APPENDIX

By Ralph W. Gerard

These findings are the most convincing ones I have seen, in fact, the first convincing ones, indicating a metabolic role of glia as "nursing" the neurons. There is a further important implication. The mere static existence of a longer axon would not demand any greater perikaryon metabolism than would a shorter axon. The greater metabolic activity implies a greater dynamic requirement in maintaining a longer axon, presumably by a more rapid material movement from soma into axon along the lines urged by Gerard,[15] Weiss,[16] and others.[17] Explicitly these results lead to the prediction that the rate of movement of materials in an axon varies as axon length—linearly as a first approximation. Experiments to test this are being initiated.

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INDETERMINISM IN INTERSPECIFIC COMPETITION

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The extensive experiments of Park and his associates[1–4] on competition between two species of flour beetles, *Tribolium castaneum* and *T. confusum*, have become one of the most-quoted examples of indeterminism in biology. When populations of the two species are kept together in cultures containing whole-wheat flour and yeast, one species invariably displaces the other. Under high temperature and high relative humidity, *T. castaneum* (hereafter designated *CS*) is the winner; when both temperature and humidity are low, *T. confusum* (designated *CF*) wins. At intermediate regimens, such as represented by 29°C and 70 per cent humidity, in the various experiments reported by Park's group (the first four in Table 1), *CS* emerged as the successful competitor in some 84 per cent of the cultures while *CF* won in 16 per cent of them. The indeterminacy is provided by the apparent unpredictability as to which species will win in any given culture. This situation has been analyzed on the basis of a stochastic model,[6] presumably on the assumption that, as stated by Cole,[7] Park "has discovered environmental conditions under which the two species are so nearly evenly matched that stochastic elements take over and mediate the outcome." The term *stochastic* here, to refer to a statistical authority in this field,[8] is synonymous with "probabilistic" and "was intended to draw attention explicitly to the random . . . aspect of population changes, due partly to the intrinsically discrete structure of populations, and in contrast with some older so-called 'deterministic' formulations." In Park's[9] own words: "The outcome of the struggle appears to be determined by something comparable to a toss of a coin." Recently Mayr,[10] in his provocative essay on cause and effect in biology, referred specifically to the Tribolium experiments as an example of unpredictability of the results of complex ecological interactions.

We wish to submit here the view that in competition experiments of the type

TABLE 1

OUTCOME OF COMPETITION EXPERIMENTS BETWEEN *T. castaneum* (CS) AND *T. confusum* (CF) MAINTAINED AT 29°C AND 70% RELATIVE HUMIDITY

(All life stages transferred monthly)

Reference	Initial population	Number of winning cultures	
		CS	CF
Park[1]	2 pairs of each species	12	6
Kennington[2]	"	19	1
Park[3]	"	24	4
Park and Lloyd[4]	"	9	1
Lerner and Ho[5]	10 pairs of each species	20	0

described, the apparent indeterminacy is largely the result of genetic heterogeneity among the founders of the populations in the different cultures, and that proper specification of the genotypes makes the results of replicate competing cultures predictable with near certainty in each individual case. This view, foreshadowed by the previous demonstration[5] of intraspecific genetic variation in competitive ability of Tribolium, is supported by the deterministic outcome of competition trials in which the genetic variability from culture to culture has been greatly reduced. This reduction has been accomplished in two types of experiments. In the first of these, a larger number of parental animals was introduced into each culture, and in the second, additionally, highly inbred lines were utilized. It should be noted in this connection that normally outbreeding organisms maintained in the laboratory as very large populations, in sharp contrast to those propagated, as in our inbred lines, by brother-sister matings, are likely to become only slightly or moderately inbred, even over periods of tens or perhaps hundreds of generations.

The first type of evidence is only mildly suggestive. As previously reported,[5] in repeating Park's experiments under the same conditions, except for initiating the competition cultures with ten pairs of beetles of each species instead of two, *CS* emerged the winner in all 20 replicates (see Table 1). The obvious interpretation, should this difference be considered significant (the P value is 0.04 using Fisher's[11] exact method for one-tailed contingency tests), is that the small sample of four beetles from a genetically heterogeneous population of *CS* used in establishing cultures has a lower probability of including representatives with superior genotypes for competitive ability than the larger samples of 20. More generally stated, the aggregate genetic effects in competition of sets of 20 genotypes taken at random are much more uniform from culture to culture than are the aggregate effects of sets of four genotypes, so that in the former case the average superiority of *CS* would almost invariably (and in our 20 tests always) prevail. Similarly,

TABLE 2

OUTCOME OF COMPETITION EXPERIMENTS BETWEEN *T. castaneum* (CS) AND *T. confusum* (CF) MAINTAINED AT 29°C AND 70% RELATIVE HUMIDITY.

