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STRUCTURE OF MYOGLOBIN

A THREE-DIMENSIONAL FOURIER SYNTHESIS AT 2 Å. RESOLUTION

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MYOGLOBIN is a conjugated protein consisting of a single polypeptide chain of about 153 amino-acid residues associated with an iron–porphyrin complex, the hæm group; its molecular weight is about 18,000, and the molecule contains some 1,200 atoms (excluding hydrogen). Two years ago a preliminary report of the first stage of an investigation of the three-dimensional structure of sperm-whale myoglobin was published in *Nature*[1] (a detailed account of this work has appeared recently[2]). Several isomorphous crystalline derivatives of myoglobin containing heavy atoms (mercury or gold) at single sites on the molecule were prepared, and by comparing the X-ray diffraction patterns of these crystals with those of the unsubstituted protein, it was possible to deduce the phases of all the reflexions in the X-ray pattern having spacings greater than 6 Å. These phases, together with the observed amplitudes, were used to compute a three-dimensional Fourier synthesis of the electron density in the unit cell (which contains two molecules) at a resolution of 6 Å. In this synthesis the polypeptide chain was visible as a rod of high electron density, folded in a complex pattern (Fig. 5*a*); in addition, the single hæm group with its iron atom, which is much more dense than any other atom in the molecule, could be identified as a disk of high electron density. The shape of the molecule could be determined with some confidence, as could most of the course of the single polypeptide chain, though there were several ambiguities where it turned through a large angle, so that the ends of the chain could not be located with certainty. Thus, the general nature of the tertiary structure of the molecule was revealed, but not the secondary structure of the polypeptide chain, though the results were consistent with a helical configuration.

More recently, Scouloudi[3] used similar methods to obtain a two-dimensional Fourier projection of the unit cell of seal myoglobin, in which the molecular arrangement is entirely different from that in sperm-whale crystals; she was able to show that the myoglobins of these two species have essentially the same tertiary structure in spite of their different amino-acid compositions. Her work, by implication, confirmed the correctness of both analyses, as well as the deductions made about the shape of the molecule. In the accompanying article[4] Perutz *et al.* now describe a three-dimensional analysis of the related protein hæmoglobin, at a slightly greater resolution, and show that each of the four sub-units of which this molecule is composed bears a close structural resemblance to myoglobin. It is apparent, therefore, that sperm-whale myoglobin possesses a structure the significance of which extends beyond a particular species and even beyond a particular protein.

We now present the results of a second stage in the analysis of sperm-whale myoglobin; in this the resolution has been increased to 2 Å., that is to say, not far short of atomic resolution. The resulting Fourier synthesis is very complicated, and a detailed study of it will take many months; in the meantime, our preliminary findings may be of interest.

Methods of X-ray Analysis

In this stage we have simply extended the methods which proved successful in the first stage of the analysis, comparing the diffraction pattern of unsub-

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stituted myoglobin crystals with those of the *p*-chloromercuribenzene sulphonate, mercury diammine and aurichloride derivatives, together with a double derivative containing the first two substituents simultaneously. Whereas myoglobin crystals give 400 reflexions having spacings greater than 6 Å., the number of reflexions with spacings greater than 2 Å. is 9,600, each of which has to be measured not only for the unsubstituted protein but also for each of the derivatives. The very much greater number of data posed many problems, both in recording intensities and in computation, and in this stage we relied much more heavily than before on the use of a high-speed computer; it was fortunate that about the time the work began the *Edsac* Mark I computer used previously was superseded by the very much faster and more powerful Mark II.

