However, there are already enough clues to justify further investigation of the non-cholinergic biochemical and physiological functions of the cholinesterases. The possible involvement of cholinesterases in cell growth and movement has far-reaching implications for our understanding of the maturation of cells in the nervous system and blood.

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**References**

1 Greenfield, S. (1984) *Trends Neurosci.* 7, 364–368
2 Silver, A. (1974) in *The Biology of Cholinesterases*, North Holland
3 Massoulie, J. and Bon, S. (1982) *Annu. Rev. Neurosci.* 5, 57–106
4 Eckenstein, F. and Sofroniew, M. V. (1983) *J. Neurosci.* 3, 2286–2291
5 Ott, P., Lustig, A., Brodbeck, U. and Rosenbusch, J. P. (1982) *FEBS Lett.* 138, 187–189
6 Paulus, J-M., Maigne, J. and Keyhani, E. (1981) *Blood* 58, 1100–1106
7 Small, D. H., Ismael, Z. and Chubb, I. W. (1987) *Neuroscience* 21, 991–996
8 Small, D. H. (1989) *Neurosci. Lett.* 95, 307–312
9 Small, D. H. (1989) *Neuroscience* 29, 241–249
10 Checler, F. and Vincent, J-P. (1989) *J. Neurochem.* 53, 924–928
11 Sikorav, J-L., Duval, N., Anselmet, A., Bon, S., Krejci, E., Legay, C., Osterlund, M., Reimund, B. and Massoulie, J. (1988) *EMBO J.* 7, 2983–2993
12 Small, D. H. and Chubb, I. W. (1988) *J. Neurochem.* 51, 69–74
13 Small, D. H. and Simpson, R. J. (1988) *Neurosci. Lett.* 89, 223–228
14 Rosenberry, T. L. (1975) *Adv. Enzymol.* 43, 103–218
15 Monard, D. (1988) *Trends Neurosci.* 11, 541–544
16 Van Nostrand, W. E., Wagner, S. L., Suzuki, M., Choi, B. H., Farrow, J. S., Geddes, J. W., Cotman, C. W. and Cunningham, D. D. (1989) *Nature* 341, 546–549
17 Hamilton, J. A., Stanley, E. R., Burgess, A. W. and Shadduck, R. K. (1980) *J. Cell. Physiol.* 103, 435–445
18 Soreq, H., Zamir, R., Zevin-Sonkin, D. and Zakut, H. (1987) *Hum. Genet.* 77, 325–328
19 Lapidot-Lifson, Y., Prody, D. A., Ginzburg, D., Meytes, D., Zakut, H. and Soreq, H. (1989) *Proc. Natl Acad. Sci. USA* 86, 4715–4719
20 Burstein, S. A., Adamson, J. W. and Harker, L. A. (1980) *J. Cell. Physiol.* 103, 201–208
21 Layer, P. G., Alber, R. and Sporns, O. (1987) *J. Neurochem.* 49, 175–182
22 Rieger, F., Shelanski, M. L. and Greene, L. A. (1980) *Dev. Biol.* 76, 238–243
23 Rotundo, R. L. and Carbonetto, S. T. (1987) *Proc. Natl Acad. Sci. USA* 84, 2063–2067

# TEXTBOOK ERRORS

## Propagation of an error: β-sheet structures

Arthur S. Edison

I have found mistakes in the diagram of both parallel and anti-parallel β-sheet diagrams in Linus Pauling's *The Nature of the Chemical Bond*[1] that have been propagated for 30 years by many of the most widely used textbooks in biochemistry.

**WHILE STUDYING** Creighton's *Proteins: Structures and Molecular Properties*[2], a required text for the course in biomolecular structure at the University of Wisconsin, I discovered that a short model of a polypeptide chain which I had built could not be oriented so that it corresponded to the diagram of β-sheet structures. Neither the parallel nor the anti-parallel drawings would fit my model, so I checked the model for the proper L-amino acids. Finding it to be correct, I soon discovered that both β-sheet diagrams in Creighton are drawn with D-amino acids.

These diagrams[2] were adapted from Pauling's *The Nature of the Chemical Bond* (3rd edn)[1]. I assumed that Creighton's diagrams had been inadvertently reversed during publication, but to my surprise, the β-sheet structures in Pauling's great text are drawn with D-amino acids. This apparent error prompted me to examine the original papers.

