cultures, whose cross-influences are apparent in many areas of Mesoamerica during the period. The art of the Olmec and their Middle Preclassic neighbors appears to reflect many fundamental patterns seen in later Mesoamerican remains, including certain political and religious motifs and themes, the use of the calendar, and the beginning of writing—although examples of the latter are rare.

The archaeological picture of what happened in the La Mojarra region during the succeeding Late Preclassic Period (around 300 B.C. to A.D. 300), after the waning of Olmec culture, has proven to be one of the most perplexing questions facing Mesoamericanists. Fortunately, the dates on the La Mojarra stela fall within this "epi-Olmec" span. Just as important is the sheer size and weight of the monument itself: Unlike the Tuxtla Statuette and several other artifacts that bear samples of the same script, it is emphatically not a portable object whose appearance by the bank of the Acula River might be ascribed to ancient or recent caprice.

Justeson and Kaufman, faced with that which brings joy to even the most staid and sober student of epigraphy and linguistics, namely, a lengthy and uncommonly clear text in what stands so far as Mesoamerica's earliest complex system of hieroglyphic signs for words and syllables, have wrested much information from the La Mojarra stela. Using it and the much shorter inscription on the Tuxtla Statuette as an independent control (for no single text can serve alone as its own key), they identify the language of the text as pre–proto-Zoquean, an ancestor of languages still spoken in the heart of Mesoamerica and, perhaps, a direct descendent of the language spoken by the Olmec themselves. Many graphic elements in the script itself, they point out, appear closely related to later Maya hieroglyphic writing.

Fully as important as these purely linguistic and epigraphic deductions is the specific content of the La Mojarra text. According to the proposed decipherment, the 21 columns of hieroglyphs constitute a sort of Late Preclassic "political poster" dealing with the accession to power of the individual portrayed. The text refers to warfare, ritual activity, astronomical events, and calendar anniversaries. Such subject matter perfectly anticipates the content of later Classic Period images and inscriptions from the Maya area and elsewhere in Mesoamerica.

The discovery at La Mojarra reminds us that much remains to be done, not only in looking for previously unrecognized examples of this unexpectedly elaborate writing system, but also in systematic programs of field investigation among the silent mounds that fill the pastures of present-day La Mojarra and at other sites in southeastern Veracruz. It is surely one of the most crucial regions for our understanding of the course of culture and civilization in ancient Mesoamerica.

Does *E. coli* Have a Nose?

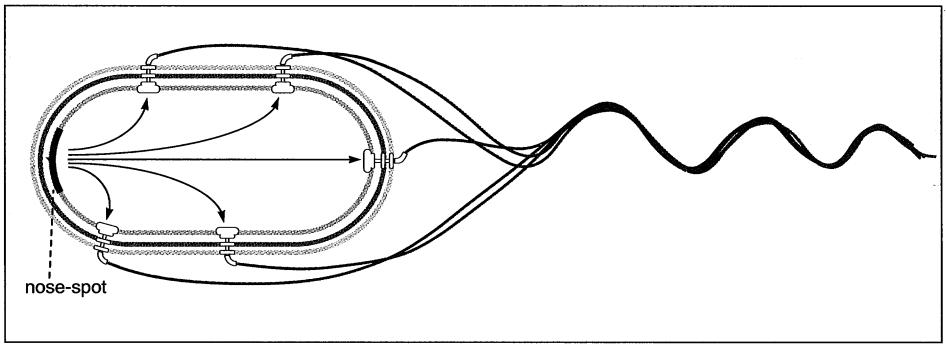
John S. Parkinson and David F. Blair

The remarkably sophisticated chemotactic behavior of *Escherichia coli* offers a tractable system for elucidating principles of sensory transduction at the molecular level. Julius Adler, who initiated modern work on bacterial chemotaxis in the 1960s, showed early on that *E. coli* has specific receptors for sensing chemicals in its environment (*1*). Although attracted to various nutrients and repelled by alcohols and other noxious compounds, the cells clearly detect the chemicals themselves, not the physiological benefits or harm they cause.

Unlike the situation in eukaryotic cells, where sensory receptors can be arranged in patches for spatial discriminations, the small size and rapid movements of bacteria effectively preclude gradient sensing based on comparison of chemical concentrations at different points on the cell. Instead, bacteria determine their heading in chemical gradients by measuring temporal concentration changes as they move about. Typical *E. coli* swimming speeds are 10 to 20 body lengths per second. By comparing current chemoreceptor occupancy with that during the previous few seconds, the cell is able to make measurements over distances of many body lengths.

If spatial discrimination is futile, how should a bacterium best deploy its chemoreceptors? The factors that limit the precision of measurements made by chemoreceptors were elaborated by Berg and Purcell (*2*). These authors concluded that for an idealized spherical cell, a uniform distribution of chemoreceptors would confer optimal sensitivity. Moreover, the capture of small molecules by cell surface receptors can be surprisingly efficient. About 3000 receptors, each with an effective radius of 1 nanometer, should be enough to capture half of all the molecules that diffuse to a cell the size of *E. coli*. Although that number of receptors represents only a small fraction of the total surface area, their capture efficiency is high because a molecule, having arrived at a cell, will usually encounter the cell surface many times again before finally diffusing away. On average, a molecule makes hundreds of "tries" at finding a receptor but does not roam widely on the cell surface. Thus, if it lands in a sizable patch of membrane devoid of receptors, it will usually escape undetected.

