Dense Active Matter

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Dense Active Matter

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Article Outline

Properties of dense systems of active objects with self-propulsion are reviewed with emphasis on glassy behavior and jamming. Experimental realizations of such systems are pointed out, and the effects of the presence of self-propulsion forces on the properties of passive glass-forming liquids are discussed, with special attention to the dependence of the observed behavior on the strength and persistence time of the self-propulsion force. Results obtained from theoretical and numerical studies of simple models of dense active systems are summarized and compared with the results of experimental studies.

Glossary

Active matter Collection of objects with self-propulsion forces.

Cytoplasm Viscous fluid that fills the inside of a cell.

Epithelial sheet Single layer of cells with every cell in direct contact with the membrane that separates it from the underlying connective tissue.

Fragility A parameter that quantifies the rate of growth of the viscosity of a liquid with decreasing temperature or increasing density.

Glass Disordered solid obtained by rapidly cooling or compressing a liquid.

Persistence time Timescale of decorrelation of the direction of the self-propulsion force.

Strength of activity Magnitude of typical self-propulsion force.

Why Study Active Matter?

Active matter consists of objects that can convert internal or ambient sources of energy into systematic motion (Schweitzer 2003). It includes any nonequilibrium condensed matter system, whether it is composed of living or nonliving matter, in which "self-propulsion" forces are present. Experimentally studied active matter includes living systems such as flocks of birds (Cavagna and Giardina 2014), schools of fish (Katz et al. 2011), swimming bacteria (Wolgemuth 2008; Peruani et al. 2012), migrating cells, (Angelini et al. 2011) and molecular motors (Kodera et al. 2010), as well as synthetic nonliving examples such as vibrated granular matter (Kumar et al. 2014), self-propelled colloids (Jiang et al. 2010; Buttinoni et al. 2013), magnetic nanopropellers (Ghosh and Fischer 2009), Quincke rollers (Bricard et al. 2013, 2015), and swimming microrobots (Peyer et al. 2013). Since active systems are characterized by self-propulsion forces that do not arise from interparticle interactions, they are outside thermodynamic equilibrium (Ramaswamy 2010; Marchetti et al. 2013). These systems have received a lot of attention in recent years because they exhibit novel collective behavior (Ramaswamy 2010; Marchetti et al.

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2013; Bechinger et al. 2016), such as flocking (Toner and Tu 1998), giant number fluctuation (Ramaswamy 2010), motility induced phase separation (Cates and Tailleur 2015), and active turbulence (Thampi and Yeomans 2016).

Definition of the Subject

In this entry, we consider dense active systems that exhibit glassy behavior or jamming (Janssen 2019; Berthier et al. 2017). When a liquid is cooled sufficiently fast so that crystallization is avoided, it enters a supercooled liquid state which, upon further cooling, undergoes a transition to an amorphous solid state that is called a glass (Binder and Kob 2011). A similar phenomenology is found when a system of hard particles is compressed sufficiently fast. The supercooled liquid state near the glass transition exhibits many interesting properties (Berthier and Biroli 2011), the most remarkable among these being a rapid growth of the viscosity and the structural relaxation time with decreasing temperature or increasing density. This growth is faster than Arrhenius in "fragile" liquids and follows the Arrhenius form in "strong" liquids (Angell 1995). Jamming, on the other hand, refers to a purely geometrical process in which the freedom of movement of the constituting particles is lost. When a system of particles without thermal fluctuations is compressed from a low density, it undergoes a jamming transition (Liu and Nagel 2010) at which macroscopic rigidity sets in. We focus on how the behavior of dense systems near the glass or jamming transition is modified by the presence of activity. Aligning interactions that may induce flocking behavior (Cavagna and Giardina 2014) are not considered and hydrodynamic interactions between active particles are neglected.

Experimental Studies

Glassy dynamics has been observed in a variety of active biological systems. Several experimental studies (Zhou et al. 2009; Nishizawa et al. 2017; Parry et al. 2014) have revealed the occurrence of glassy dynamics in the cytoplasm of cells. These studies show a transition from a fluid state to a glass as the strength of activity is reduced. Activity is also found to decrease the fragility (Angell 1995) of the liquid state. Similar results have been obtained in a study of the dynamics of micron-size particles embedded in cell nuclei (Hameed et al. 2012).

