Modelling interacting molecular motors with an internal degree of freedom

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Abstract. The mechanisms underlying the collective motion of molecular motors in living cells are not yet fully understood. One such open puzzle is the observed pulses of backward-moving myosin-X in the filopodia structure. Motivated by this phenomenon we introduce two generalizations of the ‘total asymmetric exclusion process’ (TASEP) that might be relevant to the formation of such pulses. The first is adding a nearest-neighbours attractive interaction between motors, while the second is adding an internal degree of freedom corresponding to a processive and immobile form of the motors. Switching between the two states occurs stochastically, without a conservation law. Both models show strong deviations from the mean field behaviour and lack particle–hole symmetry. We use approximations borrowed from the research on vehicular traffic models to calculate the current and jam size distribution in a system with periodic boundary conditions and introduce a novel modification to one of these approximation schemes.

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1. Introduction

Unconventional myosins, which are molecular motors that move processively on actin filaments, are primarily associated with active transportation of cargo on actin filament networks. Inside actin-based cellular protrusions, they were shown to be involved in the transport of actin-regulating proteins that play a role in the formation of filopodia. An example of such a molecular motor is myosin X (or Myo10), which is known to play an important role in the formation of filopodia at the cell membrane [1–3]. These motors have recently been observed to form density pulses which move backwards in the filopodia [4–8]. Such pulses were also observed in myosin-XV [6], myosin-III [9] and myosin-Va [7]. The velocity of these pulses seems to be close to the retrograde flow of the actin filaments, indicating that the pulses contain immobile or jammed motors. These traffic jams are dynamic as opposed to the static domain walls calculated in previous theoretical works [10, 11] (recently confirmed experimentally for Kinesin motors [12]). The mechanism driving these dynamic jams of myosin motors is not yet understood. The flow of motors from the protrusion tip back to the cytoplasm plays an important role in the overall recycling of the motors and determines the overall protein flux that they carry along the protrusion. Studying the driving mechanism might shed light on the interactions between the motors that give rise to the observed collective behaviour.

The total asymmetric exclusion process (TASEP) is of relevance to many processes in biology. It was first introduced in [13] to model mRNA translation, while over the years it has been used to model other phenomena such as the collective behaviour of molecular motors [10, 14–16] or even the transport of molecules and proteins through pores and ion channels [14]. Jams in TASEP appear only at densities greater than half-filling, while it seems that jams in the filopodia appear at lower densities. Furthermore, their size distribution is exponential; thus the probability of observing a jam that occupies a macroscopic fraction of...
the system is practically zero. The observed pulses seem to have a distinct size and do not seem to exist in the form of numerous small jams. The simple TASEP model therefore needs to be modified in order to account for the phenomenon of pulses of jams.

For inspiration, we turned to studies of vehicular traffic jams, where pulses of backwards-moving jams have been observed [17–19]. Backward-moving traffic jams are one of the main results of the Nagel–Schreckenberg (NS) model for vehicular traffic [20]. There is one big difference between the NS model and models described here. The robustness of the jams in the NS model is partially due to the parallel updating scheme [21]. When using the random sequential update rule the jams are less distinct and are destroyed due to the noise in the update scheme. It seems more plausible to model the traffic of molecular motors with a random sequential update rule: a forward step of a motor corresponds to hydrolysis of ATP, and since this chemical reaction occurs in a stochastic manner with a certain rate, it is unlikely that the reaction occurs simultaneously for all the motors.

In this paper, we introduce two modifications of TASEP that could give rise to larger and more robust jams. Firstly, we consider attractive interactions that tend to cluster adjacent motors, thus forming a jam. This model will be called the $r$-model. The second model introduces a possibility for the motors to have an internal degree of freedom corresponding to a processive and an immobile form. For myosin-X a recent study revealed that it can inhibit its own activity [22], and a similar phenomenon was also found for myosin-IIIa [23], where an auto-phosphorylation reaction between motors can lead to their inactivation. The motors are assumed here to switch stochastically between these two states. We call the model with two independent states of mobility the $s$-model. In both the $r$ and $s$ models, a simple mean field (MF) approach exhibit strong deviations from simulation results. We will study each of the two models separately and also calculate their combined effect. In order to calculate the current and jam size distribution at steady state, we use approximation schemes for vehicular traffic models [21, 24]. For the $r$-model we find an exact solution using the approximation scheme that solves the NS model [21]. For the $s$-model we introduce a novel modification to the existing approximation scheme. Both approximations are improved MF methods taking into account particle correlations.

2. The models

In this section, we describe the two models: incorporating TASEP with a short-range attractive interaction and with two states of mobility. We present approximations for the current–density relation (fundamental diagram) and for the jam size distribution. We call the models the $r$-model and the switches-model ($s$-model).

In the $r$-model, the hopping rate is reduced if two particles are at adjacent sites (see section 2.1). We define the rate as the probability for a particle to jump given that it was chosen for update. A somewhat similar model is the KLS model [25, 26] which also has nearest neighbours interactions. Our $r$-model differs from the KLS model by the asymmetry of the interaction as it does not induce greater hopping rates into sites that are adjacent to an occupied site. An interaction similar to our $r$-model was considered in [27], but the current and the jam size distribution were not calculated.

