Cell order in bacterial swarms arises from reversals of moving direction

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Short Abstract — **Using a biomechanical model, we show that periodic reversals of moving direction in populations of rod-shaped bacteria in general can lead to extensive ordering of cells, thus enabling them to effectively resolve traffic jams formed during swarming. We show that an optimal reversal period and an optimal cell length exist for producing such order. The optimal reversal period and the optimal cell length are connected by a simple relation.**

I. BACKGROUND

MANY bacteria are able to spread rapidly over surfaces by the process of swarming [1, 2]. Bacterial swarms are model systems for the study of multicellularity [3] and biological self-organization [4]. Swarming bacteria have rod-shaped cells [1], and are observed to move smoothly even when they are packed together at high density. Why don't swarming cells interfere with each others' movements?

One efficient swarmer, *M. xanthus*, reverse their gliding directions regularly with an average period of 8.8±2.1 minutes [5]. Recently we have shown that the molecular regulatory circuit for reversal in *M. xanthus* has evolved to optimize the swarming efficiency [5]. In addition, frequent polarity reversal during swarming is found in *Phormidium*, a filamentous gliding cyanobacterium, in *Flavobacterium johnsoniae* and in hyper-flagellated *E. coli*; the polarity reversal of hyper-flagellated E. coli is a unique behavior occurred in swarming and different from the usual tumbling occurred in swimming [6]. Can it be coincidental that several different bacteria reverse frequently when they swarm?

II. RESULTS

Investigating a cell-based biomechanical model of bacterial swarming in general, we found that swarming bacteria can use directional reversals to build up orientational order in dense and initially disorganized swarms [7]. An optimal reversal period and an optimal cell length exist for producing such order. Moreover, these theoretically optimal values for *M. xanthus* swarms coincide with the values found experimentally for wild type *M. xanthus*. The optimal reversal period and the optimal cell length are connected by a simple relation, which allows us to make testable predictions about the swarming of other rod-shaped bacteria, such as *E. coli*. The predicted reversal period agrees surprisingly well with a recent experimental result [6], although the mechanics of swimming of E. coli swarmer cells are fundamentally different from the mechanics of gliding in *M. Xanthus*.

III. CONCLUSION

Given the observations of reversing behavior in several bacterial genera, we suggest that swarming bacteria evolved the use of directional reversals and elongated shapes to enable their cells to flow smoothly in dense crowds or to migrate towards the source of attractants. For flagellated bacteria in a swarm, efficient running and tumbling required for performing chemotaxis would seem difficult, if not impossible, to achieve when the cell density is very high. By contrast, collisions between flexible rod-shaped cells that are always moving in the direction of their long axis while reversing regularly could change the orientation of cells and increase spatial order with high efficiency.

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