Another class of dense active systems that has received a lot of experimental attention consists of two-dimensional epithelial sheets and three-dimensional assemblies of cells. Angelini et al. (2011) have presented evidence for fragile glass-like behavior in confluent epithelial monolayers of Madin-Darby Canine Kidney (MDCK) cells. Garcia et al. (Garcia et al. 2015) have found evidence for a jamming transition in a monolayer of human bronchial epithelial cells. Recently, Henkes et al. (2020) have shown that displacement and velocity correlations in epithelial monolayers are reminiscent of those in supercooled liquids. A connection between a liquid-to-glass transition in layers of human bronchial epithelial cells and the occurrence of asthma has been demonstrated in the work of Park et al. (2015). Signatures of glassy dynamics have also been observed in three-dimensional collections of cells in embryogenesis (Schötz et al. 2013), wound healing (Vishwakarma et al. 2020), and metastasis of cancer (Palamidessi et al. 2019).

A recent study (Klongvessa et al. 2019a, b) of glass transition in synthetic active matter has considered two-dimensional layers of Janus colloids (gold particles half-coated with platinum) in which self-propulsion forces are controlled by the concentration of hydrogen peroxide. The main result of this study is the observation that the relaxation time decreases with increasing activity if the packing fraction is not very large. On the other hand, if the packing fraction is very large, such that the dynamics is nonergodic in the absence of activity, then the introduction of activity is found to slow down the dynamics. This slowing down is followed by fluidization at higher activity.

Models

Theoretical and numerical studies of dense active systems have been carried out mostly for particle-based models. The simplest particle-based model, known in the literature as Active Brownian Particles (ABPs) (Romanczuk et al. 2012), consists of particles with spherically symmetric interactions. Activity in the system is modeled by a random self-propulsion force with magnitude f and persistence time τ_p that describes the timescale of decorrelation of its direction. The overdamped equations of motion of the constituent particles in the ABP model in two dimensions are given by

$$\begin{aligned} \gamma \dot{\mathbf{x}}_i &= \sum_{j \neq i} \mathbf{f}_{ij} + f \mathbf{n}_i + \mathbf{y}_i, \\ \dot{\theta}_i &= \xi_i, \end{aligned} \tag{1}$$

where γ is a friction coefficient, $\mathbf{f}_{ij}$ is the force exerted on particle i by particle j, $f\mathbf{n}_i$ is the self-propulsion force, and $\mathbf{y_i}$ is a thermal noise with zero mean and variance $2k_BT\gamma\delta(t–t_0)$ that obeys the fluctuation-dissipation relation (T is the temperature and k_B is the Boltzmann constant). The direction $\mathbf{n}_i \equiv (\cos\theta_i, \sin\theta_i)$ of the stochastic self-propulsion force undergoes rotational diffusion described by the noise ξ_i with zero mean and correlation $\langle \xi_i(t)\xi_j(t')\rangle = 2\tau_p^{-1}\delta_{ij}\delta(t-t')$. Its effect on the x_i-dynamics is that of an exponentially correlated vectorial noise with correlation time τ_p. In Brownian dynamics simulations, these equations of motion are numerically integrated forward in time. In simulations of glassy behavior, one typically considers binary mixtures or poly-disperse systems in order to avoid crystallization. Models of active rod-like particles, such as dumbbells, have also been considered in simulations (Mandal et al. 2017). The self-propulsion force in such models is usually assumed to have a fixed magnitude f, and to act along the long axis of each rod-like particle. The persistence time of the active force is not an independent variable in these models – it is determined by system parameters such as the density, the temperature, and the strength f of the active force.

Studies of the collective dynamics of living cells in tissues involve a different class of models. These models are different from the particle-based models described above in that the cells in these models cover the entire space without any gap between neighboring cells. In vertex models (Bi et al. 2015; Barton et al. 2017) of confluent layers of epithelial cells, the cells are represented as polygons that share edges. The energy of a collection of cells is defined in terms of the areas and perimeters of these polygons. Activity is incorporated in the model by the addition of a velocity of fixed magnitude and random direction in the equation of motion of the cells. Variants of the vortex model include the Voronoi model (Bi et al. 2016) and the cellular Potts model (Chiang and Marenduzzo 2016).