In the $s$-model, each particle switches randomly to a different internal state independently of the neighbouring sites, as opposed to previously studied models where either there is a conservation law associated with the transitions [28–32] or the transition occurs only if there
Consider $N$ particles on a ring of length $L$. Each particle is picked at random for hopping. Particles can hop only in one direction and there can be only one particle at each site due to exclusion. If a particle at site $n$ is being chosen for update while site $n-1$ is occupied, it jumps with a rate $r < 1$ as shown in figure 1. This shows the attraction between neighbouring motors. Therefore, the average current is

$$ J = P(0, 1, 0) + r P(1, 1, 0), $$

where $P(x, y, z)$ represents the probability for a certain cluster of size 3 in steady state. The indices 1 and 0 represent an occupied and an empty site, respectively. Note that the $r$-model lacks the particle–hole symmetry of the regular TASEP. If the empty sites are to be considered as particles and the particles considered as holes, then we do not obtain the same dynamics. Mathematically, the current is not symmetric under the transformation $c \rightarrow 1 - c$, where $c$ is the density. Therefore, we expect that the current plot will not be symmetric around half-filling.

2.2. The $s$-model

In the $s$-model, each particle can switch between two states:

- The ‘On’ state (processive): If the next site is empty the particle jumps to it with a rate equal to 1.
- The ‘Off’ state (immobile): The particle is stationary.

The rates of switching between the ‘On’ and ‘Off’ states are $K_n$ and $K_f$, respectively, as shown in figure 2. These transitions occur independently of the states of neighbouring sites. The
Figure 2. The $s$-model. Blue filled circles are active (‘on’) particles, while red circles are inactive (‘off’) particles. Active particles move to the + end; jumps in the – end direction and jumps to occupied sites are not possible. Inactive particles do not move. Active particle can switch to the inactive state with rate $K_f$ while inactive particle can switch to the active state with rate $K_n$. Particle 1 is at the beginning of the gap, while particle 2 is at the end.

Figure 3. Comparison between holes and particles in the $s$-model. Each empty site in the particles picture corresponds to a hole particle in the holes picture. The state of the hole is determined by the state of the particle to the left.

Current in the system is

$$J = P(\text{on}, 0),$$

where $P(\text{on}, 0)$ is the probability for an active particle followed by an empty site.

As in the $r$-model, the $s$-model does not have a particle–hole symmetry. When we examine two-site states such as (on, 0) or (off, 0) it seems that the symmetry is maintained. However, when we consider a three-site state as depicted in figure 3 it is clear that the movement of the ‘on’ particle is equivalent to the movement of a hole that becomes ‘off’ due to its movement. This transformation cannot happen in the particle picture, since a particle cannot move and change its state at the same time. Therefore the particle–hole symmetry is broken. This conclusion is in disagreement with [40], where the current was found to be symmetric around $c = 1/2$ at the MF approximation. Note that particle–hole symmetry is found in two models that were solved exactly: TASEP with open or periodic boundary conditions [43] and the NS model with velocities 0, 1 [21]. Therefore a lack of this symmetry may indicate that an exact solution for the $s$-model is not a simple one.
2.3. The current–density relation

In both models, we explore the current–density relation, which is also called the fundamental diagram. The lack of particle–hole symmetry in the two models is crucial, as it shifts the maximal capacity (the density of maximal current) to values smaller than half-filling. Moreover, it was shown that the collective velocity of density perturbations is given by \[ V_c(c) = \frac{\partial J}{\partial c}. \] (3)

For densities beyond the maximal capacity the velocity is therefore negative, and the jams will move in the opposite direction to the motors’ movement.

3. Results

In this section, we calculate the current and the jam size distribution for the two models. For the \( r \)-model we use a two-cluster approximation (for details see appendix A), previously used to calculate the current for the NS model of vehicular traffic [21]. For the \( s \)-model, we introduce a new approximation scheme based on the ‘Car Oriented Mean Field’ (COMF) method, which was also used to calculate the current in the NS model [24]. We will not use COMF for the \( r \)-model since the two-cluster approximation solves the model exactly, and we will not use the two-cluster method for the \( s \)-model since it is very cumbersome and less accurate.

3.1. The \( r \)-model

An MF approximation to (1) gives
\[ J = c(1 - c)(1 - (1 - r)c). \] (4)

This approximation is consistent in the limit \( r \to 1 \), but not in the limit \( r \to 0 \). The results in figure 4 show that this expression is not accurate. We use the two-cluster method to improve the results (see appendix A).