The first proposal of β-sheet structures was made by Pauling and Corey in 1951[3,4]. During the same period of time, Pauling, Corey and Branson proposed two hydrogen-bonded helices, one of which has become known as the right-handed α-helix[5]. This work was based upon model building which incorporated the authors' knowledge of the planar peptide bond, bond angles, and bond lengths. In each of these papers[3–5] the authors were discussing L-amino acids, but the diagrams contained what we now designate D-amino acids. However, in the publication on helical configurations[5] the authors state: 'An arbitrary assignment of the R groups has been made in the figures'. At the time of this initial work in 1951, the absolute configuration of the amino acids was not known, and the authors made a random guess that was later shown to be incorrect.

Around this same time, Bijvoet and co-workers[6–8] developed the method of isomorphous replacement for X-ray crystallography which enabled them to determine the absolute configurations of a wide range of optically active compounds, many of which could be related, by chemical methods, to the naturally occurring amino acids.

In 1955, Pauling, Corey and Marsh published a paper on the structure of silk fibroin[9]. In this paper, the diagram of the anti-parallel β-sheet was drawn with the correct configuration of L-amino acids which corresponds to *S* (except for cysteine) in the *R/S* system of Cahn, Ingold and Prelog[10,11].

This shows that the papers published in 1951 and 1955 by Pauling and colleagues were correct in their representation of β-sheet structures: in 1951 because the absolute configuration of amino acids had not yet been determined, and in 1955 because they cor-

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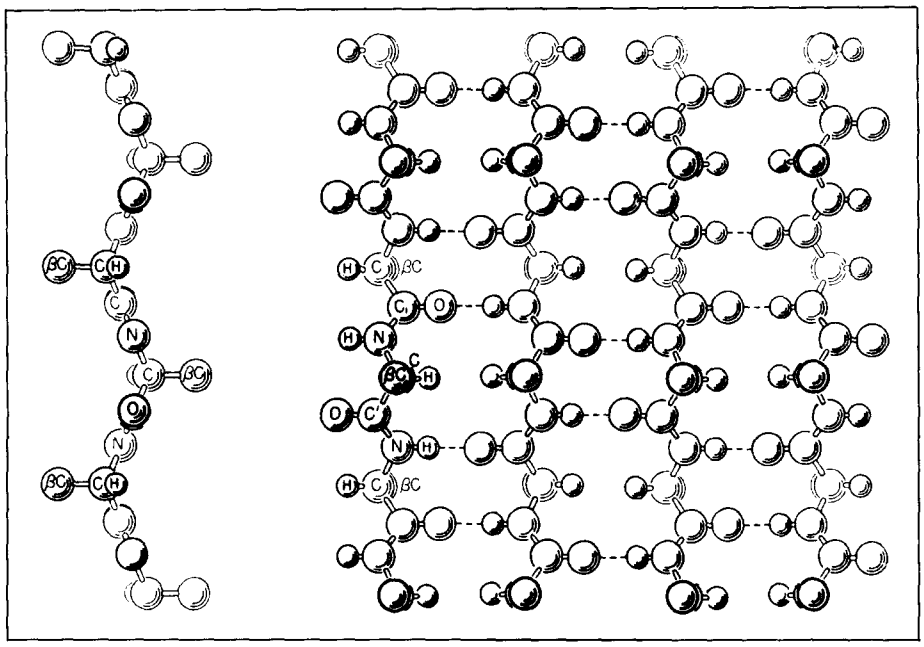

