

In addition to the broad patterns of overall diversity and group replacement, we observe patterns of change in rates of evolution both between and within major groups. Among each successive major group shown in Fig. 1, there is a general trend for an increase in the mean rate of appearance of new species and a decrease in the mean species duration (see Fig. 2). The slowest rates of species origination and longest durations are seen in groups *a* and *b*, while the highest rates and short durations are seen in the angiosperms. Even if the short species durations calculated for the flowering plants falsely result from their relatively recent appearance, their high species origination rates are not influenced by the same bias, and are an order of magnitude above those of the lowest valued group. The rates of species origination and the lengths of species duration also change in a consistent manner within each of the four major groups.

The overall pattern of increasing rates of species origination and decreasing species durations between the major groups are statistically significant. A linear regression of the average species origination rate and the mean species duration for each of the 19 suprageneric groups of Fig. 2 that go to make up the four major groups of Fig. 1 gives $r = 0.47$; elimination of the high values of the angiosperms yields $r = 0.49$ ($n = 17$). Both r -values fall between the 95–99% confidence interval, indicating a high degree of correlation between species origination rates and species durations. Studies indicate that differences in apparent speciation rates have a high correlation with plant breeding strategies and karyotypic variation⁶. Possible plant breeding strategies favouring high speciation rates involve small effective population sizes and specialized mechanisms of pollen and/or propagule dispersal, features commonly found in the most rapidly speciating angiosperm families. By contrast, large effective population size and generalist pollen and propagule dispersal features (commonly observed in gymnosperms) may favour slower speciation rates⁸.

Clearly, the many factors that have influenced the diversification of tracheophytes on the one hand, and marine invertebrates on the other, were both quantitatively and qualitatively different. Similarly, the extent of environmental stability and heterogeneity experienced in the marine and terrestrial habitats are quite distinct. Yet the patterns of diversity observed for these two groups are similar. Both indicate that there have been relatively few changes through time in the structure of the Earth's biota, and that such changes that have occurred have accompanied the radiations of major taxa and have frequently resulted in significant increases in total diversity. Further, following a period of rapid diversification, each evolutionary fauna and flora has tended to approach a levelling-off in the increase in the number of species and ultimately a decline in number as a new group radiates. However, throughout this history, the overall trend has been for a continued increase in total diversity. This suggests that similar types of interactions between developmental potential and ecological constraints may have controlled the evolution of diversity on land and in shallow marine environments.

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1. Sepkoski, J. J. Jr., Bambach, R. K., Kaup, D. M. & Valentine, J. W. *Nature* **293**, 435–437 (1981).
2. Sepkoski, J. J. Jr., Bambach, R. K., Kaup, D. M. & Valentine, J. W. *Paleobiology* **7**, 36 (1981).
3. Gøthan, W. & Weyland, H. *Lehrbuch der Paleobotanik* (Akademic, Berlin, 1954).
4. Knoll, A. H., Niklas, K. J. & Tiffney, B. H. *Science* **206**, 1400–1402 (1979).
5. Niklas, K. J., Tiffney, B. H. & Knoll, A. H. in *Evolutionary Biology* Vol. 12 (eds Hecht, M. K., Steere, W. C. & Wallace, B.) 1–89 (Plenum, New York, 1980).
6. Tiffney, B. H. in *Paleobotany, Paleocology and Evolution* Vol. 2 (ed. Niklas, K. J.) 193–230 (Praeger, New York, 1981).
7. Whittaker, R. H. in *Evolutionary Biology* Vol. 10 (eds Hecht, M. K., Steere, W. C. & Wallace, B.) 1–68 (Plenum, New York, 1977).
8. Levin, D. A. & Wilson, A. C. *Proc. natn. Acad. Sci. U.S.A.* **73**, 2086–2090 (1976).
9. Klován, J. E. & Imbrie, J. *Math. Geol.* **3**, 61–77 (1971).
10. Flessa, K. & Levinton, J. S. *J. Geol.* **83**, 239–248 (1975).
11. Joreskog, K. G., Klován, J. E. & Regment, R. A. *Geological Factor Analysis* (Elsevier, Amsterdam, 1976).
12. Smith, C. A. F. III *Paleobiology* **3**, 41–48 (1977).