The current becomes
\[ J = \frac{r(1 - c)(2c(1 - r) + r - \sqrt{r}\sqrt{r + 4(1 - r)c(1 - c)})}{2c(1 - r)}. \] (5)

In fact, we found later that the two-cluster approximation is an exact solution to the \( r \)-model, as shown in appendix B. The calculated current is compared to the simulation results in figure 4. The overall agreement seen is very good. Using (5) we can find the density at the maximum current (maximal capacity) which is plotted in figure 4(c). Beyond this density the current decreases and backward-moving jams appear.

Within the two-cluster approximation (see appendix A) the jam size distribution is expected to be exponential:
\[ C_n = \frac{P(1, 0)}{c} \left( \frac{c - P(1, 0)}{c} \right)^{n-1}. \] (6)

We calculate it in appendix A and plot it in figure 5. The results show that for small \( r \) the jam size distribution has more weight for large jams than the distribution of the regular TASEP. The calculated distribution matches very well with the simulated data.
3.2. The s-model

At first sight it might seem that the s-model is equivalent, on average, to a TASEP model with a reduced hopping rate: \( 1 \to K_n(K_n + K_f)^{-1} \). Indeed a naive MF approach predicts:

\[
J = \frac{K_n}{K_n + K_f} c(1 - c),
\]  

(7)
Figure 6. The current–density relation for $K_n = 10K_f$. Purple curves are COMF, while yellow curves are mCOMF. Green curves are a naive MF of (7), which gives the same expression for all $K_n = 10K_f$. (a) $K_n = 0.9$, $K_f = 0.09$; (b) $K_n = 0.1$, $K_f = 0.01$; inset: MF (green curve) compared to mCOMF (yellow curve) and simulation data (blue points).

Figure 7. The current–density relation for $K_n = K_f$. (a) $K_n = 1$, (b) $K_n = 0.1$; inset: MF (green curve) compared to COMF (purple curve) and mCOMF (yellow curve) and simulated data (blue points).

while from the inspection of figures 6 and 7 it is clear that the MF (7) is not valid since the maximal capacity is shifted to values smaller than half-filling. The s-model exhibits correlations between active and inactive particles which are absent in the MF calculation.

We now describe a better MF theory called COMF [24]. In the COMF framework, there is a distinction between the two internal states of the particles, thus yielding different steady state distributions for the different populations. In COMF, we look at the probabilities to have $n$ empty sites in front of a particle. We define the following variables:

- $P_n$—The probability to have $n$ empty sites in front of a particle in an ‘on’ state.
- $B_n$—The probability to have $n$ empty sites in front of a particle in an ‘off’ state.

The probabilities to be ‘on’ and ‘off’ are denoted by $\bar{K} = \frac{K_n}{K_n + K_f}$ and $\tilde{K} = \frac{K_f}{K_n + K_f}$, respectively.
Figure 8. The ratio of the simulated and COMF probabilities of different gap sizes, using $K_n = K_f = 1, c = 0.4$. Blue circles are the simulation data. The yellow curve is the result of COMF, i.e. the ratio is equal to 1. The results of mCOMF (14) and (15) are plotted in purple.

Note that

$$K = \sum_{n=0}^{\infty} P_n,$$

$$\tilde{K} = \sum_{n=0}^{\infty} B_n.$$  

We denote the probabilities to jump at the next time step by $g_1$ and to be stationary at the next time step by $g_0$:

$$g_0 = \tilde{K} + P_0,$$

$$g_1 = K - P_0.$$  

In the language of COMF, the current in (2) is

$$J = c \cdot g_1 = c \cdot (K - P_0).$$  

Therefore, we need to calculate $P_0$ at the steady state. Solving the master equations at steady state, we obtain

$$J = \frac{K_n}{K_n + K_f} c (1 - c) \frac{1}{1 + \frac{K_n}{K_n + K_f} c}.$$
Figure 9. (a) The ratio $P(\text{on}, \text{off})/(P_0\bar{K})$ versus density for $K_n = K_f$. Curves with circles are the results of simulations, while solid lines are the mCOMF results (14). (b) The ratios $P(\text{on}, \text{off})/(P_0\bar{K}) - 1$ (blue points) and $P(\text{off}, \text{off})/(B_0\bar{K}) - 1$ (green points) versus $\Lambda$ (13) in a log–log scale. The linear red curve is the theoretical approximation (13). Circles correspond to $K_n = K_f$, while squares correspond to $K_n = 10K_f$.

The COMF approximation is an MF approximation with respect to the gaps between the particles. Given a gap of size $n$, the particle at the end of the gap (see figure 2 for the definition of the end of the gap) has the MF probability to be in either internal state. For example,

$$P(\text{on}, \text{off}) = P_0\bar{K},$$

$$P(\text{on}, \text{on}) = P_0K.$$ (12)

From figures 6 and 7, one can see that this MF assumption is not valid for our $s$-model. The correlations beyond MF can be understood as an effective attraction between ‘on’ and ‘off’ motors. If a motor is jammed, it does not matter whether it is active or not, and motors will flow and accumulate in the lattice sites behind it. If the motor is not jammed (i.e. there is an empty site in front of it), only an ‘off’ state will induce a jam of incoming motors. By these considerations we expect the ratio $P(\text{on}, \text{off})/(P_0\bar{K})$ to be a monotonic decreasing function of $c$. Simulation results shown in figure 9 confirm this.

