



Introduction

How does a sperm cell find the ovum? How do white blood cells direct themselves to the site of injury or inflammation? How do unicellular microorganisms find their food and avoid hostile environments? The common answer to all these questions is: By chemotaxis (Figure 1). Similarly to a butterfly that is attracted to a flower by odor, or a male insect that is attracted to the female by pheromones, many organisms (primarily, but not solely, unicellular) and cells of multicellular organisms are attracted to their targets or repelled from certain chemicals by chemotaxis.

What is chemotaxis? Today this term is used to denote cell movement towards or away from a chemical source, defined as positive and negative chemotaxis, respectively. The chemical is defined as chemoattractant or chemorepellent, respectively. According to the common, broad definition of chemotaxis, any cell motion that is affected by a chemical gradient in a way that results in net propagation up a chemoattractant gradient or down a chemorepellent gradient is defined as chemotaxis. This definition includes three narrower definitions that were used in the past to distinguish between different behavioral mechanisms by which cells approach chemoattractants and avoid chemorepellents:

- (a) The original, narrow definition of chemotaxis, also termed topotaxis—a change in the *direction* of movement resulting from active alignment of the cell's axis according to a chemical gradient.

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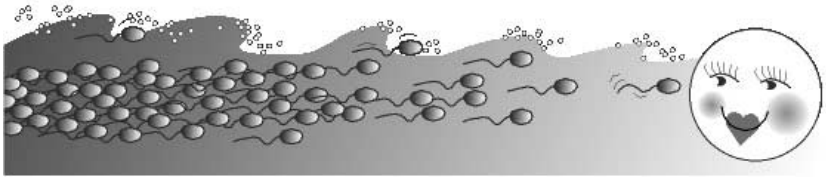


Figure 1. Chemotaxis of sperm cell to the egg: “the origin of life.”

Chemotaxis of cells with amoeboid movement (e.g., white blood cells) usually follows this mechanism (Chapters 5 and 6).

- (b) A phobic response—a decreased linear velocity in response to a chemical stimulus (normally a stop response) followed by a change of direction. Some bacteria (e.g., *Rhodobacter sphaeroides*) follow this mechanism (Chapter 3).
- (c) Klinokinesis—a change in the frequency of spontaneous directional changes in response to a chemical stimulus [7–9, 11, 14, 30, 31]. Some bacteria (e.g., *E. coli*) employ this behavioral mechanism (Chapter 3).

The common denominator of all these mechanisms is that their end result is a directional change up a chemoattractant gradient or down a chemorepellent gradient. These mechanisms should be distinguished from chemokinesis (also termed orthokinesis [7]), which is a mechanism of response that does not involve directional changes and is, therefore, not a part of the broad definition of chemotaxis. In chemokinesis, the *linear* velocity of the cell or organism is altered by the stimulus [7]. Chemotaxis and chemokinesis may occur in parallel, as in the case of the response of sperm cells to substances secreted from the egg (Chapter 7).

The outcome of positive chemotaxis would usually be accumulation of cells or organisms in a region with higher concentration of the chemoattractant. The outcome of negative chemotaxis would usually be dispersal of cells or organisms from a region with higher concentration of the chemorepellent. However, accumulation and dispersal may also be caused by chemokinesis and trapping, for which reason they alone cannot be used as a criterion for chemotaxis (Chapter 7).

Chemicals are not the only stimuli sensed by cells and organisms. Other stimuli include light, temperature, touch, etc. In all cases, the name of the response includes a prefix that describes the stimulus (chemo-, photo-, thermo-, etc.) and the suffix *taxis*, meaning moving towards or away from the stimulus. For example, movement directed by

Table 1. Nomenclature of directed movements in response to various stimuli.

Term	Stimulus	Examples of responsive species	References
Chemotaxis	Chemical	Bacteria, archaea, amoebae, white blood cells, sperm cells	This book
Elasticotaxis	Elastic force	Some gliding bacteria (<i>Myxococcus xanthus</i>)	[10]
Electrotaxis	Electrical field	Amoebae	[40]
Galvanotaxis	Electrical current	Bacteria, spermatozoa	[1, 39]
Geotaxis or gravitaxis	Gravity	Bacteria, ciliates (<i>Paramecium</i>), flagellates	[3, 12, 15, 33]
Magnetotaxis	Magnetic field	Bacteria	[5, 25, 38]
Phototaxis	Light	Bacteria, archaea, amoebae, flagellates	[2, 6, 13, 17, 18, 22, 26, 29, 32, 35, 36]
Thermotaxis	Temperature	Bacteria, ciliates, amoebae, nematodes, spermatozoa, trophoblastic cells, leukocytes	[4, 16, 19, 20, 27, 28, 34, 37]
Thigmotaxis or mechanotaxis	Touch, mechanical force	Ciliates, flagellates, endothelial cells	[21, 23, 24]

a light or a temperature gradient is termed phototaxis or thermotaxis, respectively. Table 1 includes the nomenclature of the known responses to various stimuli. When the response to the stimulus is directed growth rather than directed movement, the suffix is *tropism*, meaning growing towards or away from the stimulus: chemotropism, phototropism, etc. As will be discussed later in this book, some of these responses, e.g., bacterial chemotaxis and thermotaxis, or archaeal chemotaxis and phototaxis, share a common molecular mechanism. Others, e.g., galvanotaxis and magnetotaxis, are more passive processes.

This book reviews some of the best-characterized chemotaxis systems, from bacteria to human cells. In so doing, the book demonstrates how basic chemotaxis is to life, how widespread it is, and how versatile its physiological functions are. The book attempts to present the state of the art of a number of representative molecular mechanisms of chemotaxis, to indicate unanswered questions surrounding each mechanism, and to suggest future directions for research. In some systems, the implications for health conditions are discussed. Thus, in the next chapter (Chapter 2), Joseph Lengeler surveys the systems and phenomena in which chemotaxis appears to have a role. Some issues

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raised in Chapter 2 are dealt with again, usually in more detail, in subsequent chapters. In Chapter 3, I review in depth the behavioral and molecular mechanisms of bacterial chemotaxis—the best-understood behavioral system. In Chapter 4, Mazal Varon and David Gutnick discuss how chemotaxis may also be involved in prokaryotic cell–cell communication. In Chapter 5, Jeffrey E. Segall and colleagues do the same for eukaryotes, describing chemotaxis of amoebae and other cells of multicellular eukaryotes with amoeboid movement. In Chapter 6, Geneva M. Omann describes the physiology and the molecular mechanisms underlying chemotaxis of another fascinating system of eukaryotic cells with amoeboid movement—white blood cells. In Chapter 7, I describe what is known about chemotaxis of sperm cells. In Chapter 8, Atsushi Tamada and Fujio Murakami review how growing axons are guided in the nervous system and find their targets by multiple processes of chemotropism. Finally, in Chapter 9, I indicate points of universality and individuality, or commonality and diversity, among the mechanisms and processes discussed in this book.

This publication is aimed to serve as both a textbook for beginners and a reference book for professionals. For easier reading, each chapter that reviews a certain chemotaxis system follows a standard scheme: it starts with a description of the motility mechanism specific to the system (motility is a prerequisite for chemotaxis) and ends with a description of how this motility is modulated by chemotaxis.

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