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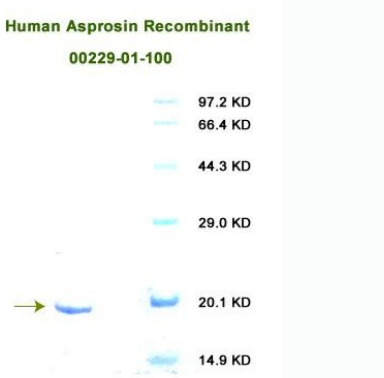
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Imprecision of Adaptation in *Escherichia coli* Chemotaxis

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Abstract

Adaptability is an essential property of many sensory systems, enabling maintenance of a sensitive response over a range of background stimulus levels. In bacterial chemotaxis, adaptation to the present level of pathway activity is achieved through an integral feedback mechanism based on activity-dependent methylation of chemoreceptors. It has been argued that this architecture ensures precise and robust adaptation regardless of the ambient ligand concentration, making perfect adaptation a celebrated property of the chemotaxis system. However, possible deviations from such ideal adaptive behavior and its consequences for chemotaxis have not been explored in detail. Here we show that the chemotaxis pathway in *Escherichia coli* shows increasingly imprecise adaptation to higher concentrations of attractants, with a clear correlation between the time of adaptation to a step-like stimulus and the extent of imprecision. Our analysis suggests that this imprecision results from a gradual saturation of receptor methylation sites at high levels of stimulation, which prevents full recovery of the pathway activity by violating the conditions required for precise adaptation. We further use computer simulations to show that limited imprecision of adaptation has little effect on the rate of chemotactic drift of a bacterial population in gradients, but hinders precise accumulation at the peak of the gradient. Finally, we show that for two major chemoeffectors, serine and cysteine, failure of adaptation at concentrations above 1 mM might prevent bacteria from accumulating at toxic concentrations of these amino acids.

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Introduction

Adaptation is an important property of many sensory systems that allows them to recover from an initial stimulation and to regain activity and responsiveness even at high levels of persistent stimulation. One of the most analyzed models for adaptation in cell signaling is bacterial chemotaxis, where the recovery from the initial attractant or repellent stimulation is mediated by changes in the methylation levels of chemoreceptors [1–3]. Receptors are methylated or demethylated on four to five specific glutamate residues by the methyltransferase CheR and the methyl-erastase CheB. CheR preferentially recognizes the inactive state of the receptors and increases receptor activity through methylation, thus counteracting the effects of chemoattractants that inhibit receptor activity. CheB preferentially demethylates active receptors and thereby lowers their activity upon removal of attractants or addition of repellents. In the absence of a gradient, these feedbacks ensure that receptor methylation and therefore activity of the receptor-associated kinase are adjusted to generate intermediate levels of the phosphorylated response regulator CheY (CheY-P). CheY-P binds to flagellar motors and induces a switch in the direction of motor rotation that results in cell tumbling and reorientation. As a consequence, an intermediate level of CheY-P that falls into the narrow working range of the motor [6] results in an intermediate switching rate and produces a random sequence

of runs and tumbles. This allows cells to explore their environment and, importantly, by the suppression of tumbles, to respond sensitively to an increase in attractant concentration thus yielding longer runs in that favorable direction [7,8].

High precision of adaptation in the presence of ambient ligand is commonly assumed to be an essential feature of chemotaxis [9–11], because it ensures that the level of CheY-P, and as a consequence the steady state tumbling bias of the cell, are adjusted within an optimal range for chemotaxis [12]. However, already an early study of *Escherichia coli* chemotaxis [8] had reported highly imprecise adaptation to high concentrations of serine, a ligand sensed by the major receptor Tar. Imprecise adaptation to several other attractants, including high concentrations of aspartate or its non-metabolizable analogue γ -methyl-DL-aspartate (MeAsp) that are sensed by another major *E. coli* receptor Tar, has also been confirmed by more recent studies [13–15].