To go beyond the COMF model, we first examine a system of two particles by neglecting the following correlations: $P(\text{on}, \text{on}) = P(\text{on})P(\text{on})$ and $P(\text{off}, \text{off}) = P(\text{off})P(\text{off})$. The approximated solution for the two particles system yields (see appendix B for more details of the calculation):

$$P(\text{on, off})/(P_0\bar{K}) = P(\text{off, off})/(B_0\bar{K}) = 1 + \Lambda,$$

where $\Lambda = K_n/(K_f + (K_n + K_f)^2).$ (13)
As in figure 9, this ratio increases as $K_n, K_f$ decreases, but maintains $K_n/K_f$ constant. The validity of this approximate solution is demonstrated for the two-particle system in figure 9(b). Note that $P(\text{off, off})/(P_0 K)$ is always above (13) while $P(\text{on, off})/(P_0 K)$ is always below, and that for larger ratio of $K_n = 10K_f$ the discrepancy between the simulation and the approximate solution increases. We can treat the two-particle case as the limit $c \to 0$ and further assume that the ratio is a simple linearly decreasing function of $c$:

$$P(\text{on, off})/(P_0 K) = F(c) = 1 + \Lambda (1 - c),$$

$$P(\text{on, on})/(P_0 K) = G(c),$$

where now $G(c)$ can be found from the constraint: $P_0 = F(c) P_0 K + G(c) P_0$. We denote this approximation as modified-COMF (mCOMF). We then use this method to calculate the average current and the jam size distribution, as described in appendix C.

From mCOMF, we can extract an expression for $P_0$. Plugging it in (10) we obtain the current, which we compare to the simulations in figures 6 and 7. We found very good agreement for a large range of parameters. In the limit of fast switching ($K_n, K_f \gg 1$), we expect to derive the MF result 7. Indeed in this limit we obtain

$$\Lambda = \frac{K_n}{K_f + (K_n + K_f)^2} \approx \frac{K_n}{(K_n + K_f)^2},$$

$$P(\text{on, off})/(P_0 K) = 1 + \frac{K_n}{(K_n + K_f)^2} (1 - c) \approx 1,$$

leading to the result of COMF (11), which in this limit becomes

$$J = \frac{k_n c (1 - c)}{1 + \frac{k_n}{(K_n + K_f)^2} c} \approx \frac{K_n c (1 - c)}{K_n + K_f},$$

as the MF predict. In the limit $K_n, 1 \gg K_f$, MF, COMF and mCOMF converge to

$$J = c (1 - c).$$

Within the mCOMF framework the jam size distribution is exponential [45]:

$$C_n = (1 - P_0 - B_0)/(P_0 + B_0)^{n-1}$$

as plotted in figure 10. We find that the simulated distribution is indeed exponential for large jam sizes, but for small values of $K_n, K_f \ll 1$ there is a clear change in the slope between small and

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**Figure 10.** Jam size distribution for $c = 0.4$ in a semi-log scale. Blue circles are simulation results, the purple curve are the mCOMF results and the yellow curve is the regular COMF. (a) $K_n = K_f = 1$, (b) $K_n = K_f = 0.1$. 

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Figure 11. Exponential jam size distribution as a function of $K_n, K_f$. In the limit of large jam sizes the distribution becomes $C_n \propto A^n$, and the values of $A$ are plotted here: circles for the simulation data, red curve for mCOMF, yellow curve for COMF and green line for the MF result where $A = c = 0.4$. Parameters of the figures: (a) $\frac{K_n}{K_f} = 10$, (b) $\frac{K_n}{K_f} = 1$.

Figure 12. Deviations from theory at low switching rates. (a), (b) The ratio of simulated probabilities and COMF probabilities for $K_n = K_f = 0.07, c = 0.4$. Blue circles indicate the data of the simulation. The probabilities for gaps of size $n > 0$ are no longer equal.

large jams (figure 10(b)). In general, there is more weight for bigger jams compared to regular TASEP. The overall agreement between the simulations and the calculation schemes is shown in figure 12 for a variety of parameters. Overall the mCOMF describes reasonably well the jam size distribution.

The mCOMF approximation begins to break down for very small values of $K_n, K_f \ll 1$ (figure 11). As we see, the simulated ratio is no longer independent of $n$ for $n \geq 1$, as assumed by mCOMF (compare with figure 8). As $K_n \to 0, K_f \to 0$ the particles will be in a static jammed phase. Each immobile particle has an infinite lifetime in this state, so it clusters active particles behind it. Note that the case $K_n = K_f = 0$ is ill-defined since the particles reach different steady states for different initial conditions.
3.3. The rs-model

We now describe a model combining both the attraction and switching properties of the $r$- and $s$-models. Intuitively, we can think of a regime where the attraction dominates and a regime where the switching dominates. From figure 13, we see that indeed for $r = 0.1$ the switching mechanism is negligible. As $r$ increases the effect of switching gets stronger. Even when the jam size distribution is similar to that of the $r$-model, we expect the current to be smaller since only the active fraction of motors will contribute to the current, while both types of particles contribute to the jams. When the parameters are such that neither of the mechanisms is dominant we find that bigger jams have a slightly higher probability. The higher fraction of inactive motors in the system makes the overall traffic limited by their intrinsic immobility rather than being limited by the attraction.

