

Main Research Areas and Selected Publications of Reinhard Lipowsky (up to 2018)

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1. Interfacial Phase Transitions and Wetting Phenomena

Surface critical phenomena at first-order phase transitions

Systems that undergo first-order or discontinuous phase transitions exhibit surface critical phenomena, arising from the appearance of another thermodynamic phase at the surface. [1, 2]. One example is provided by surface melting. [3] In the latter case, the theory has been corroborated by experiments on lead [4, 5] and ice [6].

Effective interface models and scaling regimes

A wetting layer is bounded by two interfaces. The separation of these interfaces, which corresponds to the thickness of the wetting layer, can be understood in terms of effective interface models. [7, 8] The corresponding interface potentials involve both molecular interactions (van der Waals, electrostatic, polymer-mediated) as well as fluctuation-induced interactions arising from the configurational entropy of the interfaces. The interplay between these two types of interactions leads to several scaling regimes: a mean-field regime as well as three different fluctuation regimes. [8, 9, 10] Interfacial fluctuations are particularly strong in two dimensions for which the critical behavior has been determined for all four scaling regimes. [11] In three dimensions, the fluctuations are too weak to compete with long-ranged molecular interactions [8] but lead to complex behavior in systems with short-ranged interactions. [7, 10]

Growth of wetting layers

For complete wetting, the thickness of a thin wetting layer grows as t^θ with time t . [12, 13] For liquid layers governed by van der Waals forces, for instance, layer growth by deposition from a vapor phase is characterized by $\theta = 1/4$ [12] whereas diffusion-limited growth leads to $\theta = 1/8$ [13]. The theoretically predicted growth laws have been confirmed in several experiments. [14, 15, 16]

Contact angles on heterogeneous surfaces

For a chemically and/or topographically heterogeneous surface, one often considers average contact angles as described by Cassie’s and Wenzel’s law. However, one may also derive a general equation for the *local* contact angle that varies along the contact line and directly reflects the different types of surface heterogeneities. [17, 18]

Morphological wetting transitions at structured surfaces

Liquid droplets in contact with a chemically patterned or topographically structured substrate surface undergo shape transformations or bifurcations as one varies the liquid volume. Such morphological wetting transitions were first predicted for circular surface domains [19] and then studied, both experimentally and theoretically, for striped surface domains [20, 21] and for extended grooves [22, 23]. The shape bifurcations strongly affect nucleation processes. Thus, the nucleation of a liquid droplet at a circular surface domain encounters two distinct nucleation barriers. [24] Likewise, morphological wetting transitions lead to nonisomorphic nucleation pathways as observed for the melting of alkane monolayers. [25]

Selected Publications on “Interfaces”

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2. Membranes and Vesicles

Unbinding transitions of interacting membranes

Van der Waals forces usually lead to attractive interactions between two membranes as described by a positive Hamaker constant. These interactions are renormalized by the thermally-excited shape fluctuations of the membranes. As a result, one finds continuous unbinding transitions at finite values of the Hamaker constant [1, 2] as confirmed by experiment [3]. Electrostatic interactions can generate an energy barrier in the interaction potential between the membranes. The unbinding transitions remain continuous for low barriers but become discontinuous for sufficiently high barriers. [4, 5]

Morphology of vesicles

The shapes of giant vesicles can be understood in terms of curvature elasticity. For vesicles with laterally uniform membranes, this elasticity depends primarily on two parameters, the volume-to-area ratio of the vesicles and the spontaneous curvature of the vesicle membranes. Solving the corresponding shape (or Euler-Lagrange) equation, one finds a large variety of different shapes and shape transformations even for small values of the spontaneous curvature [6], in agreement with experimental observations [7, 2]. Vesicles also undergo shape transformations when they adhere to an attractive substrate surface as shown in [8] for vanishing spontaneous curvature and variable adhesive strength. Most vesicles have the topology of a sphere but toroidal vesicles with several handles are quite interesting because they exhibit new types of incessant shape transformations corresponding to ‘conformal diffusion’ in shape space: the vesicles are able to change their shape for fixed volume and area without changing their curvature energy [9] as confirmed experimentally [10].

