

# Traffic flow of interacting self-driven particles: rails and trails, vehicles and vesicles

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One common feature of a vehicle, an ant and a kinesin motor is that they all convert chemical energy, derived from fuel or food, into mechanical energy required for their forward movement; such objects have been modelled in recent years as *self-driven* “particles”. Cytoskeletal filaments, e.g., microtubules, form a “rail” network for intra-cellular transport of vesicular cargo by molecular motors like, for example, kinesins. Similarly, ants move along trails while vehicles move along lanes. Therefore, the traffic of vehicles and organisms as well as that of molecular motors can be modelled as systems of interacting self-driven particles; these are of current interest in non-equilibrium statistical mechanics. In this paper we point out the common features of these model systems and emphasize the crucial differences in their physical properties.

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## I. INTRODUCTION

In the recent years non-equilibrium statistical mechanics has found unusual applications in research on traffic flow of various different types of objects. In this paper we consider mainly three different examples of such traffic, namely, (a) vehicular traffic [1, 2, 3], (b) ant-traffic on ant-trails [4, 5, 6, 7], and (c) intra-cellular traffic of molecular motors carrying vesicular cargo moving along cytoskeletal filaments [8]. Most of these models are essentially generalizations or extensions of the Asymmetric Simple Exclusion Process (ASEP) [9], which is, to our knowledge, the simplest model of systems consisting of interacting *driven* particles; the general aim of these investigations is to understand the interplay of self-organized *structures* and *transport* in systems driven far from equilibrium [10, 11, 12].

The aim of this article is (a) to summarize the main results of recent works on all the three systems mentioned above, elucidating the nature of various types of quenched randomness, (b) to present the challenging open problems, and (c) to indicate the possible trends of future developments in this frontier area of interdisciplinary research.

The common modeling strategy is to represent the motile elements (i.e., vehicles, ants, molecular motors) by “self-propelled” particles which convert chemical energy (derived from fuel or food) into the mechanical energy required for the forward movement. In such generic models, the mutual influences of the motile elements on the movements of each other are captured by appropriate inter-particle interactions. In the spirit of the lattice gas models, the track for the traffic movement (i.e., the highway lane or ant trail or cytoskeletal filaments) are represented as discrete lattice of “cells” each of which can accomodate at most one particle at a time. The dy-

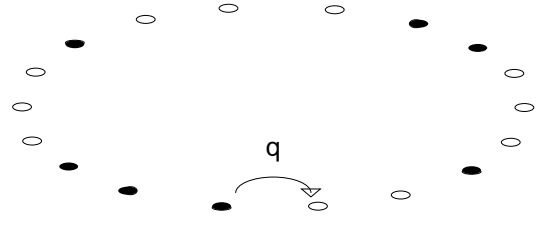


FIG. 1: TASEP with periodic boundary conditions. The hopping probability of the particles is  $q$ .

namical laws governing the forward movement of the self-propelled particles in such “particle-hopping” models are usually formulated as “update rules” in terms of cellular automata (CA) [13].

## II. VEHICULAR TRAFFIC

The simplest model of interacting self-driven particles is the so-called totally asymmetric simple exclusion process (TASEP) [9, 10, 11]. Imposition of open boundary conditions leads to richer physics as compared to those for the corresponding model with periodic boundary conditions. The states of the system are updated either in parallel or in a random-sequential manner following rules which will be explained later in this section.

### A. TASEP with periodic boundary conditions

TASEP with periodic boundary conditions is sketched schematically in fig.1. In the original formulation of TASEP, the states of the system were updated in a random sequential manner where a particle is picked up randomly and moved forward by one lattice spacing, with the hopping probability  $q$ , provided the site in front of the particle is empty.