4. Discussion

We have explored two models for motors with an attractive interaction and with an internal random switch between a processive and an immobile state. We described two methods for
Figure 14. Space–time plots (kymographs) of $c = 0.2$ (left column), $c = 0.5$ (right column). (a), (b) TASEP, (c), (d) $s$-model for $K_n = K_f = 0.1$, (e), (f) $r$-model for $r = 0.1$, (g), (h) $rs$-model for $K_n = K_f = 0.1$, $r = 0.1$. Red means occupied sites while blue means empty sites (or holes). Backward-moving density waves are robust for the right column, because the density is above the maximal capacity, except for (b) which is at the maximal capacity. The left column is below the maximal capacity. (i) Comparison between the density–current relation of the different models. Blue points: $rs$-model; yellow points: $r$-model; purple points: $s$-model. The red curve is (5) while the green curve is the mCOMF curve.
approximating the current and the jam size distribution. We introduced a novel version of the COMF approximation called modified COMF (mCOMF). These approximations are beyond MF, by taking into account correlations between motors. It seems that the main effect in the current and jam size distribution is due to correlations between the occupancy of two adjacent sites. In the s-model the correlations arise from the fact that ‘on’ particles tend to move until they jam at an ‘off’ particle, so an ‘off’ particle is more likely to have a particle behind it. This correlation is between nearest neighbours. Indeed, as one can see in figure 6, the probabilities for gaps of size \( n \geq 0 \) are more or less equal. The results also account for the lack of particle–hole symmetry. It is clearly seen for low values of \( r \) (see figure 4(b)) and \( K_n, K_f \) (see figure 7(b)). The shift of the maximum current density to values lower than half-filling indicate that backward-moving jams start forming at lower densities. It is quite surprising that our rather simple treatment of the correction for the two-site probabilities gives a current that fits the simulation results for a large range of parameter values. This framework can be checked for other types of non-equilibrium models with strong correlations.

In the biological context, many types of motors may have attractive interactions, directly through van der Waals, some electric affinity or mediated by a connecting substrate of proteins or membrane. In addition, these motors often have an inhibited (immobile) and processive states \[22\]. We demonstrate here that such characteristics change the collective behaviour of the motors on one-dimensional tracks. For example, the overall current decreases and backwards-moving jams are induced at much lower densities. Density waves that propagate backward begin to appear when the current has a negative derivative with respect to the density \[44\]. In other words, jams move backward only if the current has a negative slope. These differences in the spatio-temporal structure of the system are demonstrated in figure 14. These plots should be compared to those observed for myosin-X \[7\], for example. It is clear that the attractive interactions and the internal inhibition give rise to jams that are much more realistic (figures 14(g) and (h)) compared to the original simple TASEP model (figures 14(a) and (b)). This may be a positive indication that indeed such processes of attractive interactions and inhibition drive the observed dynamic jams in cellular protrusions.

We introduced a framework for dealing with various effects that may affect the collective behaviour of molecular motors inside cellular protrusions. These models will serve as a basis for more realistic extensions that will include the effects of the treadmilling actin filaments, and the correct (non-periodic) boundary conditions.

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*Note added in proof.* After the paper was finished we realized that our \( r \)-model falls in the category of models which have been shown to have exact solutions in the following paper: Katz S, Lebowitz J L and Spohn H 1984 *J. Stat. Phys.* 34 497–537.

**Appendix A. Details of two-cluster calculation for the \( r \)-model**

Within the two-cluster approximation all the probabilities are written in terms of two-cluster probabilities. The probability \( P(x_{i-1}, x_i, x_{i+1}) \) for a certain occupancy of sites, \( x_{i-1}, x_i, x_{i+1} \), is
Table A.1. States at time $t$ that can flow into the state $(x_i = 1, x_{i+1} = 0)$ at $t+1$. $W$ are the rates for the flow between states.

