The left-handed helix of each chain is <u>not</u> stabilized by intrapeptide H-bonds.

The three left-handed helices are twisted around each other to form a right-handed superhelical structure as shown in Fig 4.20.

The superhelical structure is stabilized by Hbonds between peptide carbonyl O atoms in one chain and peptide N-H groups in the other chains.

Since both pro and hyp residues lack a H on the peptide N, as shown below, the number of possible H-bonds is limited. The number of H-bonds between chains is maximized by the repeating sequence Gly-X-Y where X is often pro and Y is often hyp as shown in Fig. 4<sup>-</sup>18.

Collagen is arranged in staggered arrays (fibrils) as shown in Fig 7-34.

Collagen fibrils in various tissues are crosslinked through lys and his side chains as shown in Figs 4.20, 4.21, 4.22.

These cross-links increase the strength of the fibers.

The extent of cross-linking appears to increase with age and contributes to the rigid and brittle character of older connective tissue.

A number of human diseases are traced to mutations in collagen or the enzymes responsible for catalyzing cross-links that affect the stability of the fibers. The structures of  $\alpha$  keratin, silk and collagen indicate the importance of both the a.a. composition and sequence to the formation of a particular secondary structure.

Studies of proteins have further suggested a differential ability of a.a. to form particular secondary structures, i.e., each a.a. shows a different propensity to form particular secondary structures as shown in Table 8-1.

The Table is based on the relative frequency of finding an a.a. in a particular secondary structure in a large set of proteins whose structures have determined by X-ray analysis.

 $P_{\alpha} = f_{\alpha}/\langle f_{\alpha} \rangle$  which is the fequency of finding an a.a. divided by the average frequency for all a.a..

 $f_{\alpha} = n_{\alpha}/n$ , where  $n_{\alpha}$  is the number of a.a. residues of a given type that occur in  $\alpha$  helices and n is the total number of residues in  $\alpha$  helices.