The data for each derivative were recorded on twenty-two precession photographs; a separate crystal had to be used for each photograph to keep radiation damage within acceptable limits. The results from the different photographs were scaled together on the computer, the best set of scaling factors being determined by solving an appropriate 22×22 matrix[5]. The degree of isomorphism of each derivative was tested, and found adequate, by means of a computer programme which used the $h0l$ reflexions to refine the preliminary values of the heavy-atom parameters, temperature factor, etc., and then compared the values of $\delta F_{obs.}$ and $\delta F_{calc.}$ as a function of $\sin\theta$. The co-ordinates of the heavy atoms were further refined using correlation functions[6] computed by means of programmes devised by Dr. M. G. Rossmann, and finally refined again during the process of phase determination itself. The phases were determined by essentially the same method as before, but owing to the very large number of reflexions the determination was carried out on the computer rather than graphically. The 'best' phases and amplitudes[7] were computed and used in the final Fourier synthesis, to which a moderate degree of sharpening was applied. In all, some hundreds of hours of computer time were required, and the Fourier synthesis itself, which was calculated at intervals of about 2/3 Å., took about 12 hr.

The Fourier Synthesis

The electron density distribution was plotted in the form of 96 sections perpendicular to x* and spaced 2/3 Å. apart, the density in each section being represented by a series of contours. For some purposes this method of representation is unsatisfactory, and we have also constructed models of parts of the structure on a scale of 5 cm. = 1 Å., by erecting vertical steel rods parallel to y in an array corresponding to the grid of points in the xz-plane at which densities were calculated, the value of the electron density at points along the rods being indicated by coloured clips. On this scale the whole molecule is about 6 ft. cube, and about 2,500 rods each 6 ft. high are required (see Fig. 4).

The distance between singly bonded carbon atoms is 1·54 Å.; many of the common types of covalent bond present in protein molecules are shorter than this. We could not expect, therefore, that neighbouring covalently bonded atoms would be resolved in the present Fourier synthesis, and in fact such resolution was not achieved; on the other hand, the degree of resolution actually obtained is very nearly as great as theory would indicate, showing that the errors in the synthesis cannot be very large (see Fig. 2). The distances between neighbouring groups in Van der Waals contact is of the order of 3 Å., however, and as would be anticipated, we find that such groups appear as discrete regions of high density. One factor which complicates the interpretation is that similar groups (for example, peptide bonds) in different parts of the structure have substantially different densities. We attribute these differences to variation in the amplitude of thermal vibration in different parts of the molecule. Thus the terminal amino-end of the chain, which is on the outside of the molecule, has low density and is presumably relatively flexible; on the other hand, structures near the hæm group, which is surrounded by several segments of polypeptide chain running in different directions, possess high density, presumably because this part of the molecule is stabilized by many inter-chain bonds.

Fig. 1. (*a*) Cylindrical projection of a helical segment of polypeptide chain, with the α-helix structure superposed: for explanation see text. (*b*) Key to the atomic arrangement in the α-helix. The points marked β and β' are the two alternative projected positions of C_β; β is the position in a right-handed and β' that in a left-handed helix of L-amino-acids

Configuration of the Polypeptide Chain

In the 6-Å. Fourier synthesis the polypeptide chain appeared as a solid rod of high density with approximately circular cross-section; segments of the chain were more or less straight, and these were joined by dense regions where the chain turned corners. In the 2-Å. synthesis all the straight segments of chain were found to be hollow cylindrical tubes of high density; projecting at intervals from the cylindrical core are dense regions of various shapes and sizes, which are clearly the amino-acid side-chains. More detailed