| $x_{i-2}$ | $x_{i-1}$ | $x_i$ | $x_{i+1}$ | $x_{i+2}$ | $W$ |
|-----------|-----------|-------|-----------|-----------|-----|
| 0         | 0         | 1     | 0         | 0         | 1 - $\frac{1}{N}$ |
| 1         | 0         | 1     | 0         | 0         | 1 - $\frac{1}{N}$ |
| 0         | 1         | 1     | 0         | 0         | 1 - $\frac{1}{N}$ |
| 1         | 1         | 1     | 0         | 0         | 1 - $\frac{1}{N}$ |
| 0         | 0         | 1     | 0         | 1         | 1 - $\frac{1}{N}$ |
| 1         | 0         | 1     | 0         | 1         | 1 - $\frac{1}{N}$ |
| 0         | 1         | 1     | 0         | 1         | 1 - $\frac{1}{N}$ |
| 1         | 1         | 1     | 0         | 1         | 1 - $\frac{1}{N}$ |
| 0         | 1         | 0     | 0         | 0         | $1/N$ |
| 1         | 1         | 0     | 0         | 0         | $r/N$ |
| 0         | 1         | 0     | 0         | 1         | $1/N$ |
| 1         | 1         | 0     | 0         | 1         | $r/N$ |
| 0         | 0         | 1     | 1         | 0         | $r/N$ |
| 1         | 0         | 1     | 1         | 0         | $r/N$ |
| 0         | 1         | 1     | 1         | 0         | $r/N$ |
| 1         | 1         | 1     | 1         | 0         | $r/N$ |

approximated as: $P(x_{i-1}, x_i, x_{i+1}) = \frac{P(x_{i-1}, x_i) P(x_i, x_{i+1})}{P(x_i)}$ [46]. The current in (1) becomes

$$J = P(0, 1) \frac{P(1, 0)}{P(1)} + r P(1, 1) \frac{P(1, 0)}{P(1)}.$$ (A.1)

Note that on a ring $P(1, 0) = P(0, 1)$, since every jam has a beginning and an end. Furthermore, we have the following relations:

$$P(1, 1) = c - P(1, 0),$$ (A.2)
$$P(0, 0) = 1 - c - P(0, 1),$$ (A.3)

where $c$ is the averaged density. In order to obtain $J$ we need to calculate $P(1, 0)$ or more explicitly, $P(x_i = 1, x_{i+1} = 0)$:

$$P(x_i = 1, x_{i+1} = 0, t + 1) = \Sigma_{x_i} W(1, 0|x_{i-2}, x_{i-1}, x_i, x_{i+1}, x_{i+2}) \times P(x_{i-2}, x_{i-1}, x_i, x_{i+1}, x_{i+2}, t),$$ (A.4)

where $W$ is the transition rate to the desired state from another state. $t$ denotes time, and in steady state we take it off. We sum over all states that can flow into the cluster $(1, 0)$ (see table A.1).

In the approximation,

$$P(x_{i-2}, x_{i-1}, x_i, x_{i+1}, x_{i+2}) = P(x_{i-2}, x_{i-1}) \frac{P(x_{i-1}, x_i)}{P(x_{i-1})} \frac{P(x_i, x_{i+1})}{P(x_i)} \frac{P(x_{i+1}, x_{i+2})}{P(x_{i+1})}. $$ (A.5)
Considering all the states that flow into (1, 0) and denoting $P(1, 0)$ as $y$, one obtains (after some algebra) the following quadratic equation:

$$(1 - r)y^2 + ry - rc(1 - c) = 0$$

(A.6)

with

$$P(1, 0) = y^* = \frac{-r + \sqrt{r(0 + r + 4(1 - r)c(1 - c))}}{2(1 - r)}.$$

(A.7)

The current will be

$$J = ry^* + (1 - r)\frac{y^{*2}}{c}$$

$$= \frac{r(1 - c)(2c(1 - r) + r - \sqrt{r(0 + r + 4(1 - r)c(1 - c))})}{2c(1 - r)},$$

(A.8)

which is (5) in the main text. Within the two-cluster approximation we can obtain an expression for the probability of a certain jam size [45]. We will denote it by $C_n$. We can write

$$C_n \propto P(0, 1, \ldots, 1, 0) = P(0, 1) \left(\frac{P(1, 1)}{P(1)}\right)^{n-1} \frac{P(1, 0)}{P(1)}.$$  

(A.9)

After normalization and denoting $P(1, 0)$ as $y$, we obtain

$$C_n = \frac{y}{c} \left(\frac{c - y}{c}\right)^{n-1}$$

(A.10)

with the approximated $y$ (A.7) plugged in (A.10).

Appendix B. Proof that the two-cluster solution is the exact solution of the r-model

Consider the master equation of the periodic $r$-model with $L$ sites and $N$ particles:

$$P([x_n]; t+1) = P([x_n]; t) + \frac{1}{L} \sum_{j=1}^{L} (1-x_{j-1})(1-x_j)x_{j+1}P(x_1, \ldots, x_{j-2}, 0, 1, 0, x_{j+2}, \ldots, x_L; t)$$

$$+ \frac{r}{L} \sum_{j=1}^{L} x_{j-1}(1-x_j)x_{j+1}P(x_1, \ldots, x_{j-2}, 1, 1, 0, x_{j+2}, \ldots, x_L; t)$$

$$- \frac{1}{L} \sum_{j=1}^{L} (1-x_{j-1})x_j(1-x_{j+1})P([x_n]; t) - \frac{r}{L} \sum_{j=1}^{L} x_{j-1}x_j(1-x_{j+1})P([x_n]; t)$$

