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Small-Angle X-ray Scattering Study of Complexes of Individual Components from E. Coli Ribosomes*

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As part of a general X-ray scattering study on individual ribosomal components and their specific complexes, this study deals with the proteins S1, S8, S15, S16 and S20, the the S4-binding region of 16-S RNA, S4-RNA, as well as the specific complexes 5-S RNA-L18, 5-S RNA-L18-L25 and S4-RNA-S4; the proteins were prepared under non-denaturing conditions. In agreement with the previous X-ray scattering studies (Österberg, Sjöberg, Liljas & Pettersson, 1976; Österberg, Sjöberg & Garrett, 1976a; Österberg, Sjöberg, Garrett & Littlechild 1977), involving the proteins L7/L12, L18, L25 and S4, the present data indicate that the proteins are elongated. However, there are individual variations; for instance, S4, L7/L12, and S1 appear to be more elongated than S8, S15 and S16. Most of the curves can be interpreted in the form of the scattering from elongated ellipsoids, but an alternative description of the data recorded for the proteins S4 and L7/L12 takes into consideration not only the well-structured domains of the molecules but also the possibility that there might be some flexible parts. Some of the structured fragments have been prepared in pure form (Liljas & Kurland, 1976; Changchien & Craven, 1976) and that of L7/L12 has been crystallized (Liljas & Kurland, 1976). The X-ray scattering from the L7/L12 fragment is in good agreement with the data previously reported (Österberg, Sjöberg, Liljas & Pettersson, 1976).

X-ray scattering titrations of the 5-S RNA complexes of L18 and of L18 and L25 indicate that the 1:1 and 1:1:1 complexes predominate *in vivo*. There is a slight but defined increase in the radius of gyration at the stepwise binding of first L18 and then L25 to 5-S RNA, indicating that the electron-density centres of the proteins must be relatively far

The binding region for protein S4 on 16-S RNA, S4-RNA, yields an X-ray scattering curve that, in its proximal part, can be interpreted as the scattering from an oblate ellipsoid; the best-fitting two-parameter ellipsoid has the dimensions of $132 \times 132 \times 32$ Å (Österberg, Sjöberg, Garrett & Ungewickell, 1977). X-ray scattering titration data indicate that S4-RNA forms a stable S4 complex with log $K \sim 7$. The X-ray scattering from this 1:1 complex is very similar to that of S4-RNA, indicating that no major conformational change of S4-RNA takes place at the complex formation.

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Neutron Small-Angle Scattering of E. Coli Ribosomes. A Contrast Variation Study

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Neutron small-angle scattering with the contrast-variation method has established that for 50S and 70S ribosomal particles the RNA-protein distribution is such that the RNA component is located predominantly towards the interior

and the protein towards the exterior of the particle. In contrast, the 30S subunit is much more homogeneous in its RNA-protein distribution. The shape of the 50S subunit has been determined at low resolution.

from that of 5-S RNA. If the Y-shaped 5-S RNA structure (Österberg, Sjöberg & Garrett, 1976b) is assumed, then, it is possible to explain the data *via* the scattering from models where L18 and L25 interact with both of the minor arms of the Y-model (cf. Österberg & Garrett, 1977).

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Neutron small-angle scattering of *E. coli* 30S, 50S and 70S ribosomal particles provides a straightforward approach to the determination of the mutual arrangement of protein and RNA in the particles on account of the large differences in scattering density between ribosomal proteins and *r*-RNA. Recent studies (Sturhmann *et al.*, 1976) using the contrast variation method have led to a model for the 50S subunit in which a region of relatively low scattering density, rich in proteins, surrounds an RNA-rich core of higher scattering density. The separation between the centres of mass of the *r*-RNA and protein distributions is much less than that found earlier by specific deuteration (Moore, Engelman & Schoenborn, 1974). This model has been confirmed (Crichton *et al.*, 1977) with contrast variation on specifically deuterated 50S subunits.

We have extended these studies to 30S and 70S particles and find that the scattering density of the 70S ribosomes, as for the 50S subunit, decreases from the centre to the outer surface of the particle. The 30S particles are much more homogeneous (Stuhrmann et al., 1978). Thus for 70S and 50S particles the r-RNA is located mainly in the interior and the bulk of the protein is distributed concentrically on the outer surface. Comparison of the parameters obtained for the two subunits and for the 70S particle suggests that the interaction between the two subunits does not involve any major structural change in the latter. Extrapolation of a series of scattering curves to infinitely high contrast gives a scattering function $I_c(\kappa)$ which is solely dependent on the

shape of the solute molecule. For the 50S subunit the determination of the molecular shape from $I_c(\kappa)$ has been carried out (Stuhrmann *et al.*, 1977); the result is in good agreement with models of the 50S determined by electron microscopy. A detailed analysis of the scattering curves to obtain the shape of the 30S and 70S particles is in progress.

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