Summary

In this article the several theories put forward to explain the biological mechanisms underlying the aging process are examined. The only ones which attack the problem from the point of view of basic biological mechanisms are the wear-and-tear theory and the somatic mutation theory. The finding that radiation accelerates the aging process is a potent tool for attacking the problem experimentally. Experiments with mice specifically designed to verify the wear-and-tear theory showed conclusively that stress per se does not contribute to aging, and no experimental evidence could be found to support the theory.

On the other hand, a great deal of evidence now available indicates that mutations in somatic cells play a dominant role in aging. It is further shown that the organs having cells which frequently undergo cell division take part in the aging process very little, if at all. Organs having cells which seldom, if ever, divide have no opportunity to throw off either spontaneous or induced mutations, and it is these organs which are responsible for the aging of the animal. Spontaneous mutations build up at a rapid rate in these organs. A cell may continue to function normally long after it has suffered a deleterious mutation, and this accounts for much of the delay in the expression of radiation damage. It is suggested that the mutation rates for somatic cells are very much higher than the rates for gametic cells, and that this circumstance insures the death of the individual and the survival of the species (*28*).

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CURRENT PROBLEMS IN RESEARCH

The Structure of RNA

Reovirus RNA and transfer RNA have similar three-dimensional structures, which differ from DNA.

Robert Langridge and Peter J. Gomatos

The structure of deoxyribonucleic acid (DNA) was fairly well established in 1953, based on x-ray diffraction patterns, chemical analysis, and molecular model building (*1*). The very high quality of the diffraction patterns obtainable from DNA has enabled the structure to be refined in considerable detail (*2*, *3*).

The structure of ribonucleic acid (RNA) has proved to be a much more intractable problem. An extensive x-ray diffraction study (see *4*) showed that the RNA from a variety of sources gave diffraction patterns which were effectively identical, but were poorly defined and diffuse. Analytical and various physicochemical data did not provide much assistance in molecular model building, and the diffraction patterns remained uninterpretable for several years.

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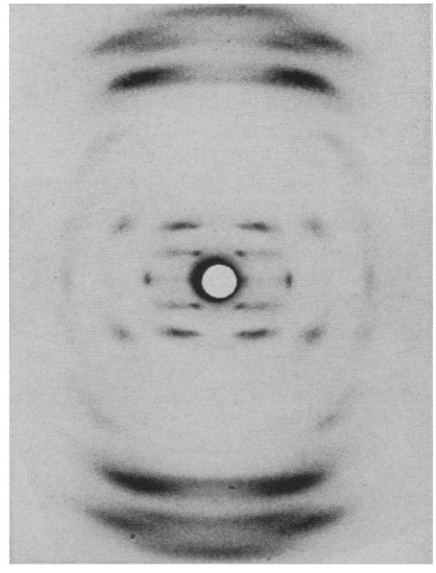
Transfer RNA

The work of Spencer *et al.* (*5*) on a preparation made from amino-acid transfer RNA extracted from yeast, finally showed that the sodium salt of this RNA has a structure which is somewhat similar to the *A* form of the sodium salt of DNA (*2*) and that the diffuse patterns given by other RNA preparations could be accounted for by a disordered form of the type of pattern obtained from transfer RNA.

There is some question about the relationship between the structure observed and the native, transfer RNA molecule, since it has recently been shown that the method of preparation yields fragments having a molecular weight of slightly less than half that of the native material (*6*). There is, however, no question that the structure observed is the structure of double-helical RNA, and the observations to be reported here show that a preparation of RNA of very high molecular weight from reovirus gives diffraction patterns which are very similar indeed to those obtained from double-helical

transfer RNA, but yield considerably better resolution on the higher layer lines, thus enabling the structure to be defined more precisely and promising a detailed determination of the three-dimensional structure of RNA.