Intramembrane domains and domain-induced budding

Biological and biomimetic membranes are fluid and contain several molecular components. As a consequence, they can undergo phase separation into two fluid phases and then form intramembrane domains. The budding of such a domain is facilitated both by the line tension of the domain boundary and by the domain’s spontaneous curvature. [11, 12] Using giant vesicles of ternary lipid mixtures, several theoretical predictions [11, 13, 14, 15, 16] have been confirmed experimentally: the growth and coalescence of small domains into larger ones [11, 15, 17]; the budding of the more flexible domains [13, 18]; and the location of the domain boundary within or close to the neck of the bud [14, 19, 20]. So far, this domain boundary location provides the only method to estimate the difference between the Gaussian curvature moduli for the two types of membrane domains. The competition between curvature and line energies can also lead to stable patterns of more than two domains as shown theoretically for freely suspended vesicles [21, 22] and for membranes adhering to corrugated surfaces [23]. It has been recently proposed that budding induced by ESCRT proteins provides another example of domain-induced budding governed by a large spontaneous curvature. [24]

Local curvature generation

In the previously mentioned studies, the spontaneous curvature was treated as a phenomenological parameter. Because the magnitude of this parameter strongly affects the behavior of membranes and vesicles, one would like to express it in terms of other quantities that can be directly measured. Such relationships have been derived for membrane-bound polymers [25, 26, 27, 28] as well as for depletion [29, 30] and adsorption [29, 31, 32] layers of rigid ‘particles’ in front of the two bilayer leaflets. Particularly interesting ‘particles’ are provided by BAR-domain proteins [31] which can be viewed as Janus nanoparticles with

strongly nonspherical shapes. [33] Experimentally, large spontaneous curvatures have been generated by the asymmetric adsorption of PEG polymers [34], by the asymmetric membrane insertion of the glycolipid GM1 [35, 36], and by the asymmetric adsorption of a water-soluble azobenzene derivative [37]. Compared to phospholipids, glycolipids such as GM1 have a bulky head group. Molecular dynamics simulations have shown that relatively small compositional asymmetries of lipids with bulky head groups can generate very large spontaneous curvature. [38]

Specific interactions between membranes

Biological membranes interact via membrane-anchored receptors and ligands (or ‘stickers’) the length of which is typically large compared to the thickness of the bilayer membrane. In order to study these specific interactions theoretically, it is useful to introduce occupation variables for the membrane-anchored molecules and to integrate over these variables. [39] In this way, one obtains effective interaction potentials for the membranes that take the spatial patterns of receptors and ligands into account. This approach has been extended to describe the clustering and pattern formation of bound receptor-ligand pairs as observed within immunological synapses [40, 41]. In addition, the same approach has revealed that the receptor-ligand binding is cooperative and leads to a quadratic dependence of the receptor-ligand concentration $[RL]$ on the individual receptor and ligand concentrations $[R]$ and $[L]$. [42, 43, 44] Cooperative binding has been recently observed for the interactions between the ‘marker of self’ protein CD47 and the macrophage receptor SIRP α . [45]

Molecular simulations of bilayer membranes

Membranes are built up from lipid bilayers, the structure of which can be studied and visualized by molecular simulations. An optimal packing of the membrane molecules leads to bilayer states with (almost) zero membrane tension, which can be obtained from the anisotropic pressure tensor of the membrane. [46, 47] In addition, the simulated spectrum of shape fluctuations implies that membrane curvature emerges on length scales that exceed about twice the membrane thickness. [48] Molecular simulations are particularly useful for membrane processes that involve non-bilayer or strongly perturbed bilayer structures. One important example is membrane fusion for which several pathways with different transition states have been discovered in molecular simulations. [49, 50, 51, 52, 53] Recent simulation studies have focussed on computing the spontaneous curvature for asymmetric bilayers from their stress profiles. [32, 30, 36, 38]