Nonuniform receptor arrangements would appear to be a poor strategy for bacteria, if efficient detection is their main concern. Yet, two papers in this issue of *Science* convincingly demonstrate clustering of chemoreceptors in *E. coli* and its distant relative *Caulobacter crescentus* (*3*, *4*). The *Caulobacter* case can be rationalized in terms of its unusual life-style: a sessile, stalked mother cell buds off motile daughters with a polar flagellum. The juvenile swarmers are chemotactic and probably seek out good neighborhoods before maturing into mother cells by shedding their flagellum and growing a stalk. The immotile mother cells have no need for chemoreceptors, so newly synthesized recep-



***E. coli*'s nose.** Localization of chemoreceptors in a patch at the leading end of the moving cell may be the best strategy for smelling attractants and eating them, too.

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tor molecules are somehow segregated to the daughter cells and arrayed around the base of the flagellum. Those chemoreceptors are subsequently degraded during the swarmer cell's transformation into a mother cell.

Alley and co-workers (*3*) found that *E. coli* chemoreceptors expressed in *Caulobacter* did not have the targeting signals for degradation in mother cells but were still correctly positioned in the swarmer cell. Might *E. coli* have a similar mechanism for localizing its chemoreceptors on a particular portion of the cell surface? To test this possibility, Maddock and Shapiro (*4*) visualized the chemoreceptors of *E. coli* with gold-labeled antibodies and thin-section electron microscopy. They found that over 70% of the membrane-associated receptors were in clusters, most often at one pole of the cell. Two cytoplasmic signaling proteins, CheA and CheW, which are known to interact with chemoreceptors in vitro (*5*), were also primarily located in polar, membrane-associated clusters. In receptorless mutants, CheA and CheW were distributed throughout the cytoplasm. Conversely, in cells lacking CheA or CheW, clustering and polar localization of the receptors were substantially diminished. These results suggest that interaction of CheA and CheW with chemoreceptors is instrumental in establishing or maintaining a clustered polar arrangement.

The mechanism of receptor localization in *E. coli* is not understood. On the one hand, the cell may have a specialized export apparatus that directs insertion of nascent receptor molecules at the poles. Subsequent complex formation with CheA and CheW could serve to aggregate the receptors in patches and somehow anchor them in place. Alternatively, receptor insertion might occur all over the cell surface. Interaction with CheA and CheW could lead to "rafts" of receptor complexes that diffuse laterally in the membrane until they drift to a cell pole, where they are somehow trapped.

Regardless of their provenance, it seems unlikely that *E. coli* would tolerate chemoreceptor patches if they were detrimental in any way. Receptor clustering should not pose any problems in communicating with and coordinating the flagellar motors because the protein molecules that convey chemoreceptor signals can diffuse from one end of the cell to the other in a fraction of a second (*6*). Still, a patch of receptors at one pole of the cell (see figure) would only detect about 10% of the chemoeffector molecules that reach the cell by diffusion. Perhaps detection efficiency is not the critical issue. The eventual aim of the cell is to ingest and use attractant chemicals—the cell must not only smell, but eat. In assessing the efficiency of different receptor arrangements, Berg and Purcell assumed that each receptor is a perfect sink. That can be true when the chemoreceptors are also membrane transporters, but for many attractants, including serine and aspartate, the chemoreceptors and transporters are distinct molecules. The chemoreceptors and the transport systems are therefore in competition for the ligand, and the competition is not entirely fair: binding to the chemoreceptor is reversible, whereas binding to the transport system will often result in transport of the ligand into the cell, out of reach of the sensory receptors.

If eating is more important than smelling, as seems likely, then ligand capture by transporters should be more efficient than capture by chemoreceptors. Faced with competition from transporters that are either numerous or very efficient at capturing the ligand, the chemoreceptors will detect only a fraction of the molecules impinging on the cell. Under these circumstances, clustering the receptors together might not make the situation much worse. Although a concentrated patch of receptors will be in the path of fewer incoming molecules than if they were dispersed, those molecules that do encounter a patch will be more likely to find a receptor first, before being swallowed by a transporter. The molecules impinging on a dense patch of receptors might even encounter several receptors and be registered more than once. Berg and Purcell showed that multiple encounters with a ligand do not convey any more information than a single encounter. However, multiple encounters could produce a stronger signal that is more likely to be tallied against background noise in the signaling pathway.

So, under some circumstances, clustering might not hurt. Could it help? Some areas on the cell receive more of the incoming molecules than others. Because *E. coli* is not spherical (a typical cell is more than twice as long as it is wide), more molecules diffuse to the ends than to equal areas near the middle. Also, swimming somewhat increases the flux at the front and decreases it at the rear of the cell. Thus, the efficiency of detection might be improved by placing the receptor-rich patches, the "nose-spots," at one or both ends of the cell. The benefit would be greatest if the nose-spot were actually at the nose, that is, the leading end of the cell.

The discovery of chemoreceptor patches in *E. coli* raises a number of intriguing new questions about bacterial behavior. How are the patches generated? Are other sensory or transport components similarly compartmentalized? (Perhaps areas rich in receptors are depleted of the corresponding transporters.) When a single receptor binds to its ligand, how strong is the signal it sends, relative to any background noise in the signaling pathway? Are receptors in patches more sensitive because they signal cooperatively? Does *E. coli* have a preferred leading end—a nose? If so, how does it know its head from its tail? Obviously, we still have a lot to learn about life from these fascinating creatures.

References and Notes

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7. We thank Howard Berg and David Goldenberg for helpful comments.