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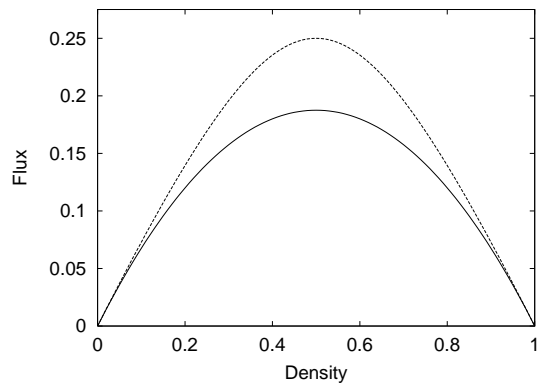


FIG. 2: Fundamental diagrams of the TASEP with periodic boundary conditions and (a) random-sequential updating (solid curve) (b) parallel updating (dashed curve), both for  $q = 0.75$ .

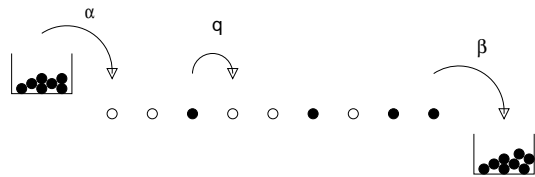


FIG. 3: TASEP with open boundary conditions.

The Nagel-Schreckenberg (NS) model [14] is a minimal CA model of vehicular traffic on idealized single-lane highways; the maximum possible (discrete) speed of the vehicles is  $V_{max}$ . However, in the special case  $V_{max} = 1$  this model reduces to the TASEP with parallel updating.

The exact fundamental diagrams of the TASEP with random-sequential updating and parallel updating are

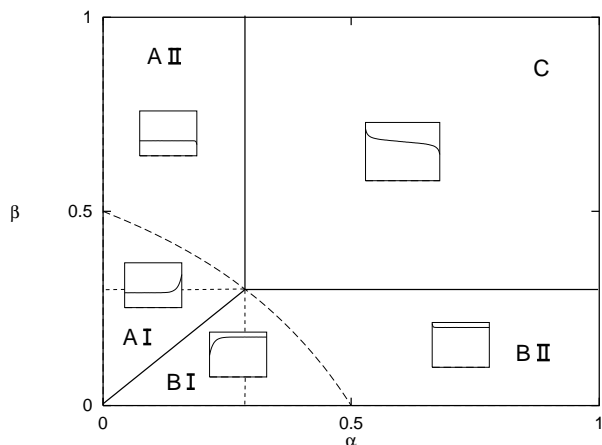


FIG. 4: Phase diagram of the TASEP for *parallel* dynamics. The inserts show typical density profiles.

given by

$$F_r = q c (1 - c) \quad (1)$$

and

$$F_p = \frac{1}{2} \left[ 1 - \sqrt{1 - 4q c (1 - c)} \right], \quad (2)$$

respectively; the two expressions (1) and (2), for identical hopping probability  $q = 0.75$ , are compared in fig.2. Note that both the expressions (1) and (2) exhibit particle-hole symmetry, i.e., these are symmetric under the interchange of  $c$  and  $1 - c$ . In section III we shall show how this symmetry is broken in a model of ant-traffic on ant-trails.

### B. TASEP with open boundary conditions

The open boundary condition is, however, closer to the real vehicular traffic on a stretch of highway. If open boundary conditions are imposed on the TASEP, additional rules must be specified to regulate the entry and exit of the particles at the two boundaries of the finite system. Usually, these are specified as follows: if the first site at the open point of entry is empty it is filled with probability  $\alpha$  whereas particles occupying the last site at the point of exit hop out of the system with probability  $\beta$  (see fig.3).

The open boundaries break the translational invariance of the system and give rise to stationary states with non-trivial density profiles. Such model systems have been investigated thoroughly over the last decade from the point of view of fundamental principles of non-equilibrium statistical mechanics. In contrast to equilibrium systems with short-range interactions, such driven non-equilibrium systems can exhibit transitions from one dynamical phase to another, even in one-dimension with only short-range interactions, with the slight change of boundary conditions [1, 15].