Colour-generating interactions across the corpus callosum

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Human vision has the remarkable property that, over a wide range, changes in the wavelength composition of the source light illuminating a scene result in very little change in the colour of any of the objects¹. This colour constancy can be explained by the retinex theory, which predicts the colour of a point on any object from a computed relationship between the radiation from that point and the radiation from all the other points in the field of view (Fig. 1). Thus the computations for colour perception occur across large distances in the visual field. It has not been clear, however, whether these long-range interactions take place in the retina or the cortex. Reports that long-range colour interactions can be reproduced binocularly when one band of wavelengths enters one eye and a different band enters the other² might seem to establish the cortex as the site of the computation. Many observers, however, see very unsatisfactory colour or no colour at all in this binocular situation, suggesting that the cortex may not be the only site at which the computation is carried out, or even the most important site. We have now tested the role of the cortex in a human subject in whom the nerve fibres connecting cortical areas subserving two separate parts of the visual field had been severed, and find that the cortex is necessary for long-range colour computations.

We obtained the subject (J.W.) with the help of Drs Norman Geschwind and Alexander Reeves, and as a preparatory step, we tested his colour vision, which proved to be normal. The subject was a 20-yr-old male who had had intractable epileptic seizures (complex limbic). In 1979 he underwent, in two stages, a complete resection of his corpus callosum, which markedly decreased the number and severity of his seizures. The subject had no obvious intellectual or physical impairment. He had been extensively tested in connection with the callosal cut. In this subject, if the site of the computation is indeed cortical, events in one visual half-field should have no influence on the appearance of objects in the other half-field. If an influence is found, the computation responsible for that influence must be retinal.

Our objective was to construct a visual scene in which there was one region, of constant luminous flux and wavelength composition, whose colour was to be reported on. This test region would span the midline of the visual field; a large second region whose illumination could be varied would be confined to one visual half-field or to the other.

We finally adopted the set-up shown in Fig. 2, where F, the point of fixation, lay within a test spot, T (Color-Aid paper RV Tint 1). A Mondrian³ of variously coloured Munsell papers lay to the left of the test spot and hence was entirely in the subject's left visual field (Fig. 2a). The parts of the field to the right of the borders of the Mondrian and test spot were black velvet. To keep the Mondrian in the subject's left visual field, we set the fixation point at 3.7° to the right of the right-hand border of the Mondrian. Beyond the experimental display, in the subject's extreme visual periphery all the surfaces in the room were low-reflection blacks.

Fig. 1 The present method of computation⁵ differs from those of previously published versions of the retinex theory⁶. To predict the perceived colour of an area in any visual scene, the computation shown here is performed. The visual field is broken into unit areas. The relative reflectance, R , of the target area, i , is computed with respect to some other area, j , along a path drawn between the two areas using the formula shown, where Λ designates the particular waveband (long, middle or short) and I is the intensity. The threshold operation on the ratios along the path is included in order to remove the effects of non-uniform illumination over the scene: variations gradual enough to be below threshold are dropped out. All others are considered significant and contribute to the computation. The average of many such computed relative reflectances is taken in order to determine the value we define as average relative reflectance at area i . Conceivably, this average of relative reflectances (not fluxes) could be taken over every area in the visual field, but as few as 100–200 is usually sufficiently accurate. The average is taken over areas from the entire visual field and not just those nearby; experiments indicate there may be nearly as much contribution from distant areas as nearby ones. As the above computation is carried out three times, once for each of the three wavebands, three numbers (designators) become associated with each unit area. These designate a point in a three-dimensional colour space, a point which proves to be invariant with large changes in quantity and composition of illumination of the field of view. Experimentally it is found that if two points in any visual scene are the same colour (even when, because of non-uniform illumination, the wavelength composition reflected from them may be very different), they will be represented at the same point or closely adjacent points in this colour space.