Numerical Studies

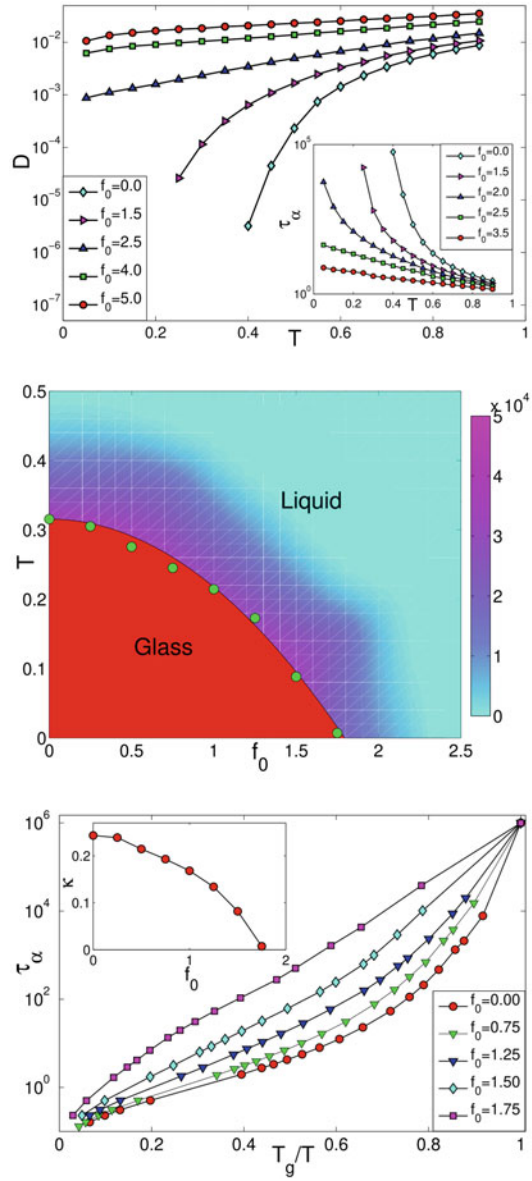
Similar to other domains in soft matter, computer simulations have been very useful to study structural and dynamical behavior of active matter systems. The standard procedure has been to consider conventional models of passive liquids whose phase behavior has been extensively characterized and introduce activity in these model systems to study how the known properties get modified. One of the first numerical studies (Ni et al. 2013) involved probing the effects of activity on the slow dynamics of a three-dimensional hard sphere system. A similar study (Berthier 2014) was carried out at about the same time for a two-dimensional system of hard disks. In both cases, it was observed that with increasing activity, the relaxation timescale decreases, at any packing fraction, which consequently pushes the glass transition density to higher values.

The effects of including activity in a well-studied model glass former, viz. the Kob-Andersen binary Lennard-Jones mixture (Kob and Andersen 1994), were studied in Ref. (Mandal et al. 2016) wherein active forces were assumed to be present for one of the constituent species. The active particles were randomly assigned self-propulsion forces of fixed magnitude f_0, chosen such that there is conservation of

the net momentum of the system. After a persistence time τ_p the directions of the active forces were randomized, while maintaining momentum conservation. The dynamical properties of this system at different temperatures were probed via the mean-square-displacement (MSD) of tagged particles, $\langle|\Delta \mathbf{r}(t)|^2\rangle$, and the self-overlap function, $Q(t)$. Relatively small values of τ_p were considered in this study.

In the absence of activity, the glass-forming mixture is a liquid at high temperatures. With the lowering of temperature, the diffusion coefficient, D, extracted from the MSD decreases, along with the increase in the relaxation timescale, τ_α, extracted from the decay of $Q(t)$. A glass transition temperature for the system can be estimated by fitting τ_α to the well-known Vogel-Fulcher-Tammann (VFT) form, $\tau_\alpha = \tau_\infty \exp\{1/(\kappa(T/T_{\rm VFT}-1))\}$, where κ is the kinetic fragility, τ_∞ is the relaxation time at high temperatures, and $T_{\rm VFT}$ is identified as the putative glass transition temperature.