The typical phase diagrams of the TASEP with open boundary conditions are sketched in fig.4; the qualitative features of the phase diagram of TASEP is practically independent of the nature of the dynamics. In the low-density phase A the flux is independent of  $\beta$  and limited only by  $\alpha$ . On the other hand, in the high-density phase B the flux is independent of  $\alpha$  and determined by  $\beta$ . However, in the maximum flux phase C the current is independent of both  $\alpha$  and  $\beta$ . Moreover, both the high- and low-density phases can be subdivided into two phases each, namely, A I, A II and B I, B II, respectively; these subphases are distinguished by the asymptotic behaviour of the density profiles at the boundaries (see the insets in fig.4). In section IV we shall see how this phase diagram is modified in models of intra-cellular transport of vesicular cargo by molecular motors.

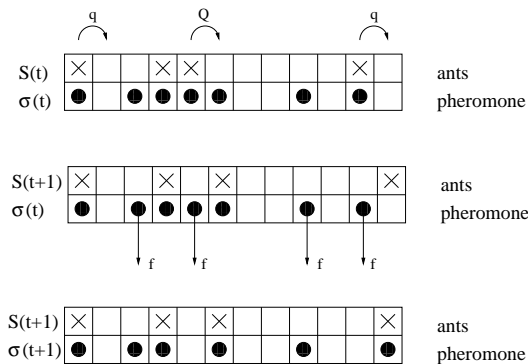


FIG. 5: Schematic representation of typical configurations; it also illustrates the update procedure. Top: Configuration at time  $t$ , i.e. *before* stage I of the update. The non-vanishing hopping probabilities of the ants are also shown explicitly. Middle: Configuration *after* one possible realisation of stage I. Two ants have moved compared to the top part of the figure. Also indicated are the pheromones that may evaporate in stage II of the update scheme. Bottom: Configuration *after* one possible realization of stage II. Two pheromones have evaporated and one pheromone has been created due to the motion of an ant.

### III. ANT TRAFFIC ON TRAILS

Ants communicate with each other by dropping a chemical (generically called *pheromone*) on the substrate as they crawl forward [16, 17]. Although we cannot smell it, the trail pheromone sticks to the substrate long enough for the other following sniffing ants to pick up its smell and follow the trail. In our recent papers [4, 5] we have developed a particle-hopping model, formulated in terms of stochastic CA, which may be interpreted as a model of unidirectional ant-traffic on a trail. Rather than addressing the question of the emergence of the ant-trail, we have focussed attention on the traffic of ants on a trail which has already been formed.

Each site of our one-dimensional ant-trail model represents a cell that can accommodate at most one ant at a time (see Fig. 5). The lattice sites are labelled by the index  $i$  ( $i = 1, 2, \dots, L$ );  $L$  being the length of the lattice. We associate two binary variables  $S_i$  and  $\sigma_i$  with each site  $i$  where  $S_i$  takes the value 0 or 1 depending on whether the cell is empty or occupied by an ant. Similarly,  $\sigma_i = 1$  if the cell  $i$  contains pheromone; otherwise,  $\sigma_i = 0$ . Thus, in contrast to TASEP, we have two subsets of dynamical variables in this model, namely,  $\{S(t)\}$  and  $\{\sigma(t)\}$ . The instantaneous state (i.e., the configuration) of the system at any time is specified completely by the set  $(\{S\}, \{\sigma\})$ .

Since a unidirectional motion is assumed, ants do not move backward. The forward-hopping probability of an ant is higher if it smells pheromone ahead of it. The state of the system is updated at each time step in *two stages*. In our ant-trail model with *parallel* dynamics, at

each stage the dynamical rules are applied *in parallel* to all ants and pheromones, respectively.

#### Stage I: Motion of ants

An ant in cell  $i$  that has an empty cell in front of it, i.e.,  $S_i(t) = 1$  and  $S_{i+1}(t) = 0$ , hops forward with

$$\text{probability} = \begin{cases} Q & \text{if } \sigma_{i+1}(t) = 1, \\ q & \text{if } \sigma_{i+1}(t) = 0, \end{cases} \quad (3)$$

where, to be consistent with real ant-trails, we assume  $q < Q$ .