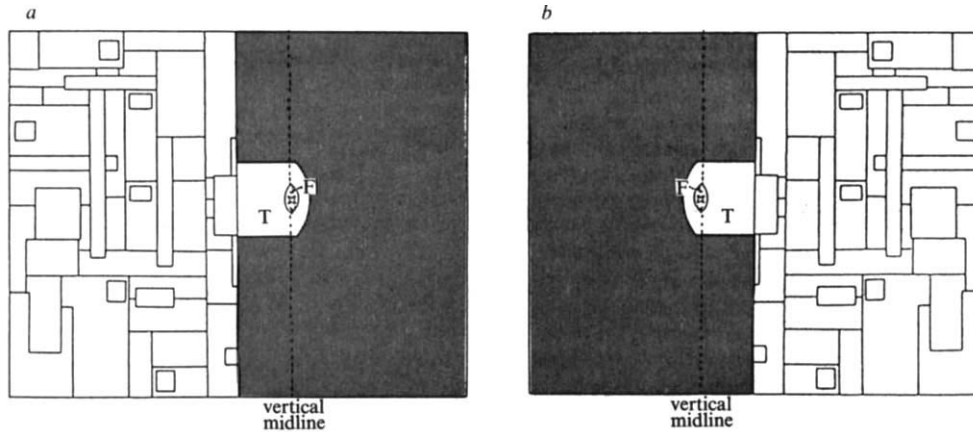
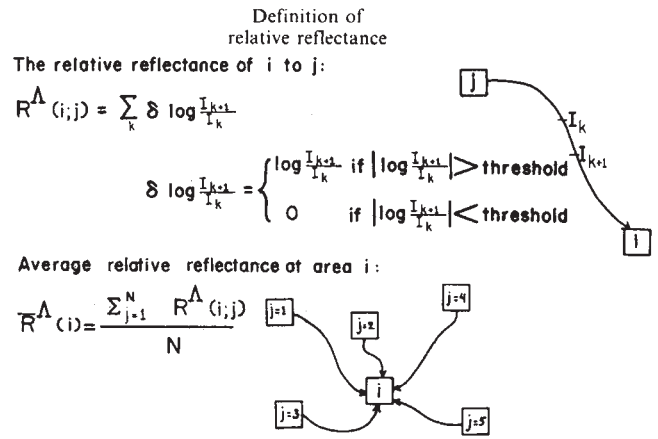


Fig. 2 A Mondrian collage of variously sized coloured matte papers, with a test spot, T, which is bordered on three sides by black velvet. A $0.75^\circ \times 1.7^\circ$ window in the test spot is at the fixation point, F. Viewed directly (a), the right-hand border of the Mondrian lies at 3.7° to the left of the vertical midline; viewed in a mirror (b), the Mondrian lies 3.7° to the right of the vertical midline. Behind the window at fixation point, F, lies a rotating disk which introduces bilaterally symmetrical letters into the window at the rate of 3.5 s^{-1} .

The fixation region was an aperture, $0.75^\circ \times 1.7^\circ$, behind which lay a rotating black disk from which a ring of bilaterally symmetrical letters (such as A, O, M, H) had been cut out. The background for the cut-out letters was a piece of paper identical to that used for the test spot. As the disk rotated, any given letter was replaced in the aperture by the one above it at the rate of 3.5 s^{-1} . We used a Mondrian instead of a uniform field, and a moving fixation target instead of a fixation point, in order to reduce the risk of after-images⁴. Another reason for using the Mondrian is that in different lighting conditions the colours (but not the brightnesses) remain virtually unchanged compared with the violent changes in colour that a uniform field would exhibit. The subject was asked to read each of the letters aloud as it appeared, and on hearing the word “colour” barked at him by the experimenter (E.H.L.), to report the colour in the test region.