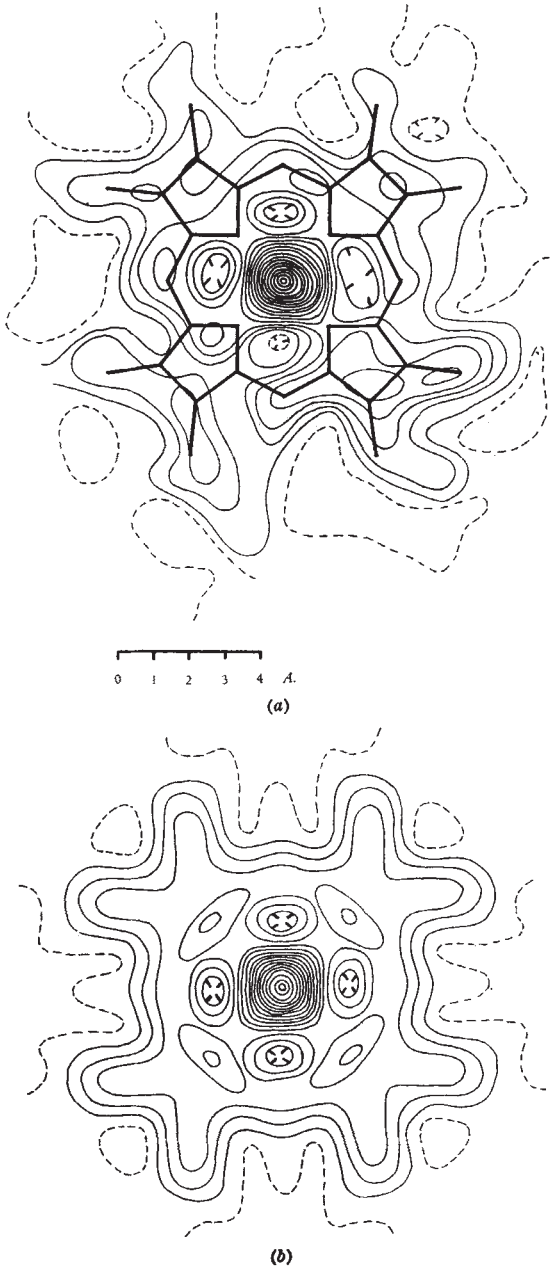
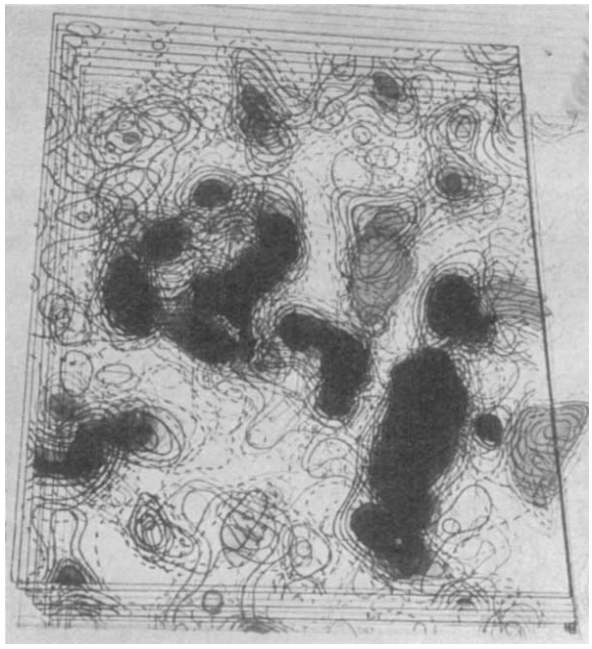


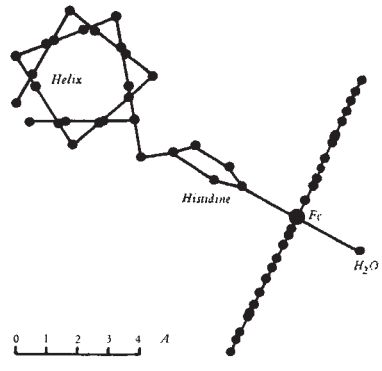
Fig. 2. (*a*) Observed electron density distribution in the plane of the hæm group, with the atomic arrangement in the group superposed. One contour interval = 0·5 electron/Å.^{3}. (*b*) Calculated electron density distribution, computed from the known atomic arrangement as described in the text. One contour interval = 0·5 electron/Å.^{3}

