A pessimistic estimate of the time required for an eye to evolve

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SUMMARY

Theoretical considerations of eye design allow us to find routes along which the optical structures of eyes may have evolved. If selection constantly favours an increase in the amount of detectable spatial information, a light-sensitive patch will gradually turn into a focused lens eye through continuous small improvements of design. An upper limit for the number of generations required for the complete transformation can be calculated with a minimum of assumptions. Even with a consistently pessimistic approach the time required becomes amazingly short: only a few hundred thousand years.

1. INTRODUCTION

When Charles Darwin (1859) presented his theory of evolution he anticipated that the eye would become a favourite target for criticism. He openly admitted that the eye was by far the most serious threat to his theory, and he wrote: 'that the eye... could have been formed by natural selection seems, I freely confess, absurd in the highest possible degree'. Although the problem is principally important, it gradually lost its scientific potency, and has now almost become a historical curiosity. But eye evolution continues to fascinate, although the question is now one of process rate rather than one of principle.

Estimates of the number of generations required to make a certain change to a simple quantitative character are easily made if the phenotypic variation, selection intensity and heritability of the character are known (Falconer 1989). The evolution of complex structures, however, involves modifications of a large number of separate quantitative characters, and in addition there may be discrete innovations and an unknown number of hidden but necessary phenotypic changes. These complications seem effectively to prevent evolution rate estimates for entire organs and other complex structures. An eye is unique in this respect because the structures necessary for image formation, although there may be several, are all typically quantitative in their nature, and can be treated as local modifications of pre-existing tissues. Taking a patch of pigmented light-sensitive epithelium as the starting point, we avoid the more inaccessible problem of photoreceptor cell evolution (Goldsmith 1990; Land & Fernald 1992). Thus, if the objective is limited to finding the number of generations required for the evolution of an eye's optical geometry, then the problem becomes solvable.

We have made such calculations by outlining a plausible sequence of alterations leading from a light-sensitive spot all the way to a fully developed lens eye. The model sequence is made such that every part of it, no matter how small, results in an increase of the spatial information the eye can detect. The amount of morphological change required for the whole sequence is then used to calculate the number of generations required. Whenever plausible values had to be assumed, such as for selection intensity and phenotypic variation, we deliberately picked values that overestimate the number of generations. Despite this consistently pessimistic approach, we arrive at only a few hundred thousand generations!

2. A MODEL OF EYE EVOLUTION

The first and most crucial task is to work out an evolutionary sequence which would be continuously driven by selection. The sequence should be consistent with evidence from comparative anatomy, but preferably without being specific to any particular group of animals. Ideally we would like selection to work on a single function throughout the entire sequence. Fortunately, spatial resolution, i.e. visual acuity, is just such a fundamental aspect and it provides the sole reason for an eye's optical design (Snyder *et al.* 1977; Nilsson 1990; Warrant & McIntyre 1993). Spatial resolution requires that different photoreceptor cells have different fields of view (Snyder *et al.* 1977). A comparison of their signals then gives information about the direction of the incident light. The smaller the field of view of each individual intensity channel, the better is the potential for accurate spatial information. It does not matter if the spatial resolution is used for measuring self-motion, detection of small targets, or complicated pattern recognition, the fundamental aspect of information is the same, and so are