In the presence of active forcing, the dynamics gets accelerated and the temperature dependence of the diffusion coefficient becomes weaker. This is illustrated in the top panel of Fig. 1 where the temperature dependence of the long-time diffusion coefficient D has been shown for different values of f_0. Similarly, the temperature dependence of the relaxation timescales, τ_α, shows a weaker increase with decreasing temperature as f_0 is increased. The phase diagram in the middle panel of Fig. 1 shows the values of $T_{\rm VFT}$ for different values of f_0, as extracted via VFT fits of the data for the relaxation time τ_α. It shows that even in the presence of finite activity, there is a thermal threshold below which the glassy regime is obtained. However, this threshold vanishes at high enough active forcing. This is qualitatively different from the behavior found in Refs (Berthier 2014). and (Ni et al. 2013) in which a (putative) glass transition was found to be present for all finite values of the strength of the activity. This important observation tells us that some of the effects of activity on the glass transition are sensitive to the nature of the system (whether controlled by temperature or density) and the details of the self-propulsion mechanism.

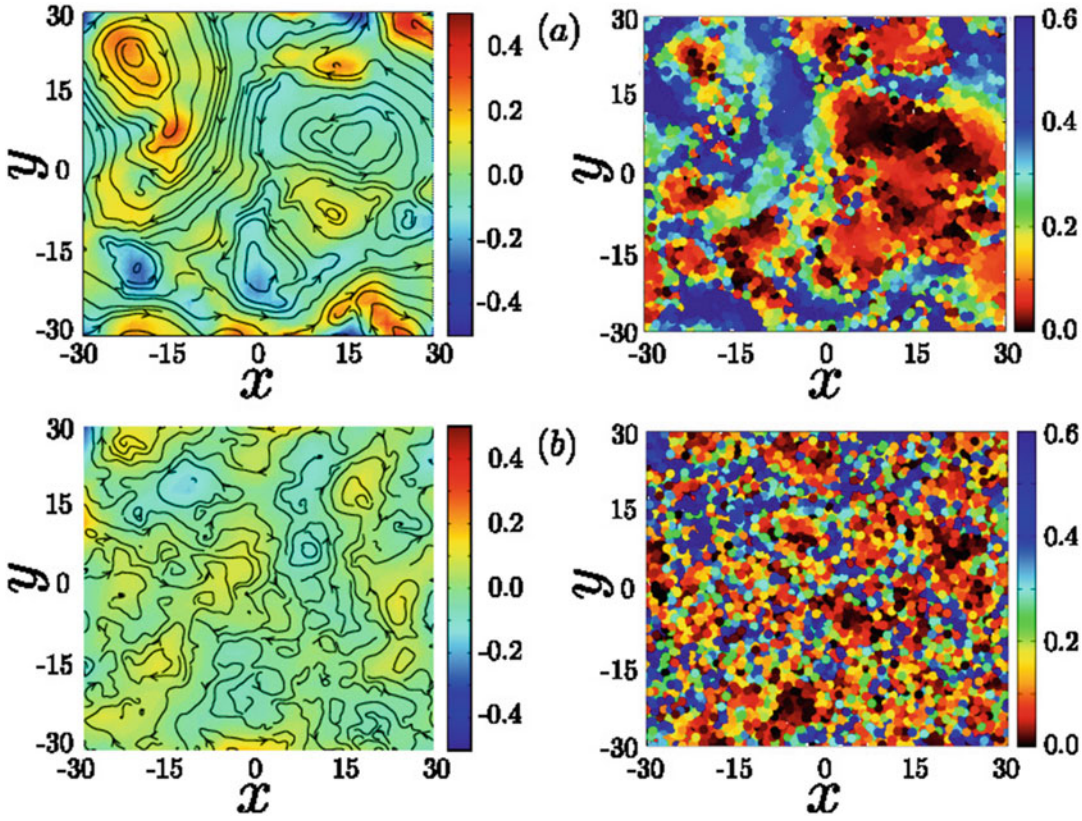


Dense Active Matter, Fig. 1 Effect of activity on a three-dimensional glass-forming liquid (Kob-Andersen binary Lennard-Jones mixture) (Adapted from Ref. Mandal et al. 2016). (Top) Diffusion coefficient (D) vs temperature (T) for $\tau_p = 4.0$ and different active forcing (f_0), as marked. The inset shows the corresponding relaxation timescales, τ_α. (Middle) Phase diagram in the T–f_0 plane. The color indicates the value of τ_α according to the colorbar. (Bottom) Angell plot, showing variation of τ_α with T_g/T for different f_0