The whole display (test spot, Mondrian, velvet) was illuminated by three tungsten slide projectors each containing a colour filter, the curves of which are shown in Fig. 3, and a choice of neutral density filters in which holes had been cut; these holes, when projected in focus from the slide position, matched exactly the shape and size of the test spot. Thus when the neutral filters were changed, the illumination of the Mondrian changed, but the illumination of the test spot remained constant. Projector intensities and neutral filters were so chosen by the

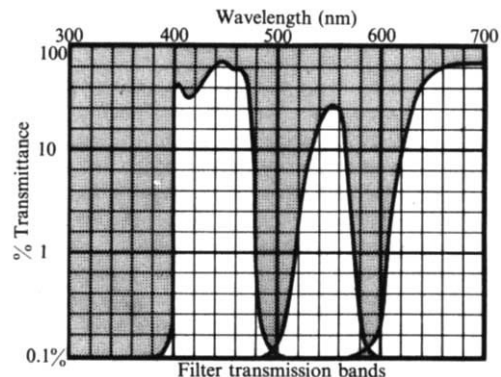


Fig. 3 The transmission bands of filters used to illuminate the display in Fig. 2. The measured test spot radiance, both when it was white and when it was purple, was $0.21 \text{ W sr}^{-1} \text{ m}^{-2}$ in the long waveband, $0.19 \text{ W sr}^{-1} \text{ m}^{-2}$ in the middle waveband and $0.073 \text{ W sr}^{-1} \text{ m}^{-2}$ in the short waveband. A piece of white paper (Color-Aid 91% reflectance) in the Mondrian in the condition in which the test spot was purple measured 0.30, 0.83 and $0.21 \text{ W sr}^{-1} \text{ m}^{-2}$ in the long, middle and short wavebands. In the situation in which the test spot was white, neutral density filters of 1.0, 1.7 and 1.2 were inserted in the respective waveband illuminators for the Mondrian only. (The test spot illumination remained constant throughout.)

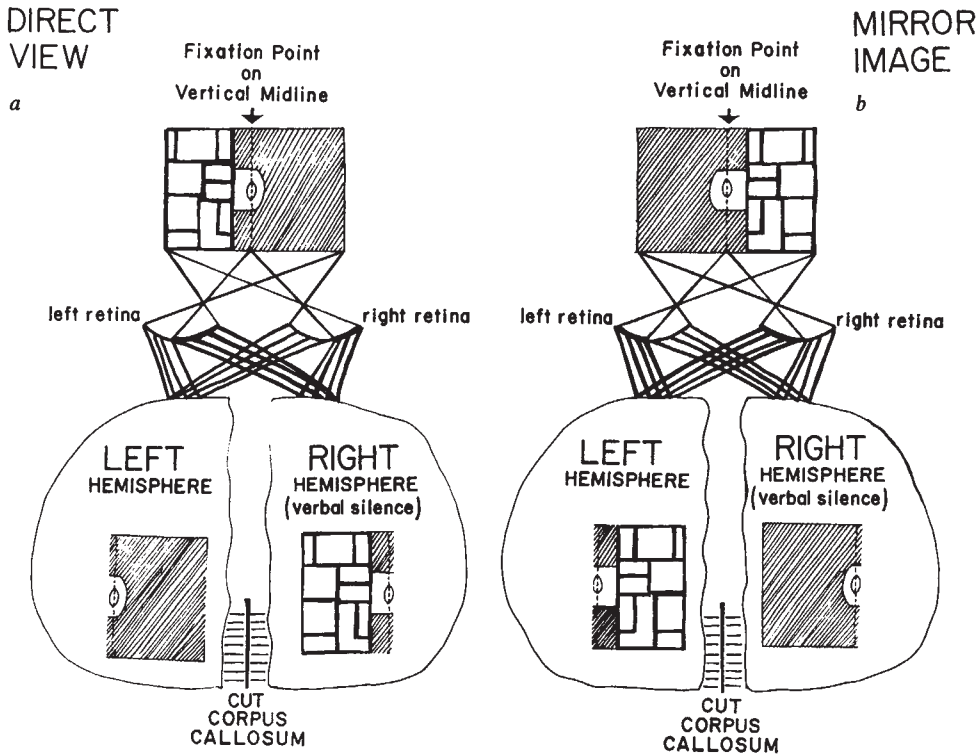


Fig. 4 A schematic representation of the information reaching the left and right hemispheres of the subject with the cut corpus callosum when he views the display depicted in Fig. 2.

computations of retinex theory (Fig. 1) that with neutral filters in place the test spot was a uniform chalky white, whereas with no neutral filters it was a uniform deep purple—although the flux from the test spot had in fact not changed at all. Most naive subjects consistently reported the test spot to be white in the first situation and purple in the second situation. A few called one “light purple” and the other “dark purple”, but any one subject’s reports were consistent.