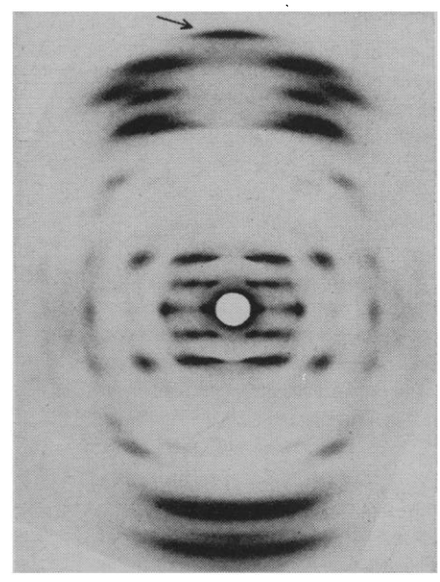


Fig. 1 (left). Reovirus RNA (sodium salt) at 75-percent relative humidity (fiber axis vertical). Fig. 2 (right). Reovirus RNA (sodium salt) at 92-percent relative humidity (fiber axis tilted 15° to the vertical). Arrow indicates tenth layer line.

Reovirus RNA

Reovirus particles are about 700 to 750 Å in diameter and contain protein and RNA. The virus shows a curious reproductive behavior by comparison with most other RNA viruses, and the particular observation that the inclusion body in reovirus-infected cells stains orthochromatically greenish-yellow with acridine orange, which is usually regarded as characteristic of DNA, led to the suggestion that reovirus RNA might be double-stranded (*7*). Further studies showed that the molar ratio of purines to pyrimidines is unity, the thermal denaturation transition is quite sharp (with a remarkably high T_m of 99°C), and that treatment with formaldehyde or pancreatic ribonuclease does not change the absorption spectrum appreciably (*8*). All these characteristics imply that the RNA is not in the single-stranded form and is most likely a double-stranded helix. For the x-ray diffraction studies to be described, the Dearing strain of reovirus 3 was cultured in mouse-fibroblast L cells, strain 929, and purified by ultrafiltration, ultracentrifugation, treatment with deoxyribonuclease, ribonuclease, and chymotrypsin, and finally by equilibrium density-gradient centrifugation in CsCl. The RNA was isolated from the virus particles with phenol at room temperature (*8*).

X-ray Diffraction Methods

The first x-ray diffraction pictures were obtained with fibers drawn from material that had been suspended in ammonium acetate buffer and lyophilized. These fibers gave pictures which, while somewhat crystalline, showed little orientation. The next preparation was made in the form of the sodium salt which was purified, precipitated with alcohol, and dried. The dried material was wetted with doubly distilled water and a fiber was pulled from the resultant gel. A fiber of approximately 0.05 mm diameter and about 3 mm long was obtained which showed good extinction between crossed polaroids. Owing to the granular appearance of the fiber it was very difficult to measure the birefringence. The fiber was mounted on a holder with a phosphor bronze leaf spring acting as a stretcher (*3*). The first few pictures showed good orientation, which was further improved when the fibers were subjected to gentle stretching. This was done by breathing on the fiber, causing it to buckle as a result of the water uptake (this seems to happen more readily with RNA than with DNA fibers); the fiber was then straightened by screwing out a stop on the phosphor bronze leaf spring. As the fiber then returned to its more normal water content it became quite tautly stretched. After several such manipulations the orientation was markedly improved.

In the cameras, the distance of specimen to film was 16 mm and 27 mm; the collimators were lead-glass capillaries, 0.06 mm inside diameter and 10 mm in length. Lead pinholes of about 0.5 mm were used on the front and rear of the collimators to shield out excess radiation, and a platinum electron-microscope aperture of 0.1-mm inside diameter was cemented to the lead exit pinhole to act as a guard. The x-ray generator was a Jarrell-Ash line-focus unit equipped with a copper target having a focal size of 0.1 by 1.4 mm; and operated at 33 kv and 5-ma beam current. Predominantly CuKα radiation of 1.54 Å wavelength was isolated with a 0.016-mm nickel filter. Ilford Industrial G film was used with exposure times of about 24 hours. To control the water content of the fibers the atmosphere in the cameras was kept at constant relative humidity by filling the camera with helium bubbled through appropriate, saturated salt solutions (*3*). A container of this saturated salt was also placed in the camera.