examination shows that, in fact, the cylindrical tubes are helices, consisting of a single strand of high density with axial repeat about 5·4 Å. The density in one such helix is shown in Fig. 1*a*. This was obtained by projecting all the density lying within a cylindrical shell of radii 1·6 and 2·3 Å. on to the surface of a cylinder of radius 1·95 Å. and co-axial with the helix; the cylinder was then cut along a line parallel to its axis and unrolled. Superposed on the contours of electron density is the cylindrical projection of an α-helix, with the dimensions given by Pauling and Corey[8]. It will be seen that the observed density follows the configuration of the α-helix with remarkable precision; and it may confidently be asserted that not only this, but also several other lengths of polypeptide chain which have been analysed in the same way, possess the α-helical configuration. It is also found that the side-chains emerge at intervals of 100° around the periphery of the helix, and at axial intervals of 1·5 Å., in conformity with the parameters of the α-helix. Several indirect lines of evidence had led to the conclusion that parts of the polypeptide chain in globular proteins are in the form of α-helixes, and in hæmoglobin Perutz[9] had found traces of an X-ray reflexion characteristic of this configuration; but these results are the first direct proof that α-helices are present and, indeed, enable them to be seen directly for the first time.

The next question is whether the α-helices are left-handed or right-handed; helices of either hand



(*a*)



(*b*)

Fig. 3. (*a*) Photograph of a set of sections normal to the plane of the hæm groups showing, from left to right, a helix in cross-section, the histidine residue nearly edge-on, the hæm group edge-on, and a presumed water molecule. (*b*) Sketch showing the atomic arrangement in Fig. 3*a*

can be built, and although the right-handed form appears to be marginally the more stable, the difference is not so great as to make it certain that left-handed helices cannot exist. To decide this question, it is necessary to determine the absolute configuration of the Fourier synthesis; this function has no centre or plane of symmetry and might be plotted in two ways, each of which would be the mirror image of the other. The absolute configuration could be settled by making use of the anomalous dispersion of X-rays from the iron atoms or the introduced heavy atoms; we have not in fact made use of this effect, but instead have proceeded in the following way. In a right-handed α-helix composed of L-amino-acids, the first atom of the side-chain (C_β) projects from the main chain in a direction *opposite* to the C—O bonds of the carbonyl groups; in a left-handed helix of L-amino-acids C_β projects in the *same* direction as the carbonyl groups (see Fig. 1*b*). By constructing a second cylindrical projection (not illustrated) of the density near a radius of 3·34 Å., corresponding approximately to the radius at which C_β is found in either case, we found that C_β was systematically on the side of the main chain opposite the oxygen atoms of the carbonyl groups. This shows that the helix must be right-handed, and we were able to plot the Fourier synthesis with the correct absolute configuration by taking account of the known absolute configuration of a L-amino-acid[10]. The molecule was then found to be of the same hand as all the closely similar sub-units in hæmoglobin, the absolute configuration of which was determined by measurements of anomalous dispersion[4]. All the lengths of α-helix in the myoglobin molecule turn out to be right-handed. Finally, it will be clear from Fig. 1 that it is possible to determine by inspection the direction in which the C—O group points, and hence to see which is the terminal carboxyl end of each segment.

The α-helices can also be located by building atomic models into the model of the unit cell made with steel rods; this has been done for all the segments of helix in the molecule, and it is found that the total number of amino-acid residues contained in these segments is 100–110, whereas the number of residues contained in the whole molecule is believed to be 153 (Edmundson, A., unpublished results). Thus, 65–72 per cent of the molecule consists of regular right-handed α-helix, made up of about eight segments, each containing between seven and about twenty residues.

When the chain turns a corner, its regular helical configuration is necessarily disrupted. At the present resolution the precise arrangement of the residues at corners is difficult to determine; we have, nevertheless, built plausible models of several corners, though we do not yet claim to have established their configurations with certainty. Most of the corners take up two or three residues, and in addition there is one region (on the extreme right of Fig. 5*a*), consisting of about 13–18 residues, in which the arrangement is irregular (part of it is helical, but probably not α-helical). Further studies will be devoted to elucidating these problems.