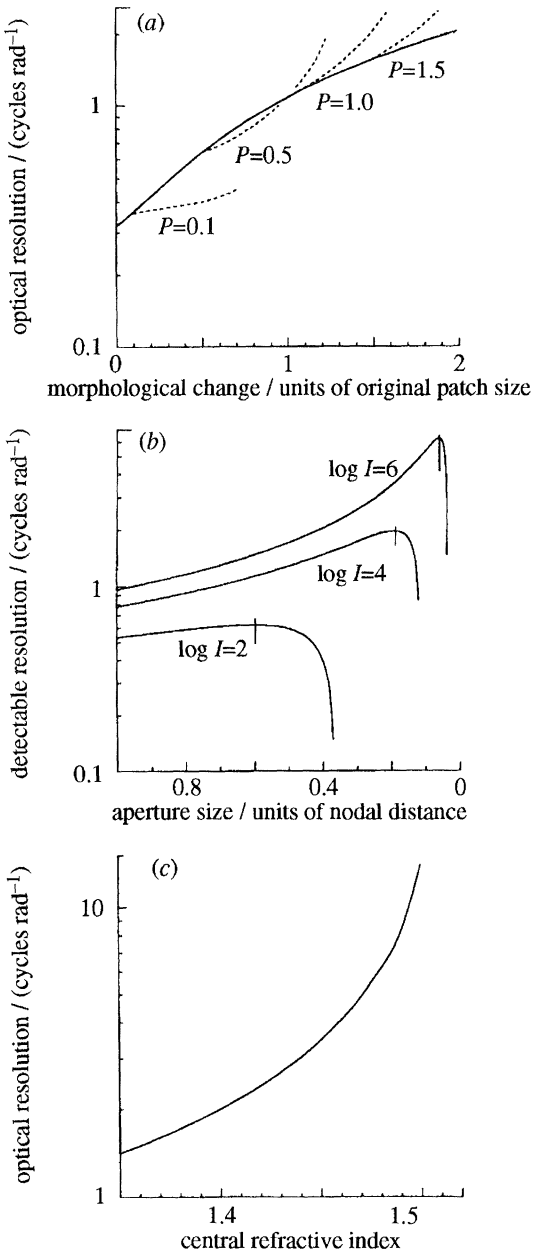

Figure 1. Strategies for improving spatial resolution in an evolving eye. (*a*) An originally flat light-sensitive patch, or retina, is gradually invaginated (solid line) to form a pit whose distal aperture keeps the size of the original patch. The optical resolution is calculated as the inverse of the field of view of a point in the centre of the retina. At various points on the curve, the deepening of the pit is interrupted and all morphological change is instead spent on constriction of the aperture (broken lines). Calculations are made for aperture constriction to start when the pit depth, P, is 0.1, 0.5, 1.0 and 1.5 times the original width of the patch. (*b*) Optimization of lensless aperture. Continuations of the dashed $P = 1$ curve in (*a*), but with photon noise taken into account with equation (1). The three curves are calculated for ambient intensities (I) separated by two log units. The upper curve is thus for an intensity 10000 times higher than that for the lower curve. The intensity is in units normalized to the nodal distance (pit depth): photons per nodal distance squared per second per steradian. The unconventional use of nodal distance instead of micrometres in the unit allows the three curves to be interpreted as eyes differing in size by a factor of 10. Assuming constant intensity, the upper curve is thus for an eye which is 100 times larger than that for the lower curve. There is an optimum aperture size, indicated by vertical lines, beyond which resolution (maximum resolvable spatial frequency) cannot be improved without a lens. (*c*) The optical resolution plotted as a function of the gradual appearance of a graded-index lens. The spherical lens is assumed to fill the aperture, and to be 2.55 lens radii away from the retina (e.g. as in fish eyes (Fernald 1990)). The central refractive index of the lens is plotted on the horizontal axis. From this value the refractive index is assumed to follow a smooth gradient down to 1.35 at the peripheral margin. The calculation demonstrates that optical resolution continuously improves from no lens at all to the focused condition where the central refractive index is 1.52. The maximum resolution in the focused condition will be limited by both photon noise, as in (*b*), and by diffraction in the lens aperture, but none of these limitations are significant within the range plotted. The vertical axis of all three graphs (*a*)–(*c*) was made logarithmic to allow for comparisons of relative improvement. A doubling of performance is thus always given by the same vertical distance.

the demands on eye design (see Warrant & McIntyre 1993).

We let the evolutionary sequence start with a patch of light-sensitive cells, which is backed and surrounded by dark pigment, and we expose this structure to selection favouring spatial resolution. We assume that the patch is circular, and that selection does not alter the total width of the structure. The latter assumption is necessary to isolate the design changes from general alterations of the size of the organ. There are two ways by which spatial resolution can be gradually introduced: (i) by forming a central depression in the light-sensitive patch; and (ii) by a constriction of the surrounding pigment epithelium. Both these morphological changes reduce the angle through which the individual light-sensitive cells receive light. The relative effects that depression and constriction have on the eye's optical resolution are compared in figure 1*a*. Initially, deepening of the pit is by far the most efficient strategy, but when the pit depth equals the width ($P = 1$ in figure 1*a*), aperture constriction becomes more efficient than continued deepening of the pit. We would thus expect selection first to favour depression and invagination of the light-sensitive patch, and then gradually change to favour constriction of the aperture. During this process a pigmented-pit eye is first formed, which continues gradually to turn into a pinhole eye (see Nilsson 1990).