Another interesting observation regarding the effect of activity on glassy dynamics is the

decrease of kinetic fragility of the liquid with increasing activity. This is illustrated via the so-called "Angell plots," shown in the bottom panel of Fig. 1, where one plots τ_α vs T_g/T, T_g being the analog of the experimentally determined glass transition temperature at which the viscosity is 10^{13} poise, obtained from the definition $\tau_\alpha(T_g) = 10^6$. The curvature of the plots gives us a measure of the fragility, κ, which is seen to decrease with increased forcing as shown in the inset of the bottom panel of Fig. 1.

The question of whether the dynamics in passive and active supercooled liquids are different was investigated in Ref. (Mandal et al. 2017) using a two-dimensional dense assembly of self-propelled dumbbells. Specifically, maps of the displacement field of the center of mass of the dumbbells were computed for state points in the (T–f_0) plane having similar relaxation timescales. In the passive limit, these maps do not reveal any spatial structures or correlations. As one increases the strength of the activity along the iso-relaxation time line, vortex-like structures become visible (see Fig. 2) and the size of these vortices increases with increasing activity. Further, the displacement maps, constructed over the structural relaxation timescales, show that the active system exhibits more dynamical heterogeneity than the passive one. The correlation lengths associated with these spatial structures increase as one moves along the path of iso-relaxation timescales in the direction of increasing activity

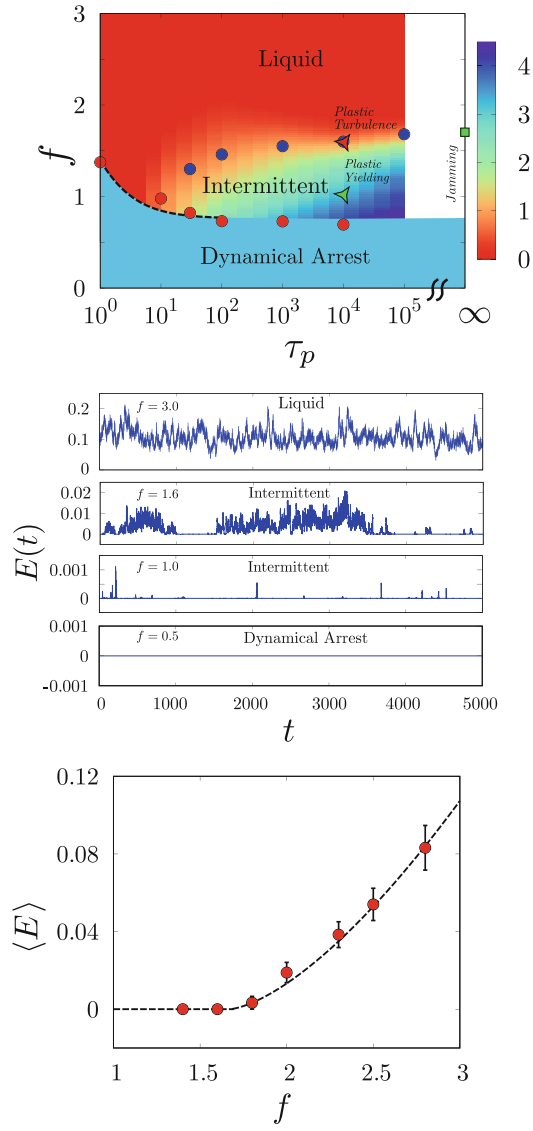


Dense Active Matter, Fig. 2 Active vs passive supercooled liquid (Adapted from Ref. Mandal et al. 2017). (left) Streamlines of displacement field computed over the relaxation timescale τ_α with the underlying colormap reflecting the corresponding values of the spatially varying vorticity. (right) Map showing the magnitude of displacement during the same time window, with blue particles being the fastest and black particles being the slowest. The top panel corresponds to the active system displaying large-scale vortical structures and extensive spatial heterogeneity, in contrast to the passive system shown in the bottom panel

(Mandal et al. 2017). The observed swirling patterns are similar to structures observed in active turbulence exhibited by a fluid of active rods (Wensink et al. 2012; Giomi 2015), and it is possible that the dynamical heterogeneity exhibited by the active glass is a remnant signature of the turbulent fluid.