#### Stage II: Evaporation of pheromones

At each cell  $i$  occupied by an ant after stage I a pheromone will be created, i.e.,

$$\sigma_i(t+1) = 1 \quad \text{if} \quad S_i(t+1) = 1. \quad (4)$$

On the other hand, any ‘free’ pheromone at a site  $i$  not occupied by an ant will evaporate with the probability  $f$  per unit time, i.e., if  $S_i(t+1) = 0$ ,  $\sigma_i(t) = 1$ , then

$$\sigma_i(t+1) = \begin{cases} 0 & \text{with probability } f, \\ 1 & \text{with probability } 1 - f. \end{cases} \quad (5)$$

We have also considered another version of our ant-trail model where the states of the system are updated in a random-sequential manner rather than in parallel [5]. Note that in both the cases, because of the periodic boundary conditions, the dynamics conserves the number  $N$  of ants, but not the number of pheromones.

This model is related to several other models. For example, in the limits  $f \rightarrow 0$  and  $\rightarrow \infty$  this ant-trail model reduces to TASEP with the hopping probabilities  $q$  and  $Q$ , respectively. Moreover, the ant-trail model may be regarded as the opposite limit of the bus-route model [18, 19] (see ref.[5] for the detailed comparison). Furthermore, the ant-trail model also has some similarities with the particle-hopping models of human trails of pedestrians [20, 21].

The typical fundamental diagrams of the ant-trail model [4] with parallel dynamics are shown in fig.6; the corresponding results in the case of random-sequential updating are qualitatively similar [5]. The unusual shapes of the curves observed over a range of  $f$  are consequences of the non-monotonic variation of the average speed of the ants with their density on the trail (see fig.7).

Both the ordinary mean-field theory (MFT), which accounts for the exact fundamental diagram of the TASEP with random-sequential updating, and 2-cluster MFT [1, 22], which successfully predicted the exact fundamental diagram of the TASEP with parallel updating, fail to capture even the qualitative features of the fundamental diagrams of the ant-trail model shown in fig.6 [5]. However, a heuristic MFT, described in ref.[5], captures at least the qualitative features of the observed flow properties of our ant-trail model.

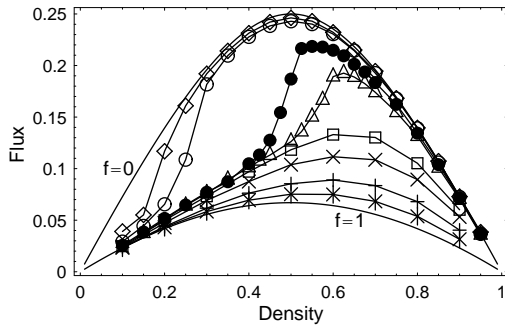


FIG. 6: Fundamental diagram of the ant-trail model with parallel updating for the parameters  $Q = 0.75$ ,  $q = 0.25$ . The discrete data points corresponding to  $f = 0.0005(\diamond)$ ,  $0.001(\circ)$ ,  $0.005(\bullet)$ ,  $0.01(\triangle)$ ,  $0.05(\square)$ ,  $0.10(\times)$ ,  $0.25(+)$ ,  $0.50(*)$  have been obtained from computer simulations; the lines connecting these data points merely serve as the guide to the eye..

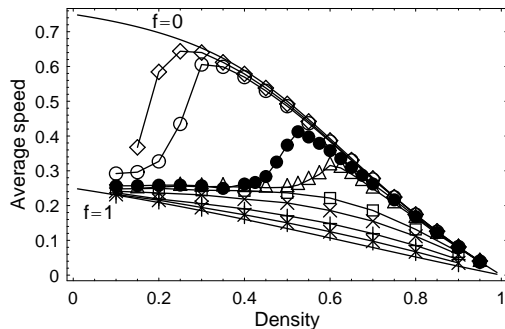


FIG. 7: Variation of the average speed of the ants in the ant-trail model with parallel updating. Same symbols in figs.6 and 7 correspond to the same values of the parameter  $f$ .