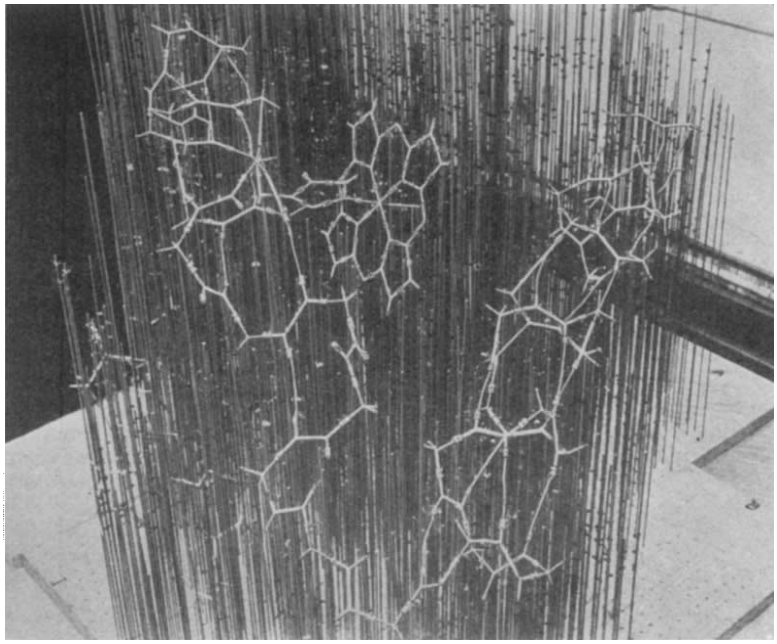


Fig. 4. Photograph of a model of part of the molecule near the hæm group, showing the vertical rods and coloured clips which indicate the electron density at each point of the grid, and atomic models of the hæm group and neighbouring helices. The terminal carboxyl end of the chain is on the extreme left

No serious attempt has yet been made to identify the side-chains, and indeed it is doubtful whether this can be done systematically at the present resolution, partly because many of them appear to be subject to considerable thermal vibration, partly because there are often interactions between two side-chains on adjacent turns of the same helix or on adjacent helices, and it is difficult to tell where one ends and the other begins. In special cases, however, identification is easy; thus, in several places two helices approach one another closely, and one or more side-chains must for steric reasons be glycine. On the other hand, some side-chains are so long that they can only be arginine or lysine. It remains to be seen how many positive identifications can be made; but it is clear that if the whole amino-acid sequence of the protein were known, it would be possible at this stage to construct a model of the complete structure with fair precision. Unfortunately, this information is not yet available; but in the meantime it may be possible to correlate and check our findings with the partial results of the sequence determination now being undertaken by Mr. A. Edmundson, of the Rockefeller Institute.

The Hæm Group

The identification of a disk of high electron density in the 6-Å. synthesis as the hæm group is confirmed by the 2-Å. synthesis; but the iron atom is now just resolved from the nitrogens of the porphyrin ring (the iron–nitrogen distance is about 1·9 Å.) and the structure of the group as a whole corresponds closely with theoretical expectation. Fig. 2*a* shows a section through the density distribution, cut in the plane of the hæm group; superposed on the section is a model of the hæm group with the dimensions

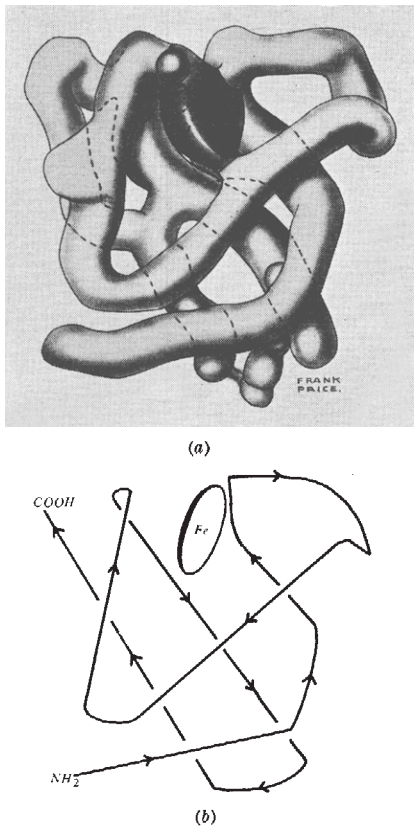


Fig. 5. (*a*) Drawing of the tertiary structure of myoglobin as deduced from the 6-Å. Fourier synthesis. (Note: the plane of the hæm group is indicated incorrectly in this drawing—see text). (*b*) The course of the polypeptide chain, deduced from the 2-Å. Fourier synthesis