Wetting of membranes by aqueous phases

Aqueous two-phase systems containing, e.g., PEG and dextran, undergo phase separation into two liquid phases. The interfacial tension between these two phases can be ultralow, reflecting the vicinity of a critical demixing point. When GUVs are exposed to these phases, a variety of wetting morphologies can be observed. [54, 55, 34, 56, 57] Quite unexpectedly, transitions from complete to partial wetting have been observed for all lipid compositions studied so far. [54, 34] For partial wetting, the capillary forces generated by the liquid-liquid interfaces lead to strong deformations of the membrane shape, even for ultralow interfacial tensions. Indeed, when viewed with an optical microscope, this shape consists of three spherical caps that meet at an apparent contact line. [57] On suboptical scales, the membrane should be smoothly curved and characterized by an intrinsic contact angle, which satisfies a relatively simple force balance equation for negligible spontaneous curvatures [55] but a fairly complex one for significant spontaneous curvatures [57]. For certain parameter regimes corresponding to small or large spontaneous curvatures, the apparent contact angles can be directly related to the tensions experienced by the different membrane

segments in contact with the different aqueous phases. [57]

Ambience-induced segmentation of membranes

A multi-component membrane that is partially wet by two aqueous phases is exposed to two different environments, which act to enrich or deplete certain molecular components of the membrane. As a result, the membrane is partitioned into two different types of segments that differ in their composition and thus in their elastic properties, which provides an example for ambience-induced segmentation of the membrane. [33] An analogous segmentation is obtained for a GUV that adheres to a rigid surface or to another membrane. [58, 59] Likewise, membrane segments can be created by protein coats as in clathrin-mediated endocytosis. [60] One interesting prediction for ambience-induced segmentation is that lipid phase separation and domain formation can occur in each individual segment separately but not in all segments at the same time. [58, 59, 33] Experimentally, the clearest examples for ambience-induced segmentation are provided by the partial wetting of GUVs by phase separated PEG-dextran solutions. In the latter case, the membrane segments in contact with the PEG-rich phase form membrane nanotubes whereas the segments in contact with the dextran-rich phase form no such tubes. [61, 34]

Spontaneous tubulation and spontaneous curvature

The spontaneous formation of membrane nanotubes, in the absence of external forces, directly implies that the corresponding membrane segment has a spontaneous curvature that is large compared to the inverse size of the segment. [31] Spontaneous tubulation was first observed for vesicles in asymmetric PEG-dextran [61, 34] and in PEG-sucrose [34] solutions. The formation of nanotubes has also been observed for phospholipid membranes doped with the glycolipid GM1 [35, 36] and for GUVs with charged membranes formed by electroformation [62] The morphology of tubulated GUVs can be analyzed in a systematic manner in order to deduce the spontaneous curvature of the vesicle membranes. Several different methods have been developed. Three methods are based on curvature elasticity alone: estimates of the tube width from the measured tube area and total tube length [34]; initial aspiration by micropipettes [35]; and pulling tubes by optical traps [31, 36]. A fourth method applies to tubulated GUVs that are partially wetted by two aqueous phases. [31, 34, 57] The latter method deduces the spontaneous curvature from the total membrane tension which can be obtained from the apparent contact angles and which is dominated by the spontaneous tension as follows from the presence of nanotubes.