In order to develop a quantitative theory for the flow properties of the ant-trail model, we have analyzed the spatial organization of the ants by computer simulations. Analyzing these observations we concluded that in the anomalous regime, loose clusters of ants dominate; the term “loose” means that there are small gaps in between successive ants in the cluster although the cluster appears to be an usual compact cluster if seen from a distance. As shown in fig.8, the fundamental diagram we calculated within the “loose”-cluster approximation (LCA) is in good quantitative agreement with the corresponding data we obtained from computer simulations of the model.

#### IV. INTRA-CELLULAR TRAFFIC OF MOLECULAR MOTORS

Molecular motors are protein molecules that convert the chemical energy, released by the hydrolysis of ATP, into mechanical energy required for its forward movement during intra-cellular transport of vesicular cargo

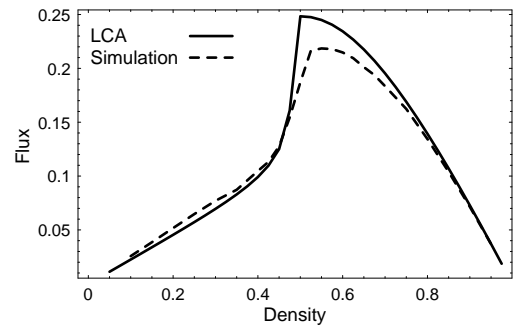


FIG. 8: Fundamental diagram ( $f = 0.005$ ) of the ant-trail model in the LCA (solid curve) compared with the simulation data (broken curve).

[23]. The minimal models developed for explaining the mechanism of directed motion of isolated motor proteins are based on Brownian ratchets [24]. In such models, each motor is represented by a particle. The essential features of the detailed mechano-chemistry of the molecular motor is captured in the Brownian ratchet models by a stochastic sequence of successive attachments and detachments of the motor with the cytoskeletal filamentary track (e.g, microtubule in the case of kinesin and dynein motors). In the simplest versions of these models [25], in the attached state, the particle representing a motor is subjected to a potential that is spatially periodic, but each period of which is asymmetric. In the detached state the particle executes an unbiased diffusive motion. In spite of its simplicity, such a minimal model can account for the directed, albeit noisy, movement of individual isolated motors.

To our knowledge, the question of the effects of interactions of the motors on the intra-cellular traffic was addressed theoretically for the first time only a few years ago [26]. In that work, the filamentary track was discretized in the spirit of the particle-hopping models described above and the motors were represented by field-driven particles. Both forward and backward movement of the particles were possible and the hopping probability of every particle was computed from the local potential. Thus, this model was a generalization of ASEP rather than TASEP where the hopping probabilities were obtained from the local potential which itself was time-dependent. The fundamental diagram of that model, computed imposing periodic boundary conditions, is very similar to those shown in fig.2. This observation indicates that further simplification in the model proposed in ref.[26] is possible to develop a minimal model for interacting molecular motors.

Recently, Parmeggiani et al.[8] have, indeed, developed such a minimal model for interacting molecular motors involved in intra-cellular transport by extending the TASEP with open boundary conditions. In this model, the molecular motors (e.g., kinesin or dynein) are represented by particles whereas the sites for the binding

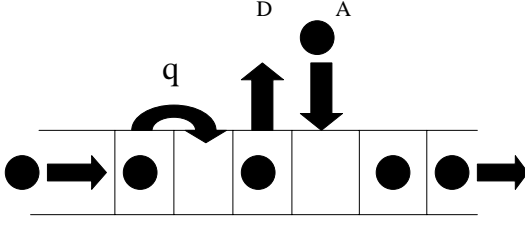


FIG. 9: Schematic representation of the model [8] of intra-cellular traffic of molecular motors carrying vesicular cargo.