Reovirus RNA Diffraction Patterns

A diffraction pattern given by a fiber of reovirus RNA mounted perpendicularly to the x-ray beam at 75-percent relative humidity is shown in Fig. 1. At 92-percent relative humidity the pattern shown in Fig. 2 is observed (this fiber was tilted at 15° to the perpendicular).

The general distribution of intensity is quite characteristic of diffraction from a helical structure, is very similar to that given by transfer RNA, and has a number of features in common with the pattern given by the sodium salt of DNA (the DNA *A* form) at 75-percent relative humidity.

It is therefore clear that reovirus RNA is a double-stranded helix. The precise form of the helix must now be determined.

Unlike the sodium salt of DNA, which changes from the *A* form (in which the bases are tilted at about 70° to the helix axis) at 75-percent relative humidity, to the *B* form (in which the bases are perpendicular to the helix

axis) at 92-percent relative humidity, the sodium salt of reovirus RNA shows only minor changes in the diffraction pattern between 15-percent and 92-percent relative humidity; this suggests fairly trivial alterations of lattice spacing and possibly of structure, but nothing comparable to the dramatic changes observed in DNA. Likewise, transfer RNA shows no major hydration-dependent structural changes from 32- to 92-percent relative humidity (*5*). The layer-line spacing on the diffraction photographs from reovirus RNA at 75-percent relative humidity is 30.5 ± 0.5 Å, a value which agrees fairly well with the 29 Å for transfer RNA (*5*).

The most noticeable difference between the diffraction patterns of reovirus RNA and transfer RNA is the greatly improved resolution of the reovirus RNA on the layer lines above the second layer line. This can be understood quite easily as due to the rather short stretches of regular helix in transfer RNA. Even if there were some end-to-end aggregation, the frequency of these irregularities would cause a broadening of the layer lines no matter how good the side-to-side regularity of the molecules in the crystallites. Reovirus RNA, on the other hand, has a molecular weight of the order of 10 million; uniform and regular lengths of very many turns of the helix are possible, and the breadth of the layer lines is limited only by other factors such as the size and orientation of the crystallites within the fiber. The much higher resolution obtainable on the higher layer lines of the diffraction patterns of reovirus RNA makes it possible to derive the structural parameters directly.

Diffraction patterns from reovirus RNA at 92-percent relative humidity and from DNA (Salmon sperm DNA, Calbiochem A grade) in the *A* configuration at 75-percent relative humidity are compared in Fig. 3. These pictures were obtained consecutively in the same x-ray camera, with the same distance of specimen to film and the same exposure. It is immediately obvious that if we confine our attention to the lower layer lines of the two patterns, they are very similar; likewise, if we consider the outer layer lines in isolation, these distributions are also quite comparable. But these maxima occur at slightly higher angles in RNA than in DNA, and, upon indexing both patterns independently, it is clear that while the three strong near-meridional layer lines in DNA are the sixth, seventh, and eighth, those of RNA are the seventh, eighth, and ninth. The sixth layer line of RNA is very weak, and in DNA it is strong; the displacement of the three strong layer lines from the meridian is somewhat less in RNA than in DNA.

The Number of Nucleotide Pairs per Turn

Since RNA structure is different from DNA, we can no longer compare them directly, and the question now arises of how many nucleotide pairs make up one turn of the RNA helix. The diffraction pattern from an undistorted helix with n residues per turn will have reflections on the meridian only for those layer lines whose index is a multiple of n. The apparent ease of making this observation is nullified by the fact that fibers always have a certain amount of disorientation so that reflections which are merely close to the meridian are sometimes smudged together and appear meridional.