As the aperture constricts, the optical image becomes increasingly well resolved, but constriction of the aperture also causes the image to become gradually dimmer, and hence noisier. It is the random nature of photon capture that causes a statistical noise in the image. When the image intensity decreases, the photon noise increases in relative magnitude, and the low contrast of fine image details gradually drowns in the noise. If we assume that the retinal receptive field, $\Delta\rho_r$, and the optical blur spot, $\Delta\rho_{lens}$, are identical Gaussians with half-widths being the angle subtended by the aperture at a central point in the retina (this effectively means that the retinal sampling density is assumed always to match the resolution of the optical image), then we can use the theory of Snyder (1979) and

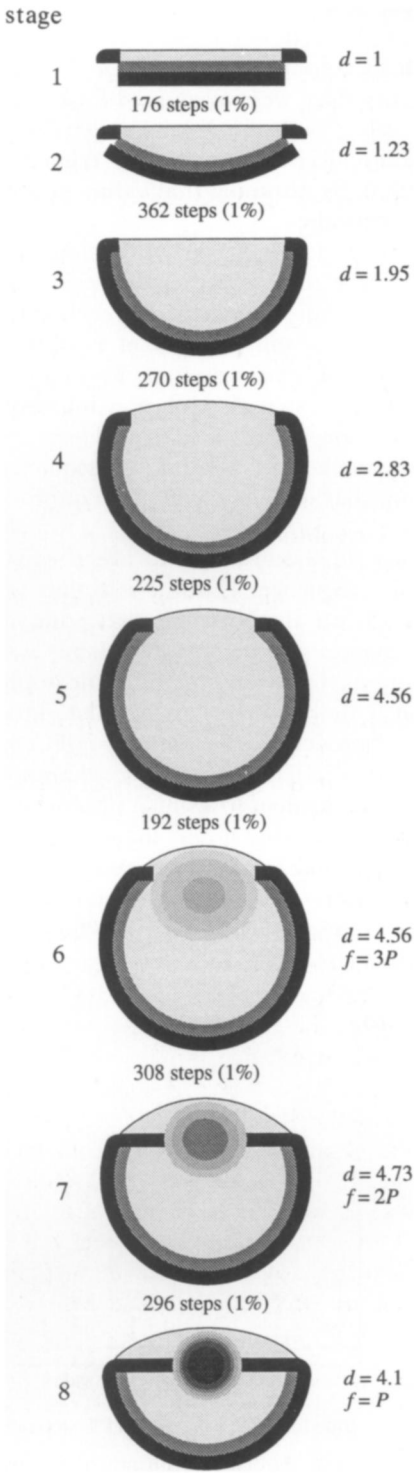

Figure 2. Representative stages of a model sequence of eye evolution. In the initial stage (1) the structure is a flat patch of light-sensitive cells sandwiched between a transparent protective layer and a layer of dark pigment. In stages 2 and 3 the photoreceptor layer and pigment layer (hereafter collectively termed the retina) invaginates to form a hemisphere. The protective layer deepens to form a vitreous body which fills the cavity. The refractive index of the vitreous body is assumed to be 1.35, which is only slightly higher than that of water, and not enough to give the vitreous body any significant optical effect. In stages 4 and 5 the retina continues to grow, but without changing its radius of curvature. This causes a gradual shift from deepening of the retinal pit to constriction of the distal aperture. The aperture size in stage 6 was chosen to reflect the typical proportions in real eyes of this type. In stages 6–8 a graded-index lens appears by a local increase in refractive index. The central refractive index of the lens grows from the initial value of 1.35 to 1.52 in the final stage. Simultaneously the lens changes shape from ellipsoid to spherical and moves to the centre of curvature of the retina. As the lens shrinks, a flat iris gradually forms by stretching of the original aperture. The focal length (f) of the lens gradually shortens, and in stage 8 it equals the distance to the retina (P), producing a sharply focused system. The relative change in receptor diameter, required to keep sensitivity constant throughout the sequence, is indicated by the normalized receptor diameter d. The anatomical change between model stages is given as the number of 1% modification steps.

Warrant & McIntyre (1993) to obtain the maximum detectable spatial frequency, ν_{max}, as:

$$\nu_{max} = (0.375P/A)\,[\ln(0.746A^2\sqrt{I})]^{\frac{1}{2}}, \quad (1)$$

where A is the diameter of the aperture, P is the posterior nodal distance, or pit depth and I is the light intensity in normalized units of 'photons per nodal distance squared per second per steradian'. We can now use this relation to plot resolution against aperture diameter (figure 1*b*). For a given ambient intensity and eye size there is an optimum aperture size where noise and optical blur are balanced in the image. A large eye or high light intensity makes for an optimum aperture which is small compared with the nodal distance. When the aperture has reached the diameter which is optimal for the intensity at which the eye is used, there can be no further improvement of resolution unless a lens is introduced.

