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Exploring the function of bacterial chemotaxis

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Bacterial chemotaxis is a classical subject: our knowledge of its molecular pathway has grown very detailed, and experimental observations, as well as mathematical models of the dynamics of chemotactic populations, have a history of several decades. This should not lead to the conclusion that only minor details are left to be understood. Indeed, it is believed that bacterial chemotaxis is under selection for efficiency, yet the underlying functional forces remain largely unknown. These aspects are discussed here by the presentation of illustrative examples related to the role of adaptation and signal integration. Both are expected to be important in ecologically relevant conditions, where chemotaxis should be strongly coupled with metabolism and growth, due to the presence of diverse chemoattractant cues and their active consumption by multiple types of bacteria competing for growth.

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The importance of orientation and active motion for the survival of many living organisms has led to the evolutionary emergence of a variety of motility mechanisms. Bacteria respond to a wide range of stimuli such as concentration of chemicals (chemotaxis), light (phototaxis), electric fields (galvanotaxis), magnetic fields (magnetotaxis), pH (pH-taxis), temperature (thermotaxis) — see [1] for an introduction. Here, we shall consider chemotaxis, whereby bacteria are able to navigate environmental landscapes of chemo-attractants and repellents. More specifically, we shall focus on the rod-shaped Gram-negative bacterium *Escherichia coli*, which is the model organism for bacteria swimming by using bundles of flagella. Assembled bundles propel the cell during phases of run, while their disassembling during tumbles leads to random reorientations of the bacterial direction of motion [2].

This mini-review will focus on the function of chemotaxis, namely adaptation and signal integration, which are major aspects that remain largely open. We briefly recall known properties of the phenomenology and the transduction pathway of *E. coli* chemotaxis that are needed in the sequel. For more details and other aspects not covered here, the reader is referred to [1,3–5].

Feedback control of *E. coli* chemotaxis is richer than perfect adaptation

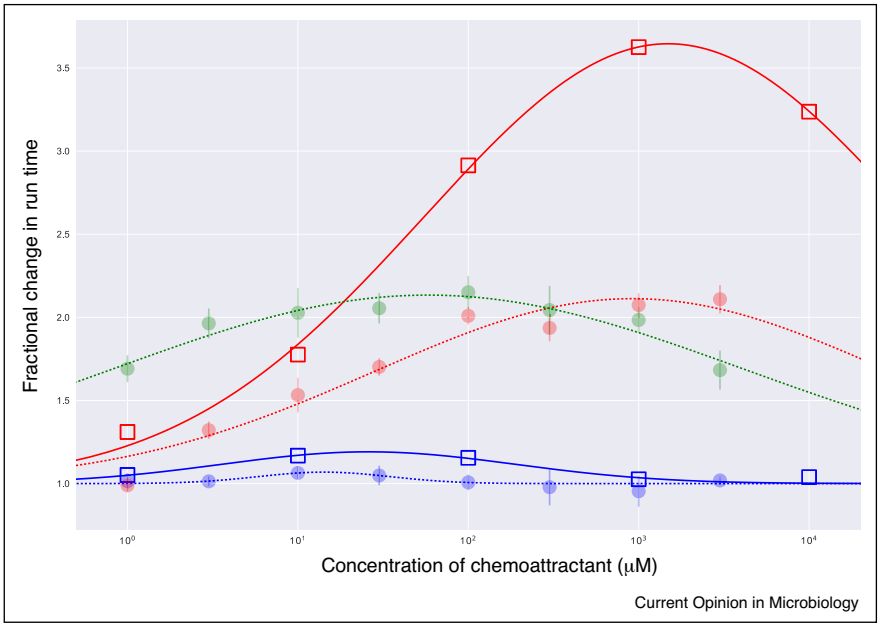
Perfect adaptation is a widespread phenomenon in biological sensing: it amounts to the sensory system being structured so as to filter out low-frequency (DC) components of the input signal. Chemotaxis towards aspartate is perfectly adapted in a wide range of concentrations [6–9]. That operationally implies that the tumbling frequency returns to its prestimulus level after the application of a step in aspartate concentration (see Figure 1). The adaptation time increases from few seconds for low steps [7], to several minutes for high steps [6], with a trend that is well captured by theoretical considerations [10]. Moreover, cells are sensitive to fold change of aspartate rather than absolute change [11], that is, the response to aspartate obeys the Weber's law found also in other sensory pathways. These striking effects and their importance for other biological systems have led studies of *E. coli* chemotaxis to focus mostly onto those aspects related to perfect adaptation.