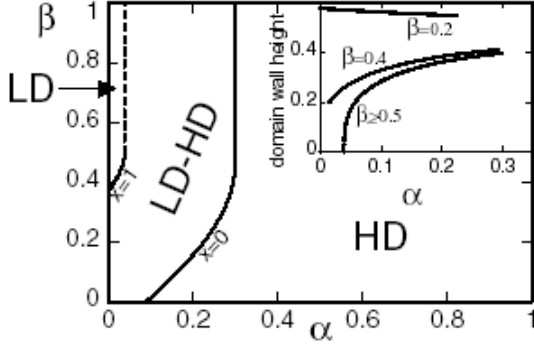


FIG. 10: The phase diagram of the model [8] of intra-cellular traffic of molecular motors carrying vesicular cargo (reproduced, with permission, from ref.[8]). The inset shows the dependence of the domain wall amplitude on  $\alpha$  for different values of  $\beta$ .

of the motors with the cytoskeletal tracks (e.g., microtubules) are represented by a one-dimensional discrete lattice. Just as in TASEP, the motors are allowed to hop forward, with probability  $q$ , provided the site in front is empty. However, unlike TASEP, the particles can also get “attached” to an empty lattice site, with probability  $A$ , and “detached” from an occupied site, with probability  $D$  (see fig.9) from any site except the end points. The state of the system was updated in a random-sequential manner.

To my knowledge, this is the first application of TASEP to intra-cellular transport phenomena although it is not the first application of TASEP in the domain of biological systems; for example, a TASEP-like model was considered earlier for protein synthesis [27]

Carrying out Monte-Carlo simulations Parmeggiani et al.[8] demonstrated a novel phase where low and high density regimes, separated from each other by domain walls, coexist (see fig.10). Using a MFT, they interpreted this spatial organization as traffic jam of molecular motors.

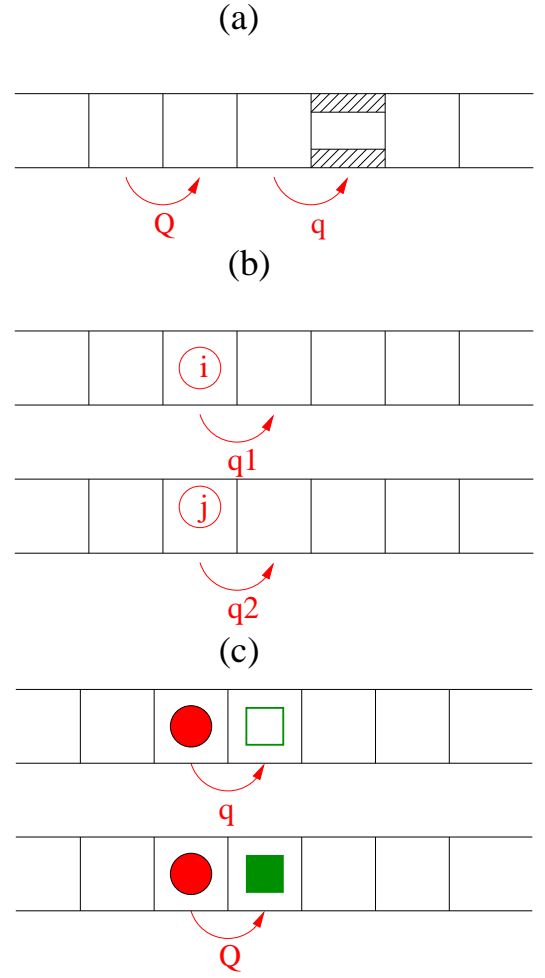


FIG. 11: Schematic representation of the different types of randomness in particle-hopping models. In (a) the randomness is associated with the track; the hopping probability  $q$  at the bottleneck (partially hatched region) is smaller than the normal hopping probability  $Q$ . In (b) the randomness is associated with the particles;  $q_1$  and  $q_2$  being the time-independent hopping probabilities of the particles  $i$  and  $j$ , respectively. In (c) the randomness arises from the coupling of the dynamics of the hopping particles (filled circle) with another non-conserved dynamical variable; the two possible states of the non-conserved variable are represented by open and filled squares.