Morphological complexity for large spontaneous curvatures

The morphologies that arise from the spontaneous tubulation of GUVs as observed in [34] and [35] are quite diverse, involving both nanobuds as well as short and long nanotubes. This complexity can be understood from the competition of two morphological transitions or bifurcations. Indeed, when we reduce the vesicle volume by a certain amount, the vesicle membrane can either form a new bud or can extend an existing bud or necklace. As we continue to decrease the volume in a step-wise manner, we create more and more “small ballons” or spherules which can be arranged in many different ways corresponding to different sequences of the two types of bifurcations. [63, 64] As a consequence, we obtain a rugged free energy landscape with multiple degenerate ground states and many metastable states. [64]

Double-membrane vesicles and autophagosomes

Many intracellular organelles such as autophagosomes are enclosed by double-membranes, i.e., by two lipid/protein membranes that are separated by a thin water layer. The initial morphology of these double-membrane organelles of

ten corresponds to an essentially flat pancake-like shape, which then closes up to form a double-membrane vesicle (or thin stomatocyte). [65, 66] The closure process is primarily driven by the spontaneous curvature of the rim of the double-membrane ‘pancake’, which can be controlled by the adsorption or desorption of proteins.

Membrane engulfment and endocytosis of nanoparticles

The adhesion and engulfment of nanoparticles by membranes is essential for many research fields such as biomedical imaging, drug delivery, nanotoxicity, and viral infection. A first theoretical study of particle engulfment was performed in [29] for zero spontaneous curvature. However, the magnitude of the spontaneous curvature, which can be positive or negative, has a rather strong effect on the engulfment process. [60, 67] Indeed, depending on the sign and magnitude of the spontaneous curvature, the engulfment process can proceed continuously via states of partial engulfment or discontinuously via a bistable engulfment regime. Furthermore, if one considers membrane domains with a protein coat that induces a certain preferred curvature, one obtains a quantitative description for the nonmonotonic size dependence of clathrin-dependent endocytosis [60] as experimentally observed in [68]. The endocytosis of nanoparticles consists of three steps: adhesion, complete engulfment, and scission of the closed membrane neck. The theoretical work in [60, 67, 69] implies that all three steps are governed by *local* stability conditions. Furthermore, theory also predicts that partially engulfed nanoparticles experience curvature-induced forces that push the particles towards curvature maxima or minima of the vesicle membrane. [70]

Formation and stability of membrane necks

During the complete engulfment of a nanoparticle, the membrane segment that is bound to the particle is still connected to the mother vesicle by a closed membrane neck. Such necks, which represent a particularly intriguing consequence of curvature elasticity, are also formed during the budding of GUVs [7, 16, 71] and play an essential role for many cellular processes such as endo- or exocytosis and cytokinesis during cell division. The stability of closed necks against neck opening is described by relatively simple conditions, as theoretically derived for uniform membranes [6, 63], intramembrane domains [13], and the complete engulfment of nanoparticles [60, 67]. These stability conditions have been generalized to include a variety of adhesive substrates as well as local constriction forces. [69] Recently, these conditions have also been applied to the adhesion-induced fission of membrane necks by ESCRT proteins. [72]

Giant vesicles with increased robustness

Conventional GUVs have only a limited capability to cope with mechanical perturbations such as osmotic inflation, adhesion, or micropipette aspiration that tend to stretch and rupture their membranes. Recently, it has been shown that the formation of nanotubes strongly increases the robustness of GUVs against such perturbations. [35] Indeed, tubulated GUVs can avoid the molecular stretching and rupture of their membranes by partial retraction of the nanotubes. This property leads to a very low mechanical tension of the GUV membranes and to a total membrane tension that is dominated by the spontaneous tension as predicted in [31]. A different method to stabilize GUVs is based on water-in-oil emulsion droplets. [73] Using microfluidic pico-injection, such a droplet can be loaded with small vesicles. Strong adhesion of these vesicles to the water-oil interface leads to vesicle rupture, and the resulting membrane patches subsequently fuse to form a GUV in contact with this interface. In a subsequent phase transfer step, the droplet-stabilized GUVs can be released into an aqueous bulk solution. [73] The advantage of the microfluidic method

is that one obtains a large population of monodisperse GUVs, the size of which can be directly controlled by the size of the emulsion droplets.

