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Phenotypic variation affecting motility in Salmonella

Motility is a bacterial character which can be studied both in populations and in individual cells. Motility behaviour of populations can be inferred from the colony patterns produced during growth on semi-solid medium, in which motile cells can swim. It seems as if many non-motile *Salmonella* strains characteristically contain a small proportion of motile cells, which do not differ genetically from the non-motile members of the strain. When pour-plates of non-motile *Salmonella* strains are incubated each viable cell produces a colony; in 20 of 47 strains tested these colonies are surrounded by smaller "Satellite" micro-colonies. On subculture, satellites yield non-motile growth indistinguishable from the parent strain. Satellites are inferred to arise from motile cells which arise during the growth of the parent non-motile strain. Satellite formation also occurs in some non-motile strains of *E.coli*, *Vibrio cholerae* and *Proteus* sp. It seems that phenotypic variation of this kind is widespread. The rate at which motile variants occur in a non-motile strain has been estimated, by making use of the Poisson Distribution. Pour-plates in gelatine agar medium are incubated at 37°C, chilled and then incubated at room temperature. The medium is solid at room temperature and no further bacterial movement can occur; but growth continues till ~~continues~~ colonies and satellites are visible. In

SW 545 (Stocker, Zinder & Lederberg, 1953, J.gen.Microbiol.9,410), about one-third of the colonies have no satellites, after five hours growth at 37°C. Assuming that "events" leading to the production of satellites occur at random amongst the population, then the mean number of such events can be calculated from the Poisson Distribution. From the number of viable cells per colony, at the time of chilling, the event frequency per cell per bacterial generation can be found. In SW 545 it is about 10^{-5}. The distribution of numbers of satellites per colony indicates, that in this strain, an event results in an average of 2-3 satellites. The frequency of events appears to be a strain characteristic - it seems as if each cell has a small, genetically determined, probability of undergoing an event during its life-time. Motile cells have been isolated from SW 545 by micro-manipulation. The majority of the progeny of such cells are non-motile. However, in most populations one, two, three or four motile cells persist amongst the non-motile progeny. The motile cells behave as if their motility results from the presence of non-multiplying motility-conferring particles.

To sum up, plate experiments indicate that, in some non-motile strains "events" occur at low frequency, each event giving rise to a small number of motile cells. Micromanipulation of single cells provides evidence for the presence of motility-conferring particles, which suggests that an "event" is the synthesis of a small number of motility-conferring particles. We now have

evidence suggesting that a motility-conferring particle corresponds with a flagellum. Presumably some sort of basal granule, secreting the flagellum, is involved. An event is probably the synthesis of a small number of flagella, by a cell; these flagella are distributed out to the progeny and are maintained for an indefinite period.

We have here a situation in which spontaneous phenotypic variation is occurring amongst cells of uniform genotype, in an environment which is as near uniform as we can make it. As described here "events" have a genetically determined, low probability of occurrence. Possibly strains showing a high proportion of motile cells have a correspondingly high event frequency. The situation in SW 545, and strains of similar behaviour, may be an extreme case of normal variability. For variation of this type we propose the term residual variation; that is spontaneous variation occurring amongst cells of uniform genotype in a "uniform" environment.

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