APPENDIX

ON THE EFFECT OF FINITE INPUT ON THE
(*TRANS/CIS*) YIELD RATIO IN BACTERIOPHAGE
COMPLEMENTATION TESTS

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In the standard test for *cis-trans* position effect the yield from the *trans* test may be less than that from the *cis* test in the absence of any true *cis-trans* effect because of the (Poisson) distribution in the numbers of particles infecting individual bacterial cells. The yields in the *trans* and *cis* cases will depend on the multiplicity of infection (m), the average number of infecting phage particles per cell, according to the particular relationship which holds between the yield and the amount of gene product of each of the genes involved. The amount of neither, one, or each of the gene products may limit the yield from mixedly infected cells. When the multiplicities of infection are high, as in the preceding study (about 10), only the case in which each of the gene products can limit the yield leads to a (*trans/cis*) yield-ratio appreciably less than one. This case is described below.

Cis configuration: Each cell, whether infected or not by a mutant phage, produces a crop of phage proportional to the frequency of wild-type particles among the infecting particles. Then, Y_c , the yield of phage in a *cis* test relative to the yield from a wild-type infected culture, is given by

$$Y_c = \sum_{M=0}^{\infty} \sum_{W=1}^{\infty} \frac{(m/2)^M e^{-m/2}}{M!} \frac{(m/2)^W e^{-m/2}}{W!} \frac{W}{W+M}$$

where W and M are the numbers of wild-type and double-mutant phage, respectively, infecting a particular cell. Y_c can be written in the closed form,

$$Y_c = \frac{1}{2} (1 - e^{-m})$$

Trans configuration: Each mixedly infected cell produces phage in a yield proportional to the frequency among the infecting particles of whichever mutant happens to be in the minority among particles adsorbed to that cell. In those cells receiving equal numbers of the two types, the yield is one-half the normal yield. Letting the number of the minority type be x and the majority type be $x + \delta$, then Y_t , the yield of phage in a *trans* test relative to the yield from a wild-type infected culture, is given by

$$Y_t = 2 \sum_{\delta=0}^{\infty} \sum_{x=1}^{\infty} \frac{x}{2x+\delta} \frac{(m/2)^{2x+\delta}}{x!(x+\delta)!} \frac{e^{-m}}{x!} - \sum_{x=1}^{\infty} \frac{1}{2} \frac{(m/2)^{2x}}{x!} \frac{e^{-m}}{x!}$$

¹ Operated by Union Carbide Corporation for the United States Atomic Energy Commission.

FIGURE A1.—The functions Y_c , Y_t and Y_t/Y_c (see APPENDIX).

The factor of 2 before the first sum arises because *either* type can be in the majority; but for the case where the two types are equal ($\delta = 0$), this results in double-counting and we must subtract the second sum to correct for this. The sums can be expressed directly in terms of Bessel Functions:

$$Y_t = e^{-m} \sum_{\delta=1}^{\infty} \int_0^m I_{\delta}(t) dt - \frac{1}{2} e^{-m} \{I_0 - 1\}$$

where I_{δ} is a modified Bessel Function of order δ (defined in ABRAMOWITZ and STEGUN 1964 equation 9.6.10). But

$$\sum_{\delta=1}^{\infty} I_{\delta}(t) = \frac{1}{2} [e^t - I_0(t)] \quad (\text{ABRAMOWITZ and STEGUN } op. cit. \text{ equation 9.6.37})$$

Therefore,

$$Y_t = \frac{1}{2} \{1 - e^{-m} I_0(m) - e^{-m} \int_0^m I_0(t) dt\}$$

Y_c , Y_t and (Y_t/Y_c) are plotted in Figure A1.

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