(B.1)

where $x_i$ denote the occupancy of site $i$ and $[x_n]$ denote the whole configuration (i.e. $[x_n] = \{x_1, \ldots, x_L\}$). The second and third terms correspond to states that can flow into state $[x_n]$ while the last two terms correspond to flow out of state $[x_n]$. Note that the allowed transitions are:

$$010 \rightarrow 001$$

$$110 \rightarrow 101.$$  

(B.2)

In steady state the difference between $P([x_n]; t+1)$ and $P([x_n]; t)$ should be zero. We now assume the two-cluster ansatz, and if it yields a zero difference it is the exact solution.
The ansatz is:

$$P (\{x_n\}) = \frac{p_{11}^{n_{11}} p_{00}^{n_{00}} p_{10}^{n_{10}} p_{01}^{n_{01}}}{Z} = \frac{p_{11}^{n_{11}} p_{00}^{n_{00}} p_{10}^{2n_{10}}}{Z}$$

(B.3)

$$\frac{p_{01}^2}{p_{11} p_{00}} = r$$

where \(n_{x,y}\) is the number of clusters \(x y\) in the configuration, \(P_{xy}\) is the steady state probability for this cluster and \(Z\) is a normalisation. Notice that the second equation in the ansatz is equivalent to the equation (A.6). From

$$L = 2n_{10} + n_{00} + n_{11}$$

(B.4)

we get:

$$N = n_{10} + n_{11}$$

we get:

$$P (\{x_n\}) = \frac{p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}}}{Z}$$

(B.5)

The number of ‘10’ clusters in a configuration is generally different from the number of these clusters in the configurations that flow into it. Consider the transition:

$$x_{j-2}010 x_{j+2} \rightarrow x_{j-2}001 x_{j+2}$$

(B.6)

where the left side is part of a state that flows into \(\{x_n\}\). Denote this state as (i). The right side is part of \(\{x_n\}\) which we denote by (ii). If \(x_{j+2} = 0\) then \(n_{10}(i) = n_{10}(ii)\), while if \(x_{j+2} = 1\) then \(n_{10}(i) = n_{10}(ii) + 1\). In the same spirit, if we look at the transition:

$$x_{j-2}110 x_{j+2} \rightarrow x_{j-2}101 x_{j+2}$$

(B.7)

we get that if \(x_{j+2} = 0\) then \(n_{10}(i) + 1 = n_{10}(ii)\); if \(x_{j+2} = 1\) then \(n_{10}(i) = n_{10}(ii)\).

Plugging the ansatz in the master equation B.1, we divide each of the first two sums to a sum over two subsets: \(J_1 = \{j | x_{j+2} = 0\}\), \(J_2 = \{j | x_{j+2} = 1\}\). Therefore, we know what is \(n_{10}\) in each sum. We get:

$$L Z \Delta P = \sum_{j \in J_1} (1 - x_{j-1}) (1 - x_j) x_{j+1} p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}}$$

$$+ \sum_{j \in J_2} (1 - x_{j-1}) (1 - x_j) x_{j+1} p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}+1}$$

$$+ r \sum_{j \in J_1} x_{j-1} (1 - x_j) x_{j+1} p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}-1}$$

$$+ r \sum_{j \in J_2} x_{j-1} (1 - x_j) x_{j+1} p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}}$$

$$- \sum_{j=1}^L (1 - x_{j-1}) x_j (1 - x_{j+1}) p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}}$$

$$- r \sum_{j=1}^L x_{j-1} x_j (1 - x_{j+1}) p_{11}^N p_{00}^{L-N} \left( \frac{p_{10}^2}{p_{00} p_{11}} \right)^{n_{10}}$$

(B.8)
Using $\frac{P_{11}^N}{P_{11}^P} = r$ we get:

$$LZ\Delta P = P_{11}^N P_{00}^{L-N} r^{n_{10}} \left[ \sum_{j \in J_1} (1 - x_j) x_{j+1} + r \sum_{j \in J_2} (1 - x_j) x_{j+1} - n_{010} - rn_{110} \right]$$

$$= P_{11}^N P_{00}^{L-N} r^{n_{10}} [n_{01}^1 + rn_{01}^2 - n_{010} - rn_{110}] \quad (B.9)$$

where $n_{xyz}$ is the number of $xyz$ clusters in $\{x_n\}$, while $n_{xy}^j$ is the number of $xy$ clusters in $J_i$.

From the definition of $J_1$ and $J_2$ we see that:

$$n_{01}^1 = n_{010} \quad (B.10)$$

$$n_{01}^2 = n_{011} = n_{110}$$

Therefore:

$$\Delta P = 0 \quad (B.11)$$

The two cluster distribution is the exact distribution in steady state.