found by Crute in his recent structure analysis of nickel etioporphyrin[11]. In the model, only the carbon atoms of the methyl groups and the first carbon atoms of the vinyl and propionic acid groups have been indicated; our analysis has not yet proceeded far enough to identify the latter groups. Fig. 2*b* is a Fourier synthesis made by calculating structure factors for the model structure in a convenient unit cell, applying to these the same temperature factor as that observed in myoglobin, and using them as terms of a Fourier synthesis cut off at 2-Å. spacings. It will be seen that the calculated and observed density distributions agree very closely; furthermore, the observed peak density (8·8 electrons/Å.^{3}) and half-width (1·8 Å.) of the iron atom agree well with the predicted values (8·2 electrons/Å.^{3} peak density, 1·8 Å. half-width). Errors are, of course, inherent in a Fourier synthesis produced from experimental results; the good agreement between the observed and calculated versions of the hæm group, and between the helical polypeptide chain and the α-helix (Fig. 1), indicate that in the present case these errors are fairly small, certainly less than we had anticipated.

In one respect the 6-Å. model now requires correction. Measurements of electron spin resonance[12] had shown that the two hæm groups in the unit cell were tilted out of the *bc* plane through 21° about an axis parallel to *c*, one in one direction and one in the other, but from these measurements one could not decide which direction of tilt was associated with the hæm group of which molecule. In the 6-Å. analysis the wrong choice was made; the new results show that the angle of tilt is indeed very close to 21°, but that it should be in the direction opposite to that shown in earlier models (including Fig. 5*a*).

Chemical studies of hæmoglobin and myoglobin have suggested that the hæm group is attached to the protein by a bond from the iron atom to a nitrogen atom of a histidine residue, and that the sixth co-ordination position of the iron atom is occupied in met-myoglobin (at *p*H's below 7) by a water molecule. Our results are in conformity with these suggestions. Fig. 3*a* is a photograph of a series of sections cut through the hæm group normal to its plane. The hæm group is seen edge-on; to its left is the histidine residue, also nearly edge-on, and to the left of that is the helix to which the histidine is attached, seen in cross-section. To the right of the hæm group is a small isolated peak which we take to be the oxygen atom of the water molecule (see Fig. 3*b*). When this structure is built with atomic models (see Fig. 4), it is found to satisfy all known requirements as to bond-lengths, angles, etc. Thus the iron–oxygen distance is close to 2·1 Å.; that between the iron and one of the histidine nitrogen atoms is 1·9 Å., while the second histidine nitrogen points with its hydrogen directly at a carbonyl group on the helix, presumably forming a hydrogen bond (forked at the carbonyl end); and finally the bonds about the C_α—C_β bond of histidine are almost exactly in the staggered configuration.

General Configuration of the Molecule

In the 2-Å. synthesis the continuity of the polypeptide chain can be followed throughout the molecule; in addition, its direction can be ascertained in each straight segment by examining the direction of the carbonyl groups in the cylindrical projections or by direct model-building. The 'run' of the chain so deduced everywhere agrees with that derived from the 6-Å. synthesis, as well as resolving several ambiguities in that model, and the terminal amino- and carboxyl-ends of the chain can now be identified. The arrangement is shown in Fig. 5 (see also Fig. 5 in the accompanying article by Perutz *et al.*). The overall shape of the molecule is as previously deduced.

Conservative estimates suggest that it may now be possible to locate with some precision at least 43 per cent of all the atoms (excluding hydrogens) in the molecule—namely, those making up the hæm group and the backbone of the regular segments of helix, together with the associated C_β's. We believe that it may be possible, either by straightforward refinement procedures or by heavy-atom methods, to extend the resolution of the synthesis to a point near the limit of the diffraction pattern of sperm-whale myoglobin crystals (about 1·5 Å.), and thus to reveal in any event most of the details of the atomic arrangement of the molecule. Further work is in hand with this end in view.