More recently, an interesting emerging direction of investigation in active glassy matter has been the so-called extreme limit wherein the magnitude of the propulsion force f is higher than that of interparticle or thermal forces and the direction of the propulsion force persists over times τ_p longer than characteristic relaxation times of the system in the absence of activity. This aspect has been numerically explored (Mandal et al. 2020) using a two-dimensional athermal assembly of soft-interacting active Brownian particles, each of mass m and driven by a stochastic self-propulsion force $f = f\mathbf{n}$ whose direction $\mathbf{n}$ undergoes rotational diffusion. Extreme activity is attained when (a) the magnitude of the active force is larger than both thermal forces and the typical force exerted on a particle by the other particles, and (b) the persistence time τ_p is larger than the characteristic relaxation time of the system in the absence of activity. In the athermal limit, condition (b) above is replaced by $Pe \gg 1$ where Pe is an active Péclet number defined as $Pe \equiv f\tau_p/(\gamma\sigma)$ (γ is a friction coefficient and σ is the particle size).

For small values of τ_p, as was discussed earlier, the system transforms from a fluid at high f to a glassy state at low f. The phase boundary is well described by an active generalization of RFOT theory (see Section VII). This is illustrated in the phase diagram shown in the left panel of Fig. 3. For intermediate values of the persistence time $\tau_p \gtrsim 10^3$, the variation of the time series of the system's kinetic energy with changing active force marks the evolution of the system through different dynamical regimes; see the middle panel of Fig. 3. At large forcing, it shows random fluctuations. However, as the forcing is decreased, the time series starts becoming intermittent, with periods of bursts followed by quiescence. The gap between these periods of bursts increases with decreasing forcing, and eventually the system gets dynamically arrested as f is decreased even further. The single particle dynamics become



Dense Active Matter, Fig. 3 Extreme active matter (Adapted from Ref. Mandal et al. 2020). (top) Phase diagram showing different dynamical regimes in the persistence time τ_p vs active forcing f plane. (middle) Time series of kinetic energy, $E(t)$, showing increasing intermittency with decreasing f, for $\tau_p = 10^4$. (bottom) In the limit of infinite persistence time, variation of the mean kinetic energy, $\langle E\rangle$, with forcing f. The system transits to a jammed state as f is decreased below $f^*(\infty) = 1.6$, with $\langle E\rangle \sim |f - f^*(\infty)|^{3/2}$ near $f = f^*(\infty)$

more heterogeneous as the phase boundary is crossed (Mandal et al. 2020). Deep inside the intermittent phase, the spikes in the time series of the kinetic energy correspond to the occurrence of local plastic events resulting from the local shear induced via the internal stirring at the scale of the active particles (Mandal et al. 2020).

An interesting limit is the case of infinite persistent time of the active particles, that is, where the direction of the active force on each particle does not change with time. In this limit, above a threshold forcing, $f^*(\infty)$, the system of particles behaves like a fluid, and below this threshold, it reaches an arrested state, consistent with similar observations in the vicinity of the jamming transition for soft harmonic disks (Liao and Xu 2018). On the approach to this arrested state, corresponding to the formation of a force-balanced configuration (Mandal et al. 2020), the kinetic energy vanishes as $\sim|f - f^*(\infty)|^{3/2}$; see the right panel of Fig. 3. A similar yielding transition was also observed (Morse et al. 2020) for the case of athermal quasi-static persistent random displacement, whereby a link to the response under macroscopic shear has also been outlined.

Further studies have tried to explore the aging dynamics in the presence of activity (Janssen et al. 2017), and different aging behavior has been observed for small and large persistence times (Mandal and Sollich 2020), with the former more similar to aging observed during thermal quenches and the latter exhibiting a two-step process with active athermal aging at short times and activity-driven aging at late times.