**Figure 1**
β-sheet diagram drawn with L-amino acids; reproduced, with permission, from Ref. 9.

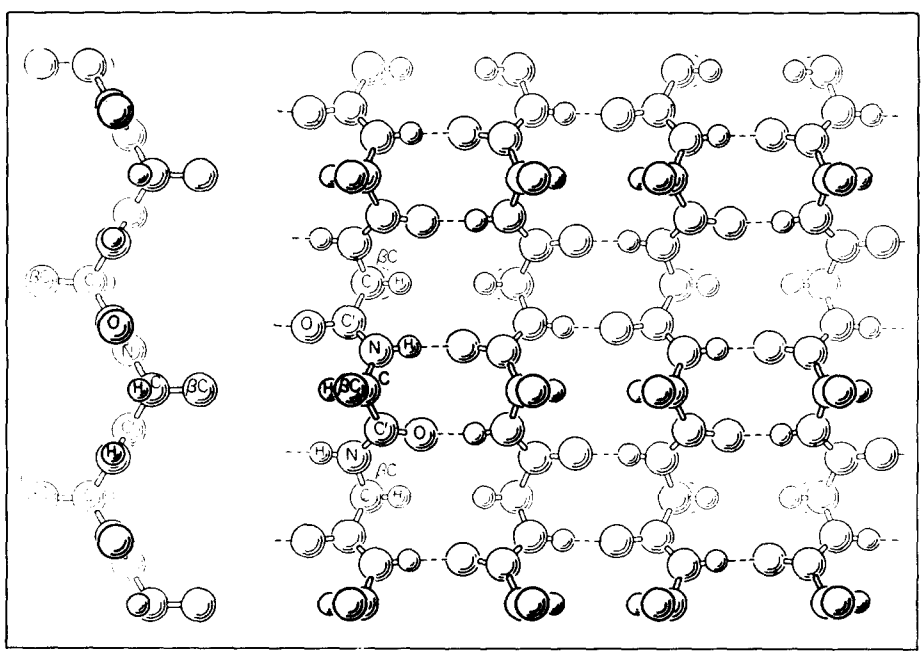

**Figure 2**
β-sheet diagram drawn with D-amino acids; reproduced, with permission, from Ref. 1.

rectly represented the known configurations of L-amino acids. However, in the third edition (1960) of *The Nature of the Chemical Bond*[1], the 1951 diagrams of β-sheets were used. As a result, the drawings incorrectly show D-amino acids.

The unfortunate, but amusing, outcome of this mistake is that many textbooks in biochemistry, biophysics and molecular biology have adapted the incorrect diagrams. During a short visit to the library, I found 11 other textbooks, including all four editions of Watson's *Molecular Biology of the Gene*, that have propagated this error[12–20]. This was just a random sampling, and I am sure that others could be found. I would doubt that an error such as this would have been propagated for 29 years had it not occurred in a book written by one of the world's greatest chemists[2].

**Acknowledgements**

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**References**

1 Pauling, L. (1960) in *The Nature of the Chemical Bond* (3rd edn), p. 501, Cornell University Press
2 Creighton, T. E. (1984) in *Proteins: Structures and Molecular Properties*, p. 174, W. H. Freeman & Company
3 Pauling, L. and Corey, R. B. (1951) *Proc. Natl Acad. Sci. USA* 37, 251–256
4 Pauling, L. and Corey, R. B. (1951) *Proc. Natl Acad. Sci. USA* 37, 729–740
5 Pauling, L., Corey, R. B. and Branson, H. R. (1951) *Proc. Natl Acad. Sci. USA* 37, 205–211
6 Bijvoet, J. M., Peerdeman, A. F. and van Brommel, A. J. (1951) *Nature* 168, 271–272
7 Bokhoven, C., Schoone, J. C. and Bijvoet, J. M. (1951) *Acta Crystallogr.* 4, 275–280
8 Trommel, J. and Bijvoet, J. M. (1954) *Acta Crystallogr.* 7, 703–709
9 Marsh, R. E., Corey, R. B. and Pauling, L. (1955) *Biochim. Biophys. Acta* 16, 1–34
10 Cahn, R. S. and Ingold, C. K. (1951) *J. Chem. Soc.* 612
11 Cahn, R. S., Ingold, C. K. and Prelog, V. (1956) *Experientia* 12, 81
12 Watson, J. W. (1965, 1970, 1976) *Molecular Biology of the Gene* (edns 1–3) W. A. Benjamin
13 Watson, J. W., Hopkins, N. H., Roberts, J. W., Steitz, J. A. and Weiner, A. M. (1987) *Molecular Biology of the Gene* (4th edn), p. 52, the Benjamin/Cummings Publishing Company
14 Schellman, J. A. and Schellman, C. (1964) in *The Proteins* (H. Neurath, ed.), Vol. II, p. 23, Academic Press
15 Mahler, H. R. and Cordes, E. H. (1971) in *Biological Chemistry* (2nd edn), p. 139, Harper & Row Publishers
16 Suttie, J. W. (1977) in *Introduction to Biochemistry* (2nd edn), p. 85, Holt Rinehart & Winston
17 Vol'kenstein, M. V. (1977) in *Molecular Biophysics*, p. 168, Academic Press
18 Vol'kenstein, M. V. (1970) in *Molecules and Life*, p. 170, Plenum Press
19 Harrow, B. and Mazur, A. (1966) in *Textbook of Biochemistry* (9th edn), p. 68, W. B. Saunders Company
20 Lehninger, A. L. (1982) in *Principles of Biochemistry* (2nd edn), p. 155, Worth Publishers

## Erratum

In the article entitled 'Tissue-specific genes for respiratory proteins' by Margaret I. Lomax and Lawrence I. Grossman (*TIBS* 14, pp. 501–503), Table I contained two errors. The two cytochrome *c* oxidase subunits *COX4* and *COX6A* are both located on human chromosome 16 and not chromosome 15.