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BIOFILMS

Shocking biofilms

Members of bacterial communities within a biofilm can coordinate to carry out specific functions through cell-to-cell communication. In addition to quorum sensing, in which small molecules are secreted and detected by bacteria in a community, bacteria have recently been found to propagate electrical signals in biofilms to coordinate group behaviour. Now, Humphries *et al.* report that these electrical signals can also influence the behaviour of distant bacteria that are not part of the biofilm.

First, the authors used microfluidics to investigate the interaction dynamics between motile cells and an electrically oscillating biofilm community of *Bacillus subtilis* and found that fluorescently labelled motile cells were attracted to the edge of the biofilm. Using a cationic fluorescent dye, they showed that the increase in the cell density at the edge of the biofilm correlated with oscillations in the membrane potential of the biofilm. In agreement with this, motile bacterial cells were not attracted to the biofilm in the absence of electrical oscillations, and the attraction was dependent on a functional flagellum.

Next, to investigate whether the observed electrical oscillations and the attraction of motile bacteria to the biofilm were due to oscillations in extracellular potassium concentration, a strong source of potassium was introduced into the microfluidic system as a potential decoy for the motile cells. Indeed, motile cells migrated towards the alternative potassium source instead of in the direction of the biofilm. Furthermore, disruption of the potassium channel function resulted in diminished electrical signalling within the biofilm and a corresponding decrease in motile cell attraction to the community was observed. These findings suggest a crucial role of the potassium ion channel for generating the electrical current, which, in turn, generates electrical signals that attract motile bacteria.

> “tumbling frequency of bacteria is influenced by the potassium gradient that is generated by the biofilm”

The authors hypothesized that the observed phenomenon was due to a functional relationship between extracellular potassium concentration, cell membrane potential of motile cells and the tumbling frequency of motile cells. In line with this theory, deletion of the major potassium pump in motile cells resulted in a negative resting membrane potential of motile cells and increased migration towards the biofilm was observed, which implies that the attraction depends on the sensitivity of motile cells to potassium gradients that are generated by the biofilm. This was confirmed by imaging 2,668 motile cell trajectories during the peak of the electrical signal, which revealed that tumbling frequency during the peak was inversely related to the distance from the biofilm, implying that the tumbling frequency of bacteria is influenced by the potassium gradient that is generated by the biofilm. Remarkably, motile *Pseudomonas aeruginosa* cells could also be attracted to *B. subtilis* biofilms. *P. aeruginosa* is a Gram-negative bacterium that is evolutionarily distant to the Gram-positive *B. subtilis*, thus it seems that electrically mediated attraction of cells to biofilms is species independent and could operate in many diverse species of bacteria. In sum, this study highlights a heretofore unappreciated role of electrical signalling in biofilm communities and in their interaction with their environment, and provides a new perspective on the formation of mixed species biofilms.

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ORIGINAL ARTICLE Humphries, J. *et al.* Species-independent attraction to biofilms through electrical signaling. *Cell* **168**, 200–209 (2017)