



Colloid Science Collides with Liquid Crystals

Nicholas L. Abbott
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motifs of transcription factors within protein-coding genomic regions are selectively devoid of sequences that contain a stop codon.

What features might permit synergistic coexistence of the regulatory and genetic codes? One major constraint of protein-coding genes is the requirement for the encoded polypeptide segment to fold into a defined tertiary structure. It is possible that in regions where folding constraints are not present, such as in intrinsically disordered regions (14), there might be increased tolerance for protein-coding genomic regions to harbor more regulatory elements that can be interpreted by different regulatory codes.

Stergachis *et al.* make a number of important genome-scale observations, but several mechanistic questions remain to be answered. For instance, although the authors report a weak tendency for transcription factors to preferentially bind to the protein-coding regions of highly expressed genes, it is unclear how the binding of a transcription factor within protein-coding regions mecha-

nistically influences the expression of a gene. Perhaps this type of binding might result in alternative promoters with different transcriptional start sites or affect the expression of neighboring genes (by acting as a distal enhancer element, for example). It is also unclear whether binding of a transcription factor within a protein-coding region may not directly affect gene expression but instead determine the formation and maintenance of higher-order chromatin structure.

Future research will need to determine the number of overlapping codes that can be tolerated by the genetic code. There is also the question of possible trade-offs, in terms of maintaining regulation and functionality, that have been made to accommodate coexistence of codes and whether this can lead to nonoptimal or deleterious consequences. For instance, protein-coding regions that cannot tolerate mutations due to multiple overlapping codes may be exploited by pathogens during host infection. The investigation of overlapping codes opens new vistas on the

functional interpretation of variation in coding regions and makes it clear that the story of the genetic code has not yet run its course.

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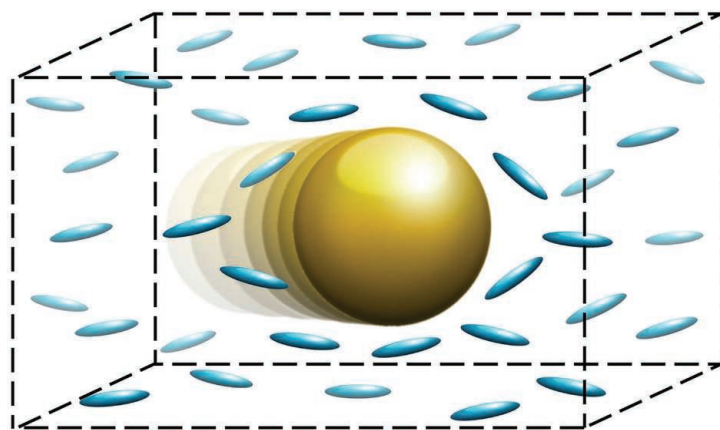
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APPLIED PHYSICS

Colloid Science Collides with Liquid Crystals

Nicholas L. Abbott

Brownian motion—the chaotic movement of colloidal particles that results from their collisions with solvent molecules—controls transport processes in systems as complex as the interior of living cells and as mundane as a film of drying paint. In a simple solvent, if you measure the distance the colloid travels (its displacement) for a sufficiently long time, the disorderly motion obeys a simple relation: The mean squared displacement (MSD) scales linearly with time. However, more recent studies of complex systems (e.g., concentrated solutions of proteins, polymers, or surfactants) revealed deviations from this classical behavior caused by local fluctuations in the composition and structure of the medium around the colloid (1–3). Now, in a strikingly elegant study described on page 1351 of this issue, Turiv *et al.* (4) unmask a



Dynamic interactions of a colloidal particle with a liquid crystalline solvent can cause its diffusion to deviate from classical Brownian motion.

Taking timely directions.

The diffusion of a colloidal particle (gold) in a liquid crystalline solvent (blue) is depicted. The solvent molecules have a local average alignment. Turiv *et al.* show that dynamic fluctuations in the alignment direction can transfer momentum to the colloid and cause the time dependence of its diffusion to deviate from classical Brownian motion.

new example of “anomalous diffusion” of colloids that involves a liquid crystal (LC), a liquid-like phase that has long-range orientational ordering. Fluctuations in the solvent-molecule orientations cause MSDs of colloids to grow nonlinearly with time.

Research on LCs and colloidal diffusion was pioneered by Planer (5) and Smoluchowski (6), both of whom worked at the

University of Lviv, Ukraine, in the late 19th century. For many decades, the fields of colloid science and LCs evolved with only occasional exchanges of ideas. That situation has changed during the past 20 years. For example, LCs can mediate intercolloidal interactions with strengths, ranges, and symmetries that result in exotic colloidal assemblies (7, 8). Emulsions with internal structures can be

Chemical and Biological Engineering, University of Wisconsin, Madison, WI 53706, USA. E-mail: abbott@engr.wisc.edu

formed with LCs that are remarkably sensitive to the presence of specific biological adsorbates (9) and can serve as templates for the synthesis of spherical and nonspherical particles with chemical patches (10). These advances are leading to LC-based colloidal systems with functional properties and potential technological impact that go well beyond traditional applications of LCs in displays.