Theoretical Studies

Most theoretical studies of dense active matter are based on modifications of theoretical descriptions of passive glass-forming liquids (Berthier and Biroli 2011; Lubchenko and Wolynes 2007) to include the effects of activity. The nonequilibrium nature of active systems is not explicitly taken into account in these descriptions. The simplest among these is the "effective temperature" description (Fily et al. 2014) in which the effects of active forces are represented in terms of an "active temperature" that adds to the bath temperature. The active force $f\hat{\mathbf{n}}_i$ in Eq.(1) differs from the thermal noise $\mathbf{y_i}$ in that it has a nonzero correlation time τ_p. If τ_p is small compared to the characteristic timescales of the system, then the active force can be treated (Mandal et al. 2016) as additional thermal noise corresponding to an active temperature T_a that is proportional to $f^2\tau_p$. The behavior of the active system at temperature T is then assumed to be the same as that of the corresponding passive system at effective temperature $T_{eff} = T + T_a$. A similar expression for the effective temperature may be obtained from an exact analytic treatment (Mandal et al. 2016; Szamel 2014) of the overdamped dynamics of a particle in a harmonic potential in the presence of an active force with correlation time τ_p. This simple description provides a qualitative understanding of several simulation results (Mandal et al. 2016) obtained for relatively small values of f and τ_p. The line drawn through the data points for the transition temperature in the middle panel of Fig. 1 was obtained from this description.

A more detailed description of the dynamics of dense active systems involves an extension (Nandi et al. 2018) of the Random First Order Transition (RFOT) theory (Berthier and Biroli 2011; Lubchenko and Wolynes 2007) of passive glassy dynamics. In the RFOT theory, the structural relaxation time is predicted to diverge at a putative thermodynamic glass transition temperature T_K (also known as the Kauzmann temperature) at which the configurational entropy density s_c associated with the multiplicity of local minima of the potential energy of the system goes to zero. Strictly speaking, s_c is not a well-defined quantity for active systems because they are not in equilibrium. Nevertheless, using a physically reasonable definition of s_c and a mean-field treatment in which the many-particle dynamics is approximated by that of an active particle in a harmonic cage potential produced by its neighbors, an expression for s_c for an active system, characterized by the activity parameters f and τ_p, can be obtained. The dependence of the relaxation time on the activity parameters f and τ_p, obtained by using the expression for s_c in the passive RFOT relation between s_c and the relaxation time, was

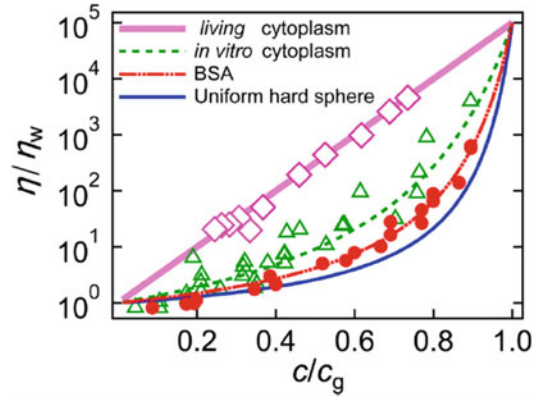
found to provide a good description of the results of several simulations. The dashed line separating liquid and dynamically arrested phases in the phase diagram shown in the left panel of Fig. 3 was obtained from this theory. The active RFOT theory also resolved apparently contradictory results for the effects of activity on the fragility obtained from different simulations. However, substantial deviations of the predicted results from those obtained from simulations were found for relatively large values of f and τ_p. A recent modification (Mandal et al. 2021) of the active RFOT theory to include nonperturbative effects arising from a large f has reduced this discrepancy between analytic and simulation results.

Mode coupling theories (Das 2004) of the dynamics of passive glass-forming liquids have also been extended to include the effects of activity (Szamel et al. 2015; Szamel 2016; Nandi and Gov 2017; Liluashvili et al. 2017; Szamel 2019). These theories start from the microscopic equations of motion or the equations of fluctuating hydrodynamics and make certain uncontrolled approximations to obtain analytic results for various time-dependent correlation functions. For passive glass-forming liquids, mode coupling theories provide an accurate description of the dynamics in the weakly super-cooled regime but fail to describe the behavior at lower temperatures. Several studies have used this formalism to look into the effects of activity on the dynamics. The predictions of these studies on the dependence of the dynamics on the activity parameters seem to depend on the nature of the approximations made in deriving the results, the details of the self-propagation mechanism, and the presence or absence of thermal noise. More work is needed to sort out these issues.

