

Structure Determination of Biological Macromolecules in Solution Using Nuclear Magnetic Resonance Spectroscopy

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Gerhard Wider
Eidgenössische Technische
Hochschule Hönggerberg,
Zürich, Switzerland

ABSTRACT

A detailed understanding of the function of a biological macromolecule requires knowledge of its three-dimensional structure. Most atomic-resolution structures of biological macromolecules have been solved either by X-ray diffraction in single crystals or by nuclear magnetic resonance (NMR) in solution. This review surveys the method of NMR structure determination. First, a brief introduction to NMR and its basic concepts is presented. The main part of the article deals with the individual steps necessary for an NMR structure determination. At the end, the discussion turns to considerations on the influence of the molecular size of the macromolecules on the structure determination by NMR. New techniques are discussed that greatly enhance the possibilities of applying NMR to large molecular systems.

INTRODUCTION

With the near completion of the human genome project, an even greater challenge awaits biologists: proteomics, the study of all the proteins coded by the genes. In many cases, it will be necessary to know the three-dimensional (3-D) structure of a protein to understand its function. The feasibility of such a structural proteomics project was recently demonstrated (10), and it was shown that two techniques will play a dominant part: X-ray crystallography and nuclear magnetic resonance (NMR). These are the two main techniques that can provide structures of macromolecules at atomic resolution. Both techniques are well established and already play a key role in biological and pharmaceutical research as a basis for a detailed understanding of molecular functions and as a foundation for protein design. Whereas X-ray crystallography requires single crystals, NMR measurements are carried out in solution under near physiological conditions. The important role that NMR plays in structural biology is illustrated by the far more than 1000 NMR solution structures deposited in the protein databank (3). NMR measurements not only provide structural data but also reach much further and can supply information on dynamics, conformational equilibria, folding and intra- as well as intermolecular interactions (14,16,28,36,57). This review focuses on the application of NMR for structure determination of proteins in solution, but the methodology is applicable to other bio-

molecules, especially nucleic acids (53).

NMR does not directly produce an image of a protein. Rather, it is able to yield a wealth of indirect structural information from which the 3-D structure can only be revealed by extensive data analysis and computer calculations. The principles of an NMR structure determination can be summarized as follows (Figure 1): preparation of the protein solution, the NMR measurements, the assignment of NMR signals to individual atoms in the molecule, identification of conformational constraints (e.g., distances between hydrogen atoms) and the calculation of the 3-D structure on the basis of the experimental constraints. These different steps will be discussed in individual sections in this review. However, the NMR technique (8,9,15,48) is first introduced in the sections "Basic NMR", "Correlations in NMR" and "Multidimensional NMR".

Structure determination by NMR is an established technique and is routinely used to determine 3-D structures of biological macromolecules in solution with molecular weights up to 30 kDa (3,13,54,55). The power of NMR over other spectroscopic techniques results from the fact that every NMR-active nucleus gives rise to an individual signal (resonance line) in the spectrum that can be resolved by multidimensional NMR techniques. This becomes more difficult for larger molecular structures and puts a practical limit to the molecular size that can be studied in detail by NMR (11,29,56). Up to now, only very few NMR structures were determined of molecules larger than 30

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