The LCs used in the study by Turiv *et al.* are low-molecular weight organic molecules that can be viewed as structured oils. The long-range orientational ordering of molecules in LCs, which gives rise to anisotropic viscosities and mechanical properties not found in simple isotropic solvents (11), is dynamic and patchy; local domains form, consisting of molecules with similar alignment. The alignment can be described theoretically with a director, a vector that represents the local average of the molecular orientations. In the late 1990s, it was shown that colloidal species dispersed in nematic LCs (the simplest type of LC that has no additional positional ordering) could locally strain the director of LCs, as well as introduce so-called topological defects. These defects are nanoscopic regions in which the LC orientational order differs substantially from the bulk (7).

The presence of these strains and defects, in combination with the anisotropic viscosities of LCs, were shown to give rise to anisotropic diffusion of colloidal particles in LCs (12, 13). However, in these earlier studies the MSDs followed the classical linear time dependence, and the measurements could be explained by construing the strain in the LC around the colloids as being static. Turiv *et al.* now demonstrate that fluctuations in the orientation of the LC director can influence the transfer of momentum from the LC to a colloid, such that the diffusion of the colloid departs from that predicted using the “static view” of the director (see the figure).

By focusing on a class of LCs with sufficiently slow fluctuations of the director, Turiv *et al.* imaged the displacements of colloids on time scales that lead to diffusive behaviors of the colloids that are faster or slower than classical Brownian motion. The measurements are striking examples of anomalous diffusion arising from purely orientational fluctuations in a solvent, and they define new questions and directions of inquiry. For example, whereas the measurements of anomalous diffusion reported by Turiv *et al.* occur on time scales consistent with the orientational fluctuations of the director in the LC, a detailed description of the dynamic coupling between the colloids and the LC is yet to be elucidated. Furthermore, the role of surface chemistry

(and, for example, colloid shape) in regulating near-particle fluctuations of the director is yet to be fully understood.

What is clear, however, is that the observations and ideas presented by Turiv *et al.* hint at new principles for manipulating colloidal transport processes. For example, one can envisage the application of time-dependent external fields (electrical, magnetic, or optical) to drive fluctuations in the director on relevant time scales and thus influence the exchange of momentum between colloids and LCs that gives rise to the anomalous diffusion. Alternatively, internally generated fields, such as those that are being explored in the context of designs of active matter (14, 15), might plausibly be harnessed to drive orientational fluctuations in LCs and thus regulate the transport of colloids.

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GENETICS

My Oldest Sister Is a Sea Walnut?

Antonis Rokas

Decoding of the ctenophore genome prompts reevaluation of the complexity of the metazoan ancestor.

With common names such as “sea walnut,” “sea gooseberry,” and “Venus’ girdle” that reflect their morphological diversity, the jelly-like creatures belonging to the phylum Ctenophora that bear distinctive “combs” of cilia are not only breathtakingly beautiful (1) but are also key to understanding early animal evolution. On page 1336 of this issue, Ryan *et al.* (2) decode the genome of the sea walnut *Mnemiopsis leidyi*, the first member of this phylum to be sequenced, and propose that ctenophores might be the earliest branch of the animal tree and the sister lineage to that of all other animals. This paints a picture of early animal evolution full of cell type complexity, as well as its loss.

The ~200 ctenophore species discovered so far live in a wide variety of marine environments and at all latitudes (3). They get their name from the eight rows of linked tiny hairs known as “ctenes” (Greek for combs) that run

alongside their body and propel the animals through water. Although superficially similar to jellyfish (cnidarians), ctenophore morphology is quite distinct from that of the other three early-branching animal phyla, the poriferans (sponges), the largely enigmatic placozoans (known solely from organisms belonging to the phylum’s single genus, *Trichoplax*), and the cnidarians (jellyfish, sea anemones, and their kin). Unlike the radially symmetrical jellyfish, ctenophores are biradially symmetrical—their main body axis is defined by a mouth at one end and a gravity-sensing apical organ at the other end. Unlike sponges and placozoans, but like jellyfish, ctenophores contain both muscle and nerve cells. The latter are organized as a diffuse net that appears to be centralized at the apical organ (4).

With the exception of poriferans, whose bodies lack tissue organization, the tissues of the other three early-branching animal phyla are thought to develop from two distinct embryonic germ layers—the ectoderm (from which the nervous system develops) and the endoderm (the layer that gives rise to the gut). By contrast, the tissues of all bilaterians—

Department of Biological Sciences, Vanderbilt University, Nashville, TN 37235, USA. E-mail: antonis.rokas@vanderbilt.edu