answer to this seems fairly clear—the basic engineering limitation of scanning systems is the amount of information which they can transmit by the single channel. The channel capacity of any nerve fibre found in nature is extremely low compared with electronic channels; at best, the maximum frequency response approaches only 10^3 pulses/second; while, for comparison, to transmit television pictures about 4×10^6 cycles/second are needed. Sophisticated perceptual systems save channel capacity by various tricks¹¹, but a vast discrepancy still remains. If, however, a scanning eye were duplicated, the elements could send down information simultaneously. This would be rather like exploring a structure with two fingers at once. There could be three fingers, four fingers . . . a thousand fingers or ommatidia. There is no need to sweep the eye of a thousand optical units across the structure, for the entire pattern can be signalled by simultaneous transmission down the many channels. Then scanning can be abandoned. The compound eye started by using a single channel, with the kind of temporal information processing of probe touch, but it can be supposed to have developed many static parallel units, to become, like the simple eye based on the pattern touch neural system, a mosaic eye. Compound eyes which have too few elements to have entirely abandoned scanning (or active exploration) by each photic probe are still found. In *Daphnia* (Fig. 3) we find a compound eye which consists of about twenty elements, and this eye is in continuous oscillatory movement. This seems to be an eye which is part-way up the sequence from the single channel scanning eye of *Copilia* to the fully developed static compound eye. In *Daphnia*, there are few units and it seems that the deficiency is made up by oscillatory scanning very like the single unit eye of *Copilia*. All compound eyes with but few elements can be assumed to scan.

I have outlined, in general terms, a possible sequence of events leading to simple and to compound eyes. Each must have taken over and developed for its own use the primordial neural mechanisms mediating touch. The simple eye took over the pattern touch system; the prototype scanning unit, which later formed compound eyes by multiplication, took over probe touch neural mechanisms. By supposing that already existing touch mechanisms were taken over for vision, the "hen and egg" problem of which came first, eye or brain, is answered. There is some justification for supposing that the first eyes took over earlier touch neural systems, which then developed to process distant information. Jumping a thousand million years or so, there may be other and deeper reasons for believing this.

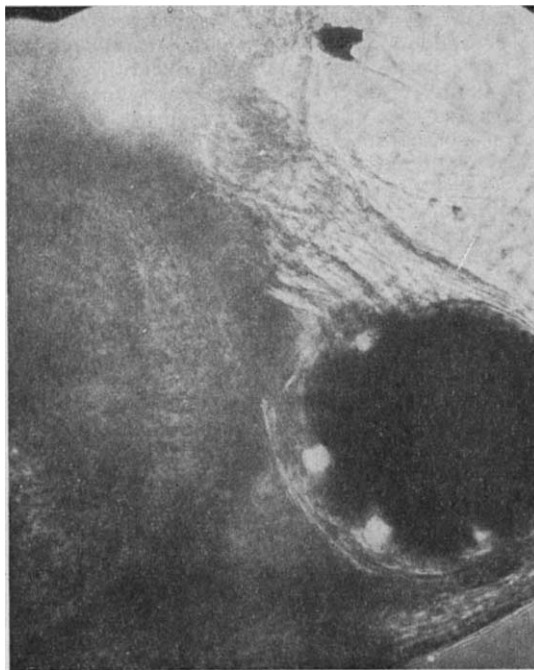


Fig. 3. Photograph of the eye of *Daphnia*; possibly a scanning eye.

Origin of visual perception. What are the essential differences between perception in primitive creatures and in higher animals, including man? It is generally believed that all primitive perception is a matter of reflex neural mechanisms, activated by more or less specific "stimuli". Perceptual learning is certainly minimal in primitive creatures; and these special visual patterns can be supposed to have taken on significance through ancestral disasters just as in the development and inheritance of more obvious structural characteristics through natural selection. Some insects do show visual learning (for example, bees learn key features of the terrain around their nests for navigation) but this ability is much greater in mammals, especially primates. Clearly perception, as it developed phylogenetically, became less and less tied to specific visual patterns, so that finally a large variety of patterns elicit the same behaviour. We may say that perception becomes geared to the response to objects, no matter how they are presented to the senses. Finally, retinal images become indicators, symbols, identifying objects. What happens is that we perceive far more than is actually sensed in each moment of perception. We "see" that a table is hard, and a chair safe to sit on. We "see"

from a smile that a person is pleased. This goes far beyond the given sensory data and yet it is usually correct. This ability of the human perceptual system to go beyond immediate data is brought out most dramatically by considering cartoons¹⁰. A few lines convey an entire story with the personality of each person and his mood. It is useful to think of perceptions as hypotheses based on, but certainly not limited by, current sensory data.

When visual information leads to behaviour appropriate to non-visual features (such as the hardness of a table, though the image of the table is not hard), then the retinal image is acting as a sign. Retinal images are symbols, like words in a language; however, like any other symbols there must be a process of initial association to acquire significance, or the symbols are in a logical vacuum and cannot represent any reality. Furthermore, retinal images are but flat projections of a three dimensional world and yet they give perception of three dimensions. There must be direct, non-visual, information of the third dimension. Other information comes from touch. It appears that any conceivable device for perceiving which relies on two dimensional images must use, at some stage, direct touch information if it is to interpret its images in terms of the three dimensions of surrounding space.

Dependence on early touch experience for visual perception is supported by cases of recovery from congenital and early blindness^{12,13}, and in animals reared in the dark^{14,15}. What is true for development of perception in the individual should also be essentially true for the development of vision in evolution, for touch must have preceded vision if touch information is required to make retinal images effective symbols of the non-optical world of objects.

If simultaneous information from the eyes and from touch is required to develop correlations between them, regions of the body which could not be seen could not give correlations. Held and Hein, in an address to the Congress of Psychology in Moscow, have shown that a monkey which is denied the sight of one of its fore limbs does not develop normal eye-limb co-ordination, though the other limb is normal. It is the fore limbs, and especially their movements, which are available to vision but not pattern touch—which is hidden from the eye by (non-transparent) objects in contact with the skin. It is active rather than passive limb movement which gives visual learning¹⁶.

In the human being we see preserved almost all the stages in the developments of vision from the simplest reflex (closing of the eyes on sudden change of illumination), to pattern recognition, and identification of objects from unusual points of view, with prediction of the immediate future based on the past. Such feats cannot be simulated with even the most advanced computers.

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