## V. DEFECTS AND DISORDER IN PARTICLE-HOPPING MODELS

At least three different types of defects and quenched randomness have been considered so far in the context of the models of interacting particles driven far from equilibrium. (a) First, the randomness may be associated with the *track* on which the particles move; typical examples are the bottlenecks on the roads (in the context of vehicular traffic) or defects on the microtubules (in intra-cellular transport), etc. For example, as shown in

fig.11(a), normal hopping probability at unblocked sites is  $Q$  whereas that at the bottleneck is  $q$  ( $q < Q$ ). This type of quenched defect and disorder of the track leads to interesting phase-segregation phenomena (see [1] for a review).

(b) The second type of randomness is associated with the hopping *particles*, rather than with the track. For example, the normal hopping probabilities of the particles may vary randomly from one particle to another (see fig.11(b)); the hopping probabilities are, however, “quenched” random variables, i.e., independent of time. In this case, the system is known to exhibit coarsening of queues of the particles and the phenomenon has some formal similarities with Bose-Einstein condensation (reviewed in [1]).

Note that in case of the randomness of type (a), the hopping probability depends only on the spatial location on the track, independent of the identity of the hopping particle. On the other hand, in the case of randomness of type (b), the hopping probability depends on the hopping particle, irrespective of its spatial location on the track. In contrast to these two types of randomness, the randomness in the hopping probabilities of the particles in some models arises from the coupling of their dynamics with that of another non-conserved dynamical variable. For example, in the ant-trail model, the hopping probability of an ant depends on the presence or absence of pheromone in front of it (see fig.11(c)). Therefore, in such models with periodic boundary conditions, a given particle may hop from the same site, at different times, with different hopping probabilities.

Defects of either (a) the cytoskeletal filaments or (b) the motor proteins or (c) the mechano-chemical coupling can cause malfunctioning of the intra-cellular transport leading to various types of diseases [28]. In order to get deep insight into the physical origin of such diseases, the recent model developed by Parmeggiani et al. [8] has been extended [29]. This modeling strategy has opened up a new horizon for further unconventional applications of non-equilibrium statistical mechanics far beyond the traditional borderlines of physics.

## VI. CONCLUSION

In this paper we began with a brief introduction to TASEP [10, 11] which is, perhaps, the simplest model

of systems of interacting driven particles. TASEP, when updated in parallel, may be regarded as a special case, corresponding to the maximum allowed speed  $V_{max} = 1$ , of the NS model [14], the minimal model of vehicular traffic on single-lane highways. We have summarized some of the main known results on the *fundamental diagram* for the TASEP with periodic boundary conditions and the *phase diagram* of the TASEP with open boundary conditions. Then, we have shown how these results for TASEP get *qualitatively* modified by the generalizations or extensions required to model ant-traffic on ant-trails [4, 5] and molecular motor traffic on cytoskeletal filaments [8].

In the context of the ant-traffic on ant-trails, we have established how a combination of analytical and numerical calculations [4, 5] can account for the unusual shape of the fundamental diagram observed in the computer simulations of the ant-trail model. We have also presented the phase diagram obtained by Parmeggiani et al. [8] from studies of their recent model for molecular motor traffic. This phase diagram suggests the possibility of coexistence of high-density regions (traffic jam) and low-density regions (freely flowing traffic), separated from each other by domain walls, in a novel phase. Finally, we have mentioned some ongoing investigations on the effects of defects and disorder on molecular motor traffic [29]. This trend of research indicates the possibility of further unconventional, but very useful, applications of statistical physics in biological systems.

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