In fact, adaptation is not perfect for all attractants and concentrations. In particular, the chemoattractant serine, preferentially bound by the Tsr receptor, is not perfectly adapted, which is witnessed by the frequency of tumbling reducing as the concentration of serine increases [2] (see Figure 1). In the linear regime, adaptation is quantified by the integral of the response to an impulse stimulus, and perfect adaptation corresponds to a vanishing integral [7]. For serine the areas of the positive and the negative lobes differ [12], and two (inverted) non-equal lobes are also observed for the chemorepulsion to leucine [12]. Even for aspartate (or its non-metabolizable analogue alpha-methyl-DL-aspartate), the *E. coli* chemotaxis pathway shows imprecise adaptation at high concentrations [13].

Coupling in the signal processing of different aminoacids

The main receptors for aminoacids, Tar and Tsr, share the same downstream pathway, namely the kinase CheA

Figure 1



Running times for perfectly adapted and non-adapted chemotactic responses. The curves report the variation of the running time with the background (uniform in space and time) concentration of an attracting aminoacid. Squares/circles refer to data in [2] for the strain AW405 and [30•] for the strain RP437, respectively. Running times have been normalized to the value for aspartate (the reason why ordinates have no units). The blue curves refer to aspartate, which is perfectly adapted: the running time is essentially constant throughout a wide range of concentrations. Conversely, the red curves for a background of serine feature substantial variations, which reflect the absence of perfect adaptation to that aminoacid. Finally, the green curve refer to the data in [30•], where a fixed background of 30 μm of serine was added to a variable background of aspartate, which is the value reported on the abscissae. The presence of the serine background induces loss of perfect adaptation to aspartate for the reasons discussed in the text and sketched in Figure 2.

that controls the phosphorylation of the second messenger CheY [1]. This sharing introduces a first strong coupling, which is further strengthened by the partial overlap in the specificity of some aminoacids for the two types of receptors Tar and Tsr [14]. Moreover, clusters mainly packed at the cell poles [15–17] are composed of a strongly coupled mixture of Tar and Tsr receptors, which is well described by allosteric models [18–20]. In particular, the so-called assistance neighborhood mechanism [21,22] makes that receptors in a cluster share the methylation sites responsible for adaptation of the chemotactic response. The notable consequence is that the presence of multiple aminoacids (even if they preferentially bind different receptors) leads to a strong level of signal integration, which modifies the combined response with respect to the individual ones, as well as the chemotactic behavior, as we shall discuss below.

E. coli ranking of different aminoacids

Couplings discussed in the previous section naturally begs the question of *E. coli* preferences among aminoacids, and whether the non-adaptation to serine might be a quirk. This possibility is ruled out by early studies [23,24] that showed variable preferences and strong chemoattraction to serine. Furthermore, recent FRET data [14] have shown that most of the chemoattractive aminoacids are also preferentially utilized during growth, and that their chemoattractant potency correlates with their order of metabolic utilization. For instance, aspartate and serine (which are the strongest binders of Tar and Tsr, respectively), are also rapidly consumed by *E. coli* in complex media [25,26]. In addition to attractant responses, repellent responses were observed for isoleucine, leucine, tryptophan or valine. Some of these amino acids are known to inhibit bacterial growth [27,28], and the repulsion might then be related to this inhibitory effect. Indeed, the identified repellents overlap strongly with the amino acids that are excreted by cells in the stationary phase [29•]. In summary, existing data point to a strong coupling between the chemotactic and the metabolic preferences of *E. coli*, in particular for the two aminoacids, aspartate and serine, that are preferential binders of Tar and Tsr receptors.

Behavioral consequences at the single-cell level

Adaptation brings the advantage of adjusting the dynamic range and avoiding saturation that would be rapidly brought by the strong nonlinearities in the chemotaxis pathway [19]. While this is a definite advantage, the above discussion for the case of serine clearly shows that partial

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