**Appendix C. Details of the two-particle system, in the $s$-model**

First we write down the equation for $P$(on, off) in steady state by equating the rates into and out from this state:

$$(K_n + K_f) P$(on, off) = $K_n P$(off, off) + $K_f P$(on, on) + $P$(on, 0, off). \quad (C.1)$$

Using two-cluster approximation, we obtain

$$(K_n + K_f) P$(on, off) = $K_n P$(off, off) + $K_f P$(on, on) + $P$(on, 0)P(0, off) + $P$(on, 0, off). \quad (C.2)$$

Approximating $P$(on, on) = $P$(on)P(on) and $P$(off, off) = $P$(off)P(off) and using probability relations, we write (C.2) as

$$(K_n + K_f) P$(on, off) = $K_n P$(off, off)P(on) + $K_f P$(on, on)P(on)

$$+ \frac{(P$(on) - P$(on, off) - P$(on)P$(on))(P$(off) - P$(on, off) - P$(off)P$(off))}{P(0)} \quad (C.3)$$

Noting that

$$P(0) = \frac{L - 2}{L},$$

$$P(on) = \frac{2K_n}{L(K_n + K_f)},$$

$$P(off) = \frac{2K_f}{L(K_n + K_f)},$$

(where $L$ is the size of the system) we can solve (C.3) to find that

$$P(on, off) = \frac{4K_nK_f(1 + K_f + K_n)}{4L^2(K_n + K_f)^3} \quad (C.5)$$
Recalling that $P_0 = P_{\text{on, off}} + P_{\text{on, on}}$, we obtain equation (13) in the main text. By repeating the same steps for $P_{\text{off, on}}$ and using $B_0 = P_{\text{off, off}} + P_{\text{off, on}}$ one finds that
\[
\frac{P_{\text{off, off}}}{B_0} = \frac{P_{\text{on, off}}}{P_0 B_0} \quad \text{as in (13)}.
\]

**Appendix D. Details of the modified car oriented mean field calculation for the s-model**

Due to the correction in mCOMF the probabilities for jumping in the next time step change accordingly:

\[
g(0|P_0, B_0) = F(c)\tilde{K} + G(c)P_0, \quad \text{and} \quad g(1|P_0, B_0) = G(c)K - G(c)P_0. \tag{D.1}
\]

We assume that $g(0|P_n, B_n)$ and $g(1|P_n, B_n)$ for $n > 0$ are independent of $n$ (motivated by figure 6). We can calculate them from the following equality:

\[
\tilde{K} + P_0 = g(0|P_0)P_0 + g(0|B_0)B_0 + \sum_{n=1}^{\infty} g(0|P_n)P_n + g(0|B_n)B_n
\]

\[
= \left( F(c)\tilde{K} + G(c)P_0 \right) (B_0 + P_0) + g(0|P_k, B_k, k > 0) \left( 1 - B_0 - P_0 \right). \tag{D.2}
\]

We are now ready to write the equations for the $P_n(t), B_n(t)$:

\[
P_0(t + 1) = P_0(t) \left( 1 - \frac{g(1, t|P_0)}{2N} - \frac{K_f}{2N} \right) + B_0(t) \frac{K_n}{2N} + \frac{P_1(t)}{2N},
\]

\[
P_n(t + 1) = P_n(t) \left( 1 - \frac{g(1, t|P_n)}{2N} - \frac{K_f}{2N} \right) + B_n(t) \frac{K_n}{2N}
\]

\[
+ \frac{P_{n-1}(t)g(1, t|P_{n-1})}{2N} + \frac{P_{n+1}(t)}{2N}, \quad n > 0,
\]

\[
B_0(t + 1) = B_0(t) \left( 1 - \frac{g(1, t|B_0)}{2N} - \frac{K_n}{2N} \right) + P_0(t) \frac{K_f}{2N},
\]

\[
B_n(t + 1) = B_n(t) \left( 1 - \frac{g(1, t|B_n)}{2N} - \frac{K_n}{2N} \right) + P_n(t) \frac{K_f}{2N} + B_{n-1}(t) \frac{g(1, t|B_{n-1})}{2N}, \quad n > 0. \tag{D.4}
\]

At steady state we obtain

\[
P_1 = P_0 \left( g(0|P_0) + K_f \right) - K_n B_0, \quad \text{and} \quad P_{n+1} = \left( 1 + g(1|P_n) + K_f \right) P_n - B_n K_n - P_{n-1} g(1|P_{n-1}), \tag{D.5}
\]

\[
B_0 = \frac{K_f}{1 + K_n - g(0|B_0)} P_0 \quad \text{and} \quad P_n K_f + B_{n-1} g(1|B_{n-1}). \tag{D.6}
\]

Solving the recursion relations (D.5) and (D.6) we can find $P_n$ and $B_n$ as functions of $P_0$ (too lengthy an expression to show here). It is now possible to calculate $P_0$ at steady state. Consider the identity

\[
\sum_{n=0}^{\infty} (n + 1)(P_n + B_n) = \frac{L}{N} = \frac{1}{c}. \tag{D.7}
\]
which comes from the fact that a particle with a space in front of it of size $n$ effectively occupies $n + 1$ sites. Plugging the results for $P_n$ and $B_n$ in (D.7) we can obtain an expression for $P_0$ (too lengthy an expression to show here). Finally, from $P_0$ we can extract the current by (10).

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