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Morphogenesis and ultrastructure of condensed DNA toroids

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DNA toroids are complex liquid crystalline objects that form spontaneously in vitro by condensation of DNA, a general behaviour of semi-flexible polyelectrolytes. These structures have intrigued biophysicists and physicists, both experimental and theoretical, because of the intrinsic beauty of these toroidal objects, and because they provide models for understanding the packaging of DNA in many biological systems such as viruses, spermatozoa or bacterial nucleoids.

Within these structures, the DNA chains locally form a hexagonal lattice, but topological defects are required to resolve the frustration resulting from several phenomena: (i) the continuity of the DNA chain and the morphogenesis of the object imposing the path of the chain within the torus [1-3]; (ii) the competition between the parallelism imposed by the compact hexagonal lattice and the tendency to twist resulting from the helicity of DNA [4-6]; and (iii) the correlations between neighbouring DNA helices (or 'electrostatic zipper' [7]).

To understand these phenomena, we analyse their ultrastructure by cryo-electron microscopy and follow their nucleation and evolution on time scales of 30 sec to several tens of minutes. We show the formation of toroidal and rod-like structures, which evolve towards equilibrium forms that are all toroidal. We show the existence of an internal phase separation, between a disordered sparse zone that would concentrate the defects of the structure and an ordered compact zone that would optimise the correlations between DNA helices everywhere else. Finally, the analysis of these correlations shows the existence of a complex link between curvature, conformation of the molecule (variation of the helical pitch) and phase of the order between helices (ferro/antiferro magnetic type order).

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