In a lensless eye, a distant point source is imaged as a blurred spot which has the size of the imaging aperture. A positive lens in the aperture will converge light such that the blur spot shrinks, without decreasing the brightness of the image. Most biological lenses are not optically homogeneous, as man-made lenses normally are (Fernald 1990; Nilsson 1990; Land & Fernald 1992). In fact, a smooth gradient of refractive index, like that in fish or cephalopod lenses, offers a superior design principle for making lenses: the optical system can be made more compact, and aberrations can be reduced considerably (Pumphrey 1961). A graded-index lens can be introduced gradually as a local increase of refractive index. As the focal length becomes shorter, the blur spot on the retina will become smaller. The effect this has on resolution was calculated by using the theory of Fletcher *et al.* (1954) for an ideal graded-index lens (figure 1*c*). Even the weakest lens is better than no lens at all, so we can be confident that selection for increased resolution will favour such a development all the way from no lens at all to a lens powerful enough to focus a sharp image on the retina (figure 1*c*).

Camera-type eyes of aquatic animals typically have a spherical graded-index lens which is placed in the centre of curvature of the retina (Land 1981; Land & Fernald 1992). With this arrangement they achieve virtually aberration-free imaging over a full 180° visual field. Another typical feature is that the focal length of the lens is 2.55 times the lens radius (Pumphrey 1961).

This relation, called Mattiessen's ratio, represents the ideal solution for a graded-index lens with a central refractive index of 1.52 (Fletcher *et al.* 1954), a value close to the upper limit for biological material. However, the best position for a lens to be introduced in a pinhole eye is in the aperture, clearly distal to the centre of curvature of the retina. Because the central and peripheral parts of the retina will then be at different distances from the lens, there is no need for the lens to be spherical. In fact, an ellipsoid lens is better because it can compensate optically for the difference in retinal distance. Furthermore, the size of the first-appearing lens is determined by the aperture, and need not have the size which will finally be required. As the lens approaches focused conditions, selection pressure gradually appears to move it to the centre of curvature of the retina, to make it spherical, and to adjust its size to agree with Mattiessen's ratio.

Based on the principles outlined above, we made a model sequence of which representative stages are presented in figure 2. The starting point is a flat light-sensitive epithelium, which by invagination forms the retina of a pigmented pit eye. After constriction of the aperture and the gradual formation of a lens, the final product becomes a focused camera-type eye with the geometry typical for aquatic animals (e.g. fish and cephalopods).

The changes in size and position of the aperture cause variations in image brightness in the model sequence. To account for this we have assumed that the receptor diameter is continuously modified such that the photon catch per receptor, and thus the signal to noise ratio, is kept constant throughout the sequence. As the model is of arbitrary size, we have used a normalized receptor diameter (d) which is 1 at stage 1 in figure 2.

3. QUANTIFICATION OF CHANGE

The model sequence of figure 2 contains a number of structural elements whose shape and size are gradually modified. To quantify these changes we calculate the number of sequential 1 % steps of modification it takes between each stage in figure 2. For example, a doubling of the length of a structure takes 70 steps of 1 % ($1.01^{70} \approx 2$). Note that the last step is twice as long as the first in this example. The principle of 1 % steps can be applied to changes of any quantitative character. Each structure of the model eye was analysed individually, as if no change follows passively from any other.

There are unavoidable ambiguities in measuring morphological change, because a product will have to be compared with a subjectively chosen origin. It would thus be possible to claim that a doubling in length of a structure is really a three times stretching of the outer half. Both views are correct, but they give different quantifications of the change. Measurements of phenotypic variation in a population suffer from the same type of subjectiveness. As we are going to relate our measures of morphological change only to general estimates of phenotypic variation, we will be safe as long as we avoid unorthodox and strange ways of comparing origin and product. Our principles have been to use whole length measurements of straight structures, arc length of curved structures, and height and width of voluminous structures. Changes in the radius of curvature were accounted for by calculating the arc length of both the distal and proximal surfaces of the structure. Refractive index was related to protein concentration, by assuming that values above 1.34 are due to proteins alone.