In this work, we aimed to better understand both the limits of precise adaptation in *E. coli* chemotaxis and the importance of imprecise adaptation. We show that adaptation becomes increasingly imprecise at high ligand concentrations, most likely due to saturation of available methylation sites. Using computer simulations we show that a limited precision of adaptation has little effect on the rate of the chemotactic movement in a gradient, but reduces the ability of bacteria to accumulate at exactly the peak of



Enterohemorrhagic e.coli 0157. Enterohemorrhagic e. coli toxin. Enterohemorrhagic e.coli treatment. Enterohemorrhagic e. coli food. Enterohemorrhagic e. coli.

Enterohemorrhagic E. Coli (EHEC) Real-time PCR Silent Kit PDPS-AR017 Silence Creative Biogene Nucleic Acid Type: DNA Species: Bacteria Storage Status: Store -20°C View AllClose *Escherichia coli* is (*E. coli*) a gram-negative microorganism that can be an innocuous resident of the gastrointestinal tract, but also has the pathogenic tract to cause gastrointestinal diseases. The pathogenic variants of *E. coli* (patovars or patotypes) cause a lot of morbidity and mortality around the world, because they have low infectious doses and are transmitted through ubiquitous means, including food and water. Of the strains that cause diarrhoeal diseases, six pathotypes are recognized: Enterohaemorrhagic *E. coli* (EHEC), Enterotoxigenic *E. coli* (ETEC), Enteroinvasive *E. coli* (EIEC), Enteropathogenic *E. coli* (EPEC), Enteraggregative *E. coli* (EAaggEC), and *E. coli* (EPEC). In addition, different strains of *E. coli* may belong to more than one group of patotype due to the expression of different virulence factors. Enterohaemorrhagic *E. coli* (EHEC) is a subset of *E. coli* (STEC) toxin producer Shiga, also called verotoxine producing *E. coli*. STEC is a diverse group of food pathogens that cause a wide spectrum of human diseases, ranging from mild diarrhea to severe human diseases, including hemorrhagic colitis (HC) and hemolytic uremic syndrome (HUS). Its virulence is partly related to its ability to produce Stx1 and/or Stx2, powerful cytotoxins that inhibit the synthesis of proteins from host cells. In addition, the typical EHEC is often characterized by the production of an external membrane protein called intimin, the *hlyE* gene. This protein mediates the tight attachment of bacteria to enterocytes. The lesions (both attachment and narrow (injuries a/e)) in the colon. 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Examples of serotypes of STEC include : E. coli O157:H7; E.coli O157:NM; E.coli O26:H11; E. coli O145:NM; E. coli 0103:H2; and E. coli O111:NM. STEC are sometimes referred to as verocytotoxigenic E. coli (VTEC) or as Enterohemorrhagic E. coli (EHEC). EHEC are a subset of STEC which can cause hemorrhagic colitis or HUS. [Rev. 8/19/2015 11:40:02 AM] [NAC-446 Revised Date: 8-15] CHAPTER 446 - FOOD ESTABLISHMENTS. GENERAL PROVISIONS. 446.010 Definitions.. 446.0102 "Accessible ..." [Rev. 8/19/2015 11:40:02 AM] [NAC-446 Revised Date: 8-15] CHAPTER 446 - FOOD ESTABLISHMENTS. GENERAL PROVISIONS. 446.010 Definitions. . 446.0102 "Accessible ..." Examples of serotypes of STEC include : E. coli O157:H7; E.coli O157:NM; E.coli O26:H11; E. coli O145:NM; E. coli 0103:H2; and E. coli O111:NM. STEC are sometimes referred to as verocytotoxigenic E. coli (VTEC) or as Enterohemorrhagic E. coli (EHEC). EHEC are a subset of STEC which can cause hemorrhagic colitis or HUS. Examples of serotypes of STEC include : E. coli O157:H7; E.coli O157:NM; E.coli O26:H11; E. coli O145:NM; E. coli 0103:H2; and E. coli O111:NM. STEC are sometimes referred to as verocytotoxigenic E. coli (VTEC) or as Enterohemorrhagic E. coli (EHEC). EHEC are a subset of STEC which can cause hemorrhagic colitis or HUS. [Rev. 8/19/2015 11:40:02 AM] [NAC-446 Revised Date: 8-15] CHAPTER 446 - FOOD ESTABLISHMENTS. GENERAL PROVISIONS. 446.010 Definitions. . 446.0102 "Accessible ...

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