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3. Biomolecular Motors and Nanomachines

Chemomechanical coupling of cytoskeletal motors

Molecular motors are able to convert the chemical free energy released from nucleotide hydrolysis into mechanical work. This chemomechanical coupling exhibits some universal features [1] and has to satisfy several thermodynamic constraints in the form of balance conditions for the possible enzymatic pathways or motor cycles. [2, 3] In fact, molecular motors with several catalytic domains are governed by several competing motor cycles as has been explicitly shown for kinesin. [4, 3] The chemomechanics of two elastically coupled motors leads to rather complex chemomechanical networks, which involve, however, only two parameters in addition to those that describe the activity of a single motor. [5]

Traffic of molecular motors and cargo particles

The cytoskeletal filaments of eukaryotic cells are typically crowded by cargo particles that are pulled by molecular motors. Each cargo particle undergoes directed motion on the filaments and diffusive motion in the surrounding medium. The resulting exclusion processes lead to a build-up of traffic jams [6, 7], to active pattern formation [6, 7, 8] characterized by steady states with spatially nonuniform density and flux patterns, and to genuine traffic phase transitions [7, 9, 10] between different steady states far from equilibrium.

Cargo transport by teams of motors

The cargo transport in cells is usually performed by small teams consisting of several motor molecules. If all motors belong to the same molecular species, their cooperative action leads to uni-directional transport with a strongly increased run length and a characteristic force dependence of the velocity distributions. [11, 12]. The run length may also be enhanced by crosslinking the cargo to the filament via additional molecules that bind to and diffuse along the filament. [13] In general, the motors interfere by mutual strain forces that act to pull the motors from the filament or stall their preferred movement. [14] If two antagonistic species of motors pull on the cargo in opposite directions, they perform a stochastic tug-of-war which leads to several distinct patterns of bi-directional transport. [15] Two important control parameters for such a tug-of-war are the maximal numbers of active plus-directed and active minus-directed motors. [16] The latter numbers can change by motors that hop on to and off from the cargo as observed in kinesin- and dynein-based transport of endosomes. [17] The force balance between two elastically coupled motor teams strongly depends on the unbinding rates of the individual motors. [18]

Filament transport by solid-supported motors

The interactions of cytoskeletal motors and filaments can also be studied by gliding (or motility) assays, in which the motors are immobilized on solid surfaces and act to pull the filaments along these surfaces. As one increases the surface density of the filaments, these systems undergo isotropic-nematic phase transitions. [19] The nematic ordering is enhanced by increasing the motor density because the motors lead to an effective lengthening of the filaments. The transport of individual filaments by two species of motors, slow and fast ones, leads to different motility regimes with distinct transport patterns [20], in close analogy to the stochastic tug-of-war between two antagonistic teams of motors [15].

(De)polymerization of actin filaments

Actin filaments grow and shrink by attachment and detachment of G-actin monomers at the two filament ends. These processes, which can be studied by Brownian Dynamics simulations [21, 22], are coupled to nucleotide hydroly-

ysis, a two-step process consisting of ATP cleavage and phosphate release. In principle, both processes could be cooperative, i.e., could depend on the local neighborhood of the subunit or protomer in the filament. [23] Recent single filament experiments provide strong evidence, however, that phosphate release represents a random, non-cooperative process. [24, 25] Furthermore, a systematic theoretical analysis of the experimental data on intermittent depolymerization of actin filaments revealed that this process is caused by photo-induced dimerization of actin protomers. [26] Each interruption of depolymerization represents the delayed dissociation of a single actin dimer, a single molecule event that can be directly observed in the optical microscope.