The calculated number of 1 % changes required between each of the stages (see figure 2) was plotted against the optical performance of each stage, which was calculated as the number of resolvable image points within the eye's visual field (figure 3). The graph shows that spatial resolution improves almost linearly with morphological change. There are thus no particularly inefficient parts of the sequence, where much change has to be made for little improvement of function.

Altogether 1829 steps of 1 % are needed for the entire model sequence. Natural selection would act simultaneously on all characters that positively affect the performance. In our model there are several transformations that would speed up the improvement of function if they occurred in parallel. True to our pessimistic approach, we deliberately ignored this and assumed that all 1829 steps of 1 % change occur in series. This is equivalent to a single structure becoming 1.01^{1829} or 80129540 times longer. In terms of morphological modification, the evolution of an eye can thus be compared to the lengthening of a structure, say a finger, from a modest 10 cm to 8000 km, of a fifth of the Earth's circumference.

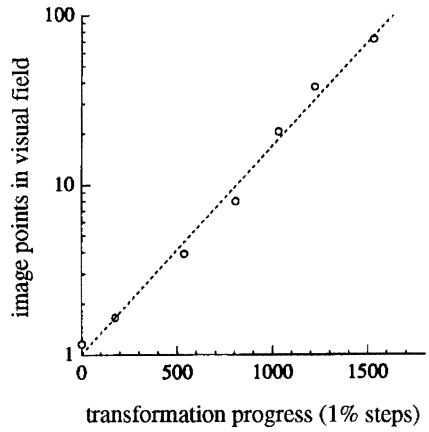

Figure 3. Potential optical performance of the model sequence plotted against transformation progress. The geometry of each stage in figure 2 sets an upper limit to the spatial resolution of the eye. The smallest resolvable detail is given by the solid angle of the field of view of a point in the centre of the retina. The number of resolvable picture elements that can be fitted into the hemispherical visual field of the eye gives a measure of the number of image points that the eye can maximally resolve. When this estimate of the eye's optical performance is plotted on a logarithmic scale against the transformation progress, it forms an almost straight line. The last stage of figure 2 is not included because its performance is strongly dependent on ambient light intensity and the absolute size of the eye. If the intensity is high and the eye large, the number of image points in the last stage may be up to six orders of magnitude larger than in the penultimate stage.

4. THE NUMBER OF GENERATIONS REQUIRED

Having quantified the changes needed for a lens eye to evolve, we continue by estimating how many generations such a process would require. When natural selection acts on a quantitative character, a gradual increase or decrease of the mean value, m, will be obtained over the generations. The response, R, which is the observable change in each generation is given by the equation

$$R = h^2 i \sigma_p \quad \text{or} \quad R = h^2 i V m, \tag{2}$$

where h^2 is the heritability, i.e. the genetically determined proportion of the phenotypic variance, i is the intensity of selection, V is the coefficient of variation, which measures the ratio between the standard deviation, σ_p, and the mean, m, in a population (Falconer 1989). For our estimate we have chosen $h^2 = 0.50$, which is a common value for heritability, while deliberately low values were chosen for both i (0.01) and V (0.01) (see Lande 1980; Futuyma 1986; Barton & Turelli 1989; Falconer 1989; Smith 1989). The response obtained in each generation would then be $R = 0.000\,05m$, which means that the small variation and weak selection cause a change of only 0.005 % per generation. The number of generations, n, for the whole sequence is then given by $1.000\,05^n = 80\,129\,540$, which implies that $n = 363\,992$ generations would be sufficient for a lens eye to evolve by natural selection.

5. DISCUSSION

Eyes closely resembling every part of the model sequence can be found among animals existing today (Salvini-Plawen & Mayr 1977). From comparative anatomy it is known that molluscs and annelids display a complete series of eye designs, from simple epidermal aggregations of photoreceptors to large and well-developed camera eyes (Salvini-Plawen & Mayr 1977; Land & Fernald 1992). The structural components of our model have counterparts with different embryological origin in different groups. For modelling purposes these differences are irrelevant because selection for the various functions will operate on whatever tissue is present at the place where the function is needed.

The development of a lens with a mathematically ideal distribution of refractive index may at first glance seem miraculous. Yet the elevation of refractive index in the lenses of both vertebrates and cephalopods is caused by proteins that are identical or similar to proteins with other cellular functions (Doolittle 1988; Goldsmith 1990; Winstow & Kim 1991; Land & Fernald 1992). Selection has thus recruited gene products that were already there. Assuming that selection operates on small but random phenotypic variations, no distribution of refractive index is inaccessible to selection. It is an inevitable consequence of selection for improved resolution that the population average is continuously adjusted towards the ideal distribution of refractive index. The lens should thus be no more difficult to evolve than any other structure of the model.