In the diffraction patterns so far obtained from untilted fibers of the sodium salt of reovirus RNA (Fig. 1) the ninth layer line appears to be meridional. However, diffraction photographs obtained with the fiber tilted about 15° from the perpendicular to the x-ray beam, show that this layer line is off meridional, and brings up another layer line which indexes as the tenth and which appears to have its maximum on the meridian (Fig. 2). We must caution, however, that the orientation of the fibers so far obtained is not good enough to make this completely unequivocal.

Other pictures taken with the fiber tilted at different angles and with longer exposures show a reflection which appears to be on the 11th layer line and which also appears to be meridional. It is, however, slightly broader than the tenth layer line reflection, suggesting that it might arise from two disorientated near-meridional reflections. It is also possible that reovirus RNA is a nonintegral helix. If this were so, the upper layer lines would not fall on the same system of layer lines as the lower ones, and some layer-line splitting would occur. Neither of these possibilities is observed, though they cannot be completely ruled out as yet. Until fibers are obtained with better orientation and the question can be studied more precisely, we will proceed on the assumption that the tenth layer line is indeed meridional.

This implies that reovirus RNA is a tenfold helix. The Bragg spacing of the tenth layer line is 3.04 Å, corresponding to the translation per nucleotide pair. Each pair will be rotated 36° in relation to its neighbor. It is virtually certain that the helix is right-handed, for while our x-ray diffraction results cannot directly distinguish left- and right-handed helices, molecular model building demonstrates that a left-handed helix is stereochemically much less satisfactory than a right-handed helix.

Since the translation per nucleotide pair is only 3 Å, while the perpendicular distance between the bases cannot be less than about 3.4 Å, the bases must be tilted, as in the *A* form of DNA. The exact angle of tilt of the bases cannot be deduced without extensive model building and calculation, since no one part of the diffraction pattern can be explained by any single feature of the molecular model, but the mean displacement of the maxima of the higher layer lines from the meridian is strongly dependent on the angle of tilt of the bases. This displacement is about 10° to 15° in the RNA diffraction pattern and about 20° in the pattern of the *A* form of DNA. Since molecular model building and calculation for the *A* form of DNA have shown that in this case the bases are tilted at about 70° to the helix axis, we might expect the bases in RNA to be tilted about 5° to 10° less, that is, about 75° to 80° to the helix axis. This is consistent with the probable translation per nucleotide of 3 Å in RNA compared with 2.5 Å in the DNA *A* form and 3.4 Å in the DNA *B* form (in which the bases are about 90° toward the helix axis).

Comparison of Reovirus RNA and Transfer RNA

As pointed out, the breadth of the upper layer lines at present precludes a precise independent determination of the structure of transfer RNA. However, a careful comparison of the reovirus RNA pattern with the published patterns from transfer RNA (*5*, *9*) leads us to suspect strongly that these structures are almost, if not completely, identical. The distribution of intensity on the higher layer lines is very similar indeed. In both types of RNA

the middle member of the trio of strong near-meridional layer lines is displaced outward, a pattern different from that given by DNA. Although the assignment cannot be made with precision, the interpretation of the published diffraction photographs of transfer RNA seems somewhat more consistent if the three strong maxima in the near-meridional outer regions of the patterns are assigned to the seventh, eighth, and ninth layer lines as in reovirus RNA rather than the sixth, seventh, and eighth as in the *A* form of DNA. Such agreement in the wide-angle portions of a diffraction diagram can only be obtained if the two structures are similar in both outline and detail.

Recent measurements on improved diffraction patterns from transfer RNA (*10*) indicate that the spacing of the higher layer lines is indeed more consistently accounted for if, with a distance of 30 Å between each turn of the helix, the three strong near-meridional reflections are assigned to the seventh, eighth, and ninth layer lines—thus agreeing with our results on reovirus RNA. The tenth layer-line maximum also appears to be meridional in the patterns from tilted fibers of transfer RNA, but this can only be regarded as consistent with the observations on reovirus RNA and in no way confirms the suggestion that the tenth layer-line maximum is meridional.

