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EDITORIAL

Classic Spotlight: the Discovery of Bacterial Transduction

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Transduction, an indispensable genetic tool in many microbial systems, is the transfer of genetic information from a donor to a recipient cell via a virus particle. Although bacteriophages were first described early in the 20th century (1, 2), their ability to transduce bacterial genetic traits was not appreciated until almost 4 decades later. The discovery and initial mechanistic description of transduction were reported in 1952 by Norton Zinder and Joshua Lederberg in the *Journal of Bacteriology* (3). The Zinder and Lederberg paper represents a key conceptual advance in microbial genetics but is not a particularly easy read for modern-day biologists. The experiments are presented blow-by-blow in a detective yarn style that features quaint language and arcane terminology. But what elegant experiments they were!

Zinder, a graduate student in Lederberg's laboratory at the University of Wisconsin, was attempting to demonstrate genetic exchange in *Salmonella* species using the approach developed by the Lederberg group that had revealed conjugation in *Escherichia coli*. Accordingly, he created a series of doubly auxotrophic *Salmonella* strains from different parental lines and plated pairwise mixtures of them on minimal medium to look for prototrophic recombinants. The reason for using multiply mutated strains was to reduce the background of spontaneous revertants and thereby enhance detection of any rare recombinants. This approach had worked well with the *E. coli* conjugation system, but only one pairwise combination of Zinder's 20 *Salmonella* lines consistently produced prototrophs above background levels. The productive strains were designated LT-2a and LT-22a (where "a" indicates multiply auxotrophic). Analysis of unselected genetic markers in the strains indicated that the prototrophic recombinants arose from the LT-22 parent, never the LT-2 parent. Two fortuitous factors, which only came to light subsequently, proved critical to this positive result. First, strain LT-22 harbored a temperate phage, now known as P22, that could infect and lyse the P22-sensitive LT-2 strain. Second, the two auxotrophic mutations in the LT-22 parent just happened to be tightly linked, allowing them to be corrected by a single transducing fragment, an amazing stroke of luck (4).

Zinder and Lederberg investigated the mechanism of genetic exchange with the productive LT-2/LT-22 strain pair. Their best-known experiment, prominent in microbial genetics texts, employed a U-tube and filter apparatus like the one devised by Bernard Davis to show that bacterial conjugation required cell-cell contact between the parental strains (5). Each strain was put in one arm of the U-tube, separated from the other by a filter impermeable to bacterial cells. This experiment showed that, in contrast to conjugation, the transduction of prototrophic alleles from LT-2 to LT-22 did not require cell-cell contact. Further U-tube experiments showed that transductants could be produced by mixing LT-22 with a sterile filtrate of an LT-2 culture but only if the LT-2 cells had prior exposure to a sterile filtrate of an LT-22 culture. A filtrable agent (FA) was evidently responsible for transduction activity. It must have moved from the LT-22 culture through the filter to the LT-2 side of the U-tube, where it induced FA activity, which then moved back across the filter to produce prototrophic recombinants in the LT-22 cells.

In further tests, FA exhibited many chemical, physical, and genetic properties synonymous with those of bacteriophage particles. (i) FA and P22 exhibited a common adsorption specificity, in which most "smooth" *Salmonella* strains adsorbed FA and phage P22 whereas "rough" strains did not. (ii) The time course of FA production paralleled that of phage P22 production after infection of LT-2 cells. (iii) FA and phage particles copurified and shared a common filtration endpoint. (iv) FA and phage particles were resistant to chloroform, toluene, and ethanol, impervious to proteases, RNase, and DNase, and inactivated by formalin.

Zinder and Lederberg concluded that FA "conforms to the genotype of the cells from which it comes . . . [and] has many activities, producing many different transductions. . . . FA may be considered as genetic material which enters the fixed heredity of the transduced cell. . . . There is good reason to identify the particle with bacteriophage. Nevertheless, the phage particle would function as a passive carrier of the genetic material transduced from one bacterium to another. This material corresponds only to a fragment of the bacterial genotype."

Clearly, Zinder and Lederberg had discovered a versatile way to transfer small bits of genetic material from one bacterium to another. Their discovery marks the birth of *Salmonella* genetics, and transduction soon became a useful genetic tool for *E. coli* as well (6). Today, transduction enables microbiologists to map and manipulate genes in a wide variety of bacteria and archaea. I encourage readers who are not familiar with Zinder and Lederberg's landmark study to give it a read to see how outstanding scientists thought about and carried out microbial genetics experiments before much was known about the nature of the gene. An excellent retrospective article by Zinder (4) provides a rich historical context for the transduction story.

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