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DEVELOPMENTS IN GAMMA-RAY OPTICS

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DURING the past decade, several phenomena that had previously been observed with light or with X-rays have been studied with nuclear γ-rays, where the quantum energy is typically 100 keV.–10 MeV. and the wave-length correspondingly short, 10^{-9} to 10^{-11} cm. Some new phenomena, specifically nuclear or specifically high-energy, have been added: but most of the experiments, though often technically more difficult, are extensions of those familiar at lower energies.

An excellent example of such an extension is the curved-crystal γ-ray spectroscopy of γ-rays, achieved with great elegance and precision by DuMond[1] and his collaborators. It will suffice to quote their value for the wave-length of electron–positron annihilation radiation, namely, $24{\cdot}262 \pm 0{\cdot}0033$ mÅ., and to mention that this radiation, when generated within a metal, has been observed to possess a spectral width which reflects the spread of energy of the conduction electrons.

A second example is the observation in the γ-ray region of Rayleigh scattering, a name taken over from visual optics to describe scattering of photons by the electronic structure of an atom without change of the atom's quantum state and therefore without any change of the photon's energy, except the small fraction taken by the recoil of the atom necessary to conserve momentum. This is the 'unmodified line' of X-ray scattering terminology, as opposed to the 'modified line' that arises from Compton scattering. The existence and (if it existed) the origin of elastic scattering at higher energies was a matter of controversy in 1930–33, but it is now clear that Meitner and Kösters observed it[2] and that its origin was electronic, not nuclear. In taking up the study of this scattering process with the wider range of monoenergetic lines provided by artificial radionuclides, Moon[3], Storruste[4] and Wilson[5] were able to verify semi-quantitatively the calculations of Franz[6] regarding its intensity and angular distribution, and many other workers have since made accurate experiments at energies above 1 MeV. where Franz's theory (which is essentially a Debye form factor) must be replaced by the more accurate relativistic treatment of Brown, Peierls and Woodward[7].

Two phenomena not observable in the X-ray region were predicted to be interwoven with the Rayleigh scattering; first, the classically calculable 'Thomson' scattering of photons by the nucleus, which oscillates in the electric field of the incident wave and radiates at the same frequency; secondly, scattering by virtual pair production in the field of the nucleus, which is a specifically quantum phenomenon.

The interest in the nuclear Thomson scattering seems to date from 1950, when it was remarked[3] that it should be coherent with Rayleigh scattering, but the process must surely have been considered long before then; the virtual pair production process was suggested as long ago as 1933 by Delbrück in a note to the paper of Meitner and Kösters[2].

Both processes were difficult to identify because the scattering radiation is of exactly the same frequency as the Rayleigh scattering but, at ordinary γ-ray energies, of much smaller intensity. The Thomson scattering was plausibly identified by the fact that the observed angular distribution of the total elastic scattering agreed much better with theory when this component was added into the calculation; its existence and its interference with the Rayleigh component were positively established by Sood's[8] measurements of the polarization of the elastic scattering at about 1 MeV., at which energy the Rayleigh and nuclear Thomson components have substantially different polarizations. The use of polarization for examining elastic scattering of γ-rays is pleasingly reminiscent of Lord Rayleigh and the blue of the sky.

The characteristic features of the Delbrück process are that its magnitude increases as a high power of the quantum energy and its angular distribution is strongly peaked around 0°. It has at last been unquestionably observed by Moffatt and Stringfellow[9] in Oxford, using 90-MeV. radiation from an electron synchrotron and working at angles of about 0·1°.

Another process of elastic scattering of γ-rays is that associated with the excitation of a nucleus from its ground-state to an excited state followed by the re-emission of a photon. This is the nuclear analogue of the optical resonance radiation so beautifully demonstrated by R. W. Wood in the early years of this century. It was sought experimentally at intervals over twenty years, the difficulty being not that the process is intrinsically weak (its cross-section, like that of any comparable resonant process, can be of the order of $\lambda^2/4\pi$) but that γ-ray lines are so narrow that the loss of energy to nuclear recoil ($h^2\nu^2/2Mc^2$ on emission and equal amount on absorption) destroys the resonance[25].