If a more detailed comparison confirms the view that reovirus RNA and transfer RNA have identical structures within the limits of measurement, the further refinement of RNA structure by means of fiber-diffraction techniques will probably be made with reovirus RNA [or an equivalent such as wound tumor virus RNA (*8*)] since the resolution obtainable is so much better. However, small single crystals of transfer RNA material have already been observed (*9*), and, if these can be grown to a much larger size, a complete single crystal structure determination is possible. Neither DNA nor reovirus RNA has as yet formed single crystals.

The Structural Difference between DNA and RNA

The main structural parameters of the sodium salts of DNA and RNA are summarized in Table I. It might be argued that the structural difference between DNA and RNA could be caused by the presence of uracil in RNA in place of the thymine in DNA. This is a priori unlikely, and recent work by Langridge and Marmur (*11*) has shown that the DNA from *Bacillus subtilis* bacteriophage PBS2, which contains uracil in place of thymine (*12*), has a DNA-like structure. Although 60 percent of the guanines and 20 percent of the cytosines are glucosylated in this DNA, and, like the similarly glucosylated T2 phage DNA, it exists only in the *B* configuration, this evidence makes it unlikely that the replacement of thymine by uracil can be implicated in the clear structural difference between DNA and RNA. The only remaining major chemical difference between DNA and RNA is the presence of the 2′-hydroxyl in RNA. The fact that transfer RNA does not show the transition to the *B* form (with the bases perpendicular to the helix axis) as the water content is raised may be due, as suggested by Spencer *et al.* (*5*), to hydrogen-bonding from the 2′-hydroxyl either to the ring-oxygen atom of the neighboring ribose, or to an oxygen atom of the adjacent phosphate group. This could also apply to reovirus RNA, and it seems probable that this mechanism can be cited to explain the difference between RNA and DNA structures.

The Generality of RNA Structure

RNA extracted from all sources including ribosomes, viruses (other than reovirus), and noncrystalline transfer RNA gives effectively identical diffraction patterns which are too diffuse and disorientated to be interpreted directly. It was shown by Spencer *et al.* (*5*) that the broad distribution of intensity in these diffuse patterns is very similar to the patterns given by crystalline transfer RNA. The highly detailed patterns now obtained from reovirus RNA also have a similar general intensity distribution.

There must therefore be regions within all the RNA's so far studied which have double-helical structure similar to reovirus RNA.

It should be emphasized that the absolute amount of helix present in the materials giving the diffuse patterns is very difficult to estimate. We can only state that regions of regular structure would tend to dominate the patterns, but a simple measurement of background to peak height does not suffice—one of the main reasons being that we do not know precisely what "background" means in this case.

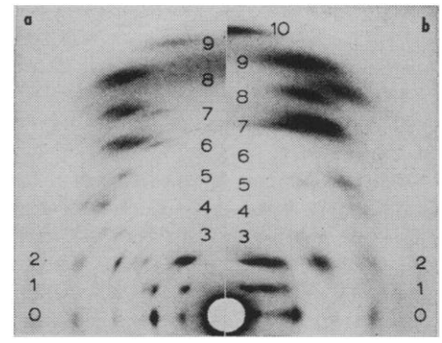


Fig. 3. *a*, Salmon sperm DNA (sodium salt) at 75-percent relative humidity (fiber axis tilted at 15° to the vertical). *b*, Reovirus RNA (sodium salt) at 92-percent relative humidity (fiber axis tilted 15° to the vertical). The layer lines are numbered; the relative spacing increases at higher angles of diffraction and the lines curve on each side of the meridian.

Reovirus RNA offers a better opportunity for making such calculations, but it is still difficult to produce figures which are better than the upper and lower limits of a rather broad range. With present data it seems reasonable to suggest that at least 50 percent of the RNA must be in the double-helical form, and that the patterns are consistent with 90- to 100-percent double helix.