It is important that the model sequence does not underestimate the amount of morphological change required. The only real threat to the usefulness of our model is that we may have failed to introduce structures that are necessary for a functional eye. Features of many advanced eyes, such as an adjustable iris and structures for distance accommodation, may in this context seem to be serious omissions from the model sequence. The function of these structures is to make the eye more versatile so that it can perform maximally over a greater range of distances and ambient intensities. However, the improved function brought about by the sequence of modifications in our model does not in any way depend on the existence of these auxiliary structures. It is in fact the other way around: evolution of these refinements requires the existence of the structures that develop in our model

Vertebrates and cephalopods have a vascularized layer, the choroid, and a supporting capsule, the sclera, in their eyes (Walls 1942; Messenger 1981). The demand for blood supply and structural support comes from the general lifestyle and size of these animals, and the demands involve the entire body, not just the eyes. The complete absence of choroid and sclera in the well-developed camera eyes of polychaetes and gastropod molluscs (Salvini-Plawen & Mayr 1977; Messenger 1981) shows that such structures are not mandatory for eye evolution, and thus are not needed in our model.

The organization and specialization of the cells in the retina require some attention. The photoreceptor cells of advanced eyes are certainly not identical to those of simple light-sensitive spots (Eakin 1963; Goldsmith 1990), but even primitive photoreceptors should be good enough to make improvements of optical resolution worthwhile. Improvements of efficiency, and specializations for polarization sensitivity and colour vision, are in no way required for selection to favour improvements of spatial resolution. The nervous tissue in the vertebrate retina can also be ignored as this is clearly a part of the nervous system which just happens to reside in the eye. No invertebrate eyes have an arrangement of this kind (Salvini-Plawen & Mayr 1977).

As far as we can tell, no structure of the eye has been omitted whose presence or development would in any way impede the evolutionary process. Further, we can be sure that real selection would outperform our model sequence in finding the modifications that give the best improvement of function for the least morphological change.

Can we be sure that our calculations do not underestimate the number of generations required for the optical structures to evolve? Throughout the calculations we have used pessimistic assumptions and conservative estimates for the underlying parameters. Should one or perhaps even two of these assumptions or estimates in fact be optimistic, we can trust that the remaining ones will at least compensate for the errors made. It is more likely, though, that the complete

calculation substantially overestimates the number of generations required.

If we assume a generation time of one year, which is common for small and medium-sized aquatic animals, it would take less than 364000 years for a camera eye to evolve from a light-sensitive patch. The first fossil evidence of animals with eyes dates back to the early Cambrian, roughly 550 Ma ago (Salvini-Plawen & Mayr 1977; Land & Fernald 1992). The time passed since then is enough for eyes to evolve more than 1500 times!

If advanced lens eyes can evolve so fast, why are there still so many examples of intermediate designs among recent animals? The answer is clearly related to a fact that we have deliberately ignored, namely that an eye makes little sense on its own. Although reasonably well-developed lens eyes are found even in jellyfish (Piatigorsky *et al.* 1989), one would expect most lens eyes to be useless to their bearers without advanced neural processing. For a sluggish worm to take full advantage of a pair of fish eyes, it would need a brain with large optic lobes. But that would not be enough, because the information from the optic lobes would need to be integrated in associative centres, fed to motor centres, and then relayed to the muscles of an advanced locomotory system. In other words, the worm would need to become a fish. Additionally, the eyes and all other advanced features of an animal like a fish become useful only after the whole ecological environment has evolved to a level where fast visually guided locomotion is beneficial.

Because eyes cannot evolve on their own, our calculations do not say how long it actually took for eyes to evolve in the various animal groups. However, the estimate demonstrates that eye evolution would be extremely fast if selection for eye geometry and optical structures imposed the only limit. This implies that eyes can be expected to respond very rapidly to evolutionary changes in the lifestyle of a species. Such potentially rapid evolution suggests that the eye design of a species says little about its phylogenetic relationship, but much about its need for vision. It follows that the many primitive eye designs of recent animals may be perfectly adequate, and simply reflect the animal's present requirements. In this context it is obvious that the eye was never a real threat to Darwin's theory of evolution.

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