Ribosomes and protein synthesis

Ribosomes are complex molecular machines that translate the codon sequences of mRNA molecules into amino acid sequences, the primary structure of proteins. This translation process involves numerous ribosomal states and individual transitions that can be studied in vitro but not in vivo. A general computational method has been recently developed by which one can deduce the in-vivo rates from their in-vitro values. [27, 28] The deduced rates have been validated by three independent sets of in-vivo data. Other interesting aspects of translation are provided by the formation of polysomes, i.e., the simultaneous translation of the same mRNA by several ribosomes and by the relatively short life time of the mRNA. [29] This aging effect leads to translation rates that decrease with increasing mRNA length [30] and to a non-exponential decay of mRNA numbers [31]. The stochastic modelling of the translation process has been recently extended to analyze the co-translational motion of the nascent peptide chain into the exit tunnel of the ribosome. [32] This analysis revealed that the kinetics of translation of the same codon depends on the position of the codon within the mRNA.

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4. Additional Fields of Interest

Conformations of semi-flexible polymers

On molecular scales, semi-flexible polymers behave as semi-rigid rods that keep their spatial orientation up to the so-called persistence length. On larger length scales, the polymers lose their orientation and attain random coil conformations. This behavior implies a renormalized, scale-dependent bending stiffness that decays to zero on large scales. [1] When a weak stretching force is applied to a semi-flexible polymer, it primarily acts to reduce the amplitude of thermally excited shape fluctuations. A strong stretching force, on the other hand, probes the molecular bonds between the monomers or subunits of the polymer. The full range of forces is covered by the semi-flexible harmonic chain model [2], which was originally introduced for the hydrocarbon tails of lipid molecules [3]. When a compressive force is applied, the semi-flexible polymer undergoes a buckling (or Euler) instability at a critical buckling force, which is also affected by thermal fluctuations. [4, 5] A rather interesting class of semi-flexible polymers is provided by oligo- and polysaccharides. Even though the backbone of an oligosaccharide assumes an essentially straight conformation in the absence of external forces, it can be easily bent by forces of physiological magnitude as revealed by molecular simulations. [6, 7]

Unbinding transitions of filament bundles

Semi-flexible polymers such as cytoskeletal filaments form long bundles, in which the filaments are essentially parallel to each other. These bundles are stabilized, e.g., by attractive van der Waals forces or molecular crosslinkers. The competition between these attractive interactions and the entropy loss of the confined filaments leads to unbinding or unbundling transitions as one increases the temperature or decreases the concentration of the molecular crosslinkers [8], in close analogy to the unbinding transitions of interacting membranes [9, 10]. The critical behavior of two interacting filaments in $1 + d$ dimensions can be obtained exactly from the fluctuations of the unbound filaments via a duality relation. [11] Thicker bundles containing more than two filaments exhibit different morphologies, including kinetically trapped states consisting of several sub-bundles, but undergo a single transition, at which all filaments unbind simultaneously. [8] At this transition, the bundle thickness changes in a discontinuous manner whereas other bundle properties exhibit scaling laws characterized by critical exponents, in agreement with recent experiments [12].

Dynamical processes on networks

Networks composed of vertices (or nodes) and edges (or links) provide a general theoretical framework for the representation of many different systems. First, any system with a discrete state space can be viewed as a network, in which the vertices represent the different states of the system and the edges correspond to possible transitions between these states. One example is provided by network representations of molecular motors. [13, 14] Second, composite systems that consist of many different but similar components can also be viewed as networks, in which the vertices represent the different components and the edges correspond to “interactions” between these components. In general, the different components of the system can attain several internal states that evolve with time. The simplest case is provided by binary variables that can be active or inactive. [15, 16, 17, 18, 19] At any given time, the state of the composite system is then characterized by an activity pattern of the network, and the system’s dynamics is described by the time evolution of this pattern. Depending on the initial pattern, the system will reach one of the dynamical attractors that govern the system’s long-time behavior. Scale-free networks without degree-degree correlations are characterized by only two stable fixed points [15, 16]. In contrast,

degree-degree correlations within these networks lead to a large number of fixed points and limit cycles [17] and to sequences of genuine phase transitions [19].

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