We also note that reovirus RNA has an apparently "normal" complement of the four nitrogeneous bases, while transfer RNA has a rather more exotic base composition, yet the three-dimensional structures of the two are identical within the limits of our pres-

Table 1. A comparison of the properties of the sodium salts of DNA and RNA. (All are double-stranded helices, in which the polynucleotide chains run in opposite directions and are joined together by Watson-Crick base-pairs.)

Relative humidity (%)	Helix repeat (Å)	Number of residues per turn	Translation/residue (Å)	Helix-plane angle* (deg)
		DNA A form		
75	28	11	2.5	About 70
		DNA B form		
92	34	10	3.4	90
		RNA		
15 to 92†	30	10‡	3‡	About 75 to 80

* Angle between helix axis and plane of bases. † Hydration changes have little effect. ‡ These figures cannot yet be regarded as definitive (see text).

ent comparison, and different from DNA.

This suggests that provided base pairing can take place, the actual structure of double-helical RNA does not depend on the type of bases taking part.

The apparent generality of the double-helical RNA structure means that the DNA's from wound tumor virus, the postulated double-helical segments of ribosomal RNA, transfer RNA, and the regions of secondary structure in a single-stranded RNA such as tobacco mosaic virus RNA probably adopt this configuration.

We might speculate that, when single-stranded RNA acts as a "messenger," the double-helical regions might be the punctuation marks in the code. The similarity in structure to transfer RNA could cause the messenger to occupy the transfer RNA site on the ribosome when these regions are reached during the "reading of the code," thus displacing the completed polypeptide chain.

In any case a careful analysis of the excellent diffraction patterns given by reovirus RNA should provide a detailed knowledge of the structure of all double-helical RNA and may form a basis for an understanding of its biological function.

Summary

X-ray diffraction patterns from fibers of the sodium salt of reovirus RNA are the most detailed so far obtained from RNA. The structure differs from any presently known form of DNA. The diffraction patterns given by reovirus RNA and transfer RNA show very similar features, which suggests that these structures are identical, and which implies that all double-helical RNA adopts this configuration (see *13*).

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The Humanities in the Scientific Curriculum

In both North and South America greater emphasis on the humanities is needed in secondary education.

Marcel Roche

The confusion between science and technology has arisen only since man, after watching the effect of their combined power, has become convinced that their large-scale development is necessary. Practical evidence of this effect—such as the speed of a plane, the cure of a disease, or the ability to destroy one's enemy—has filled man with awe and reverence. Francis Bacon had prophesied that his new philosophy would not "come down to the apprehension of the vulgar except by its utility and effects" (*1*).

This is only natural—and political as well—since public opinion, and no longer the good pleasure of a Prince, is what determines the spending of state funds. Scientists themselves have contributed to this point of view. To sway politicians, most of whom think of the future as within the scope of a single political mandate, scientists have emphasized only a by-product of science: practical application. They deem it necessary to justify pure science, and to apologize for it. It is a well-worn cliché that theoretical studies lead to unexpected applications. The saying is true and easy to prove. That it should have to be constantly repeated shows that the contemplative nature of science is not generally appreciated.

Now, anything valid which will help to further knowledge has my wholehearted support. I have myself used such arguments, and their value as motivators cannot be denied. But what worries me is that such considerations may obscure the true nature of science. For when the contemplative aspects of science are given their proper emphasis, the gap between science and the humanities disappears. Both are seen as manifestations of man's creativity, hence as activities that should be supported primarily because of their intrinsic value, not because of their practical usefulness. Lest I be accused of mysticism, let me hasten to say that "contemplation" for me is not belly-button-gazing and a nirvana of the will but rather an active, purposeful, and systematic perception of reality.

Inventive Technology

Even the difference between science and the humanities on the one hand and technology on the other is not as clear as it seems. There is an inventive technology which implies creative spirit, imagination, and, I should say, a humanistic point of view. For the humanities embrace any en-

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