The subject is right-handed and it had been previously determined that his speech centre was in his left hemisphere (A. Reeves, personal communication). He could therefore verbally describe things seen in his right visual field, but not things seen in his left visual field.

When the test apparatus was arranged so that the Mondrian was entirely in the left visual field with the test spot spanning the vertical midline (Fig. 4a), the split-brain subject consistently reported that the test spot was “white” regardless of the illumination of the Mondrian, even though to a normal observer it appeared purple when the Mondrian was fully lit and white when the lighting of the Mondrian was appropriately attenuated by the set of neutral filters. When he viewed the set-up in a mirror (Fig. 4b), the Mondrian was in his right visual field and the test spot again spanned the vertical midline. Now, with the Mondrian lit, he first stated that he saw “all colours, green and brown”, but on questioning it turned out that he was describing the entire Mondrian, something he had apparently not been able to do when it was presented to his nonverbal hemisphere. Thereafter, having been instructed to describe only the test spot, he reported it as “purple” when the Mondrian was lit without attenuators and “white” when the lighting of the Mondrian was attenuated by neutral filters, in complete agreement with the appearances to a normal observer.

We alternated viewing sessions so that the Mondrian was entirely in the right visual field (Fig. 4b) or entirely in the left visual field (Fig. 4a). When the Mondrian was in his left visual field, the subject almost always called the test spot “white”, occasionally “purple”, but not correlated at all with the appearance to a normal observer. When he viewed the set-up in a mirror, thus transposing the Mondrian to the right visual field,

his responses were always in accord with the appearance to a normal observer.

It could be objected that the part of the test spot reported on by the subject in the first (mirrorless) situation was farther from the Mondrian, by about 4° , than in the control situation, in which the two abutted each other; and that as a consequence the influence of Mondrian on test object might have fallen to insignificance in that 4° distance. For two reasons we are convinced that this was not so. First, when the Mondrian was confined to the left visual field, and then a 3° circular test spot, entirely surrounded by black velvet, was placed at varying distances along the horizon in the right visual field, normal observers continued to see a clear alternation from white to purple in the two lighting situations, even when the separation was extended to 30° or when, in simulation of what the subject presumably saw in configuration a of Fig. 4, the test spot was a $1^\circ \times 3^\circ$ crescent 4° from the right-hand border of the Mondrian. Second, to a normal observer the test spot, in either of the mirror symmetry situations, appeared absolutely uniformly purple or white (as predicted by retinex theory).

Since J.W. gave normal responses when the Mondrian was in his right visual field, his visual system is clearly capable of generating the long-range interactions that occur in a normal observer. What he failed to do was to transfer the information which would enable him to make a computation based on the whole field of view across the vertical midline. Therefore the calculation could not have occurred solely or largely in the retina and must have occurred in the cortex, where regions representing the two halves of the visual field are joined by the corpus callosum.

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1. Land, E. H. *Proc. natn. Acad. Sci. U.S.A.* **45**, 115–129, 636–644 (1959); *Am. Scient.* **52**, 247–264 (1964).
2. Geschwind, N. & Segal, J. R. *Science* **131**, 608 (1960).
3. Land, E. H. *Proc. R. Instn Gt Br.* **47**, 23–58 (1974).
4. Daw, N. W. *Nature* **196**, 1145 (1962).
5. Land, E. H. *Proc. natn. Acad. Sci.* (in the press).
6. Land, E. H. & McCann, J. **61**, *J. opt. Soc. Am.* **61**, 1–11 (1971).