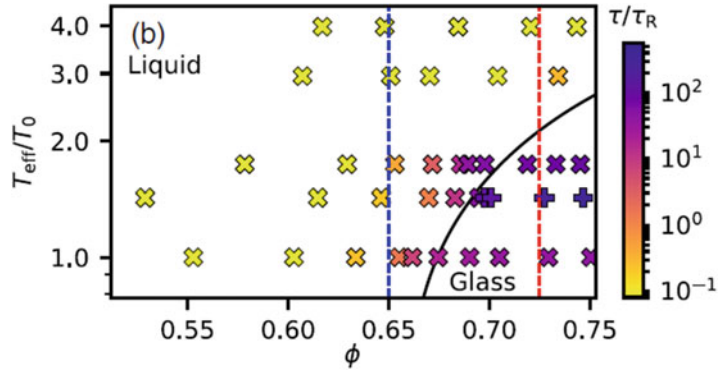
Comparison with Experiments

The simple model systems considered in theoretical studies do not provide a realistic description of biological active matter studied in experiments. Nevertheless, some of the results obtained from analytic and numerical studies of these simple models are found to be qualitatively similar to those of experiments on biological systems. For example, the dependence of the fragility parameter on the strength f of the active force found in simulations (Mandal et al. 2016) (see the bottom panel of Fig. 1) and the active RFOT theory (Nandi et al. 2018) is quite similar to that observed in experiments on in vitro and living cytoplasm (Nishizawa et al. 2017) – in both cases, the fragility decreases as the activity is increased (see Fig. 4). It has been shown in Ref. (Henkes et al. 2020) that several features of experimentally observed displacement and velocity correlations in epithelial cell monolayers can be reproduced in theoretical and numerical studies of simple models. Another example is the observation (Park et al. 2015) of a jamming transition in confluent monolayers of human bronchial epithelial cells at a value of a geometrical parameter associated with cell shapes that is close to the value at which a similar transition occurs in simulations (Bi et al. 2015) of the vertex model mentioned above.

There is a closer connection between theoretical models and experimentally studied systems of synthetic active matter. As shown in Fig. 5, the



Dense Active Matter, Fig. 4 Viscosity (scaled by the viscosity of water) as a function of scaled concentration for BSA – a globular protein – (red circles and the dash-dot-dot curve), for cell extracts from *E. coli* (green triangles and the dotted curve), and for cytoplasm in a living cell (pink diamonds and the solid line). Higher curvature of the plot indicates larger fragility (from Ref. Nishizawa et al. 2017). The dependence of the fragility on activity is similar to that shown in the bottom panel of Fig. 1



Dense Active Matter, Fig. 5 Phase diagram of a two-dimensional system of Janus colloids in the activity (T_{eff}/T_0) vs. packing fraction (ϕ) plane (from Ref. Klongvessa et al. 2019a). The colorbar indicates the value of the relaxation time. Increasing the packing fraction in this system is similar to decreasing the temperature in a thermally driven system. This phase diagram is similar to that in the middle panel of Fig. 1 – activity promotes fluidization in both cases

phase diagram obtained in an experimental study of a system of Janus colloids (Klongvessa et al. 2019a) for which the packing fraction is the control parameter is qualitatively similar to that found in simulations (Mandal et al. 2016) of a model of thermally driven active particles (see the middle panel of Fig. 1). In both cases, the activity is found to promote fluidization in a similar way.

Conclusion and Future Directions

This short review attempts to provide a summary of the current state of affairs in the developing field of dense active matter. The primary interest in studies of dense active matter derives from the biological importance of understanding the behavior of two- and three-dimensional collections of cells. As discussed above, analytic and computational studies of simple models of active matter are beginning to make contact with experiments on cell assemblies. However, there is a need for incorporating biologically important features in these models. Experiments on synthetic active systems that are closer to the theoretical models are also being performed. More effort in this direction would make it easier to connect theoretical predictions with experimental results. On the theoretical side, the behavior of dense active matter with relatively small values of f and τ_p is fairly well-understood. However, there is little theoretical understanding of several interesting features observed in simulations (Mandal et al. 2020) of extreme active matter with large f and/or τ_p. More theoretical work and experiments on extreme active matter would be most welcome.

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