

12th November 1975

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Dear Hank

This is in reply to your letter of 30th October. I am glad you have seen the light about the toroidal and interwound helices. This conversion, as you imply, is a matter of mechanics. You will find it discussed in Brock Fuller's paper (PNAS, 1971, 68, 815-819) - see his figure 1 - but the discussion is so brief that it could be overlooked on first reading (page 817, Section 4: especially "The consequence of this is that any linking number . .").

The rest of the letter shows you to be in a state of confusion and unable to distinguish the linking number (which is a topological property and for DNA is necessarily an integer for a complete circle from the twist, which is a metrical property and can have any value. If you cannot understand Brock Fuller I had better send you a rough first draft of my paper "Writhing numbers for Birdwatchers" - or did I give you one already!

About Vinograd's estimate: the 'number of superhelical turns' is the linking number (or more correctly the true linking number minus $n/10$ where n is the number of base pairs in the DNA circle). This is a topological property and cannot be altered without nicking the helix and resealing after a relative twist of the two ends. It does not depend at all on mechanical properties. Moreover the method of measuring, which is done by counting the number of possible superhelical species one can produce by nicking and rejoining (not that this is necessarily an integer) counts the number from the initial superhelical state to the unstrained state when there are no superhelical turns. Thus at the 'end point' there is no strain, so you can see that strain has nothing to do with it. Thus Vinograd's value of about $1\frac{1}{2}$ per nucleosome must stand, at least for SV40.

You also seem to me unclear about solenoidal coiling. Take a cylinder and wrap a piece of tape round it, with the tape flat to the cylinder, for, say, 5 complete turns (and then join the

ends of the tape together in a straightforward way). Then (apart from end effects) the linking number (for the two edges of the tape) is exactly 5 whatever the angle (α) of the helix. However the twist imposed on the tape over these 5 turns (see Brock Fuller, legend to Fig 1) is $5 \sin \alpha$, and therefore does depend on how steep the helix is. Unless you can understand this you cannot get the grips with the problem. Naturally DNA when wound helically may or may not be twisted. If you want DNA to be untwisted between kinks then you must have just the right amount of twist at the kinks to give the correct value to $N \sin \alpha$. If this is done then the linking number is exactly one per turn. (Incidentally, it is not possible, without experience, to derive the linking number of a complicated structure by guessing it. You can easily go wildly wrong).

Thus your argument for 2 kinked left-handed simple toroidal turns (the DNA between kinks being in the 13 form) giving a linking number of -1.2 is quite false.

We are very interested in your 45° kink if only because it makes a smoother circle, when kinked every 10 bp, than a coil with 90° kinks every 20 base-pairs. I should like to be satisfied that the bases do not foul (or prevent hydrogen bonding to NH's) for all 10 possible pairs of base-pairs adjacent to the helix. I assume you have built it with a dyad. Such a structure is defined by 4 parameters (see our Nature paper on the kinky helix) of which the 45° angle is only one. What are the others? Please be sure to estimate the dihedral angle correctly. Do remember that between the first base-pair of a stretch of 10 base-pairs and the last base-pair there is a rotation of only 324° not 360° . Incidentally Aaron tells me that the trick of getting a novel 'bend' by altering one of the sugars to the other form is used several times in tRNA.

Looking forward to hearing from you.

Yours sincerely

F H C Crick