(All cultures initiated with 10 pairs of each species. Adults discarded at monthly transfer. Some of the results shown have already been reported by Lerner and Ho.[5])

Generations inbred at outset of experiments	Competitors	Number of cultures Won by CS	Won by CF	Outcome uncertain
0	CS synth-CF synth	89	1*	0
13	CS 2-CF 9	10	0	0
	CS 2-CF 11	10	0	0
	CS 12-CF 9	10	0	0
	CS 12-CF 11	9	1	0
	CS (2 × 12)-CF 9	10	0	0
	CS (2 × 12)-CF 11	10	0	0
	CS 2-CF (9 × 11)	7	1	2†
	CS 12-CF (9 × 11)	0	10	0
	CS (2 × 12)-CF (9 × 11)	10	0	0
16–18	CS 3-CF 1	0	10	0
	CS 3-CF 11	0	10	0
	CS 5-CF 1	10	0	0
	CS 5-CF 11	8	0	2‡
	CS (3 × 5)-CF 1	10	0	0
	CS (3 × 5)-CF 11	10	0	0
	CS 3-CF (1 × 11)	0	10	0
	CS 5-CF (1 × 11)	0	10	0
	CS (3 × 5)-CF (1 × 11)	10	0	0
	CS synth-CF (1 × 11)	20	0	0
18	CS synth-CF (9 × 11)	10	0	0
	CS 12-CF synth	0	10	0
	CS 12-CF (9 × 11)	0	10	0

* The CF winning culture was infected with *Nosema*, see Lerner and Ho.[5]
† Percentages CS at termination were 54 and 79, respectively.
‡ Percentages CS at termination were 61 and 67, respectively.

under environments in which *CF* has more than a trivial advantage, larger foundation populations should lead to invariable victories for *CF*.

Evidence from the second type of experiment, based in part on published results and in part on new data, is presented in Table 2. Procedures followed in the 320 competition cultures reported require some amplification. As has been noted in our previous publication,[5] Park's standard technique of transferring all life stages of the competing beetles to fresh medium monthly has been modified, the adults being discarded at each transfer. The outcome of competition was found to be identical with that using Park's original method (in both instances, however, starting with ten pairs of beetles of each of the species) but in general arrived at much more rapidly. This modification has been adopted as a timesaving device.

We have found, however, that even under these conditions the period of complete elimination of one of the species is very much prolonged in the few situations to be seen in Table 2 when the outcome is not completely determinate for the whole set of replicates.

The synthetic populations of the two species in which the unsuccessful attempt to select directly for competitive ability has been previously described are represented in the table as *CS synth* and *CF synth*, respectively. The other designations refer to various inbred lines (e.g., *CS 2*, *CF 1*, etc.) propagated by brother-sister matings for the number of generations specified *prior* to the initiation of the experiment. When the initial competitors were F_1 crosses between these inbred lines, the appropriate designation (e.g., *CS* (*2* $\times$ *12*)) is shown.

Examination of the data in the table (populations in a few of the cultures have not yet reached 100 per cent of the winning species, but all of these have approached this state within a few per cent) clearly shows that when genetic heterogeneity of the founding population is largely eliminated, so is most of the "indeterminacy." The further the inbreeding progresses, the more true this is. Had, for instance, the experiments initiated after 16 or more generations of inbreeding been treated as a single set of replicates, the outcome of the cultures carried to the terminal point would be given as 78 wins for *CS* and 60 wins for *CF*. Considering subsets only, within each group of replicates the winning species is invariably the same. Identification of the genotype apparently removes the random effect regarding the outcome, though it should be, of course, noted that the details of the eliminatory process of one of the species, such as duration and pattern, may still be mediated by stochastic events within the populations.

The kinds of factors responsible for lack of uniformity of outcome in replicated competition experiments may be briefly considered. Indeterminacy may result from interculture differences existing at the initiation of populations in such factors as phenotypic differences in fitness traits, ages, genotypes for reproductive or competitive ability, possible infections of parental individuals, and variation in quantity and quality of food provided. Other influences, similar in affecting cultures as units but different in that they are still unresolved in newly established populations, include, for example, temperature and humidity to the extent that their variations from culture to culture are inadequately controlled.

Contrasting with these factors are influences dependent on accidents, coincidences, and, in general, chance phenomena within the individual populations themselves. Certainly belonging to this class are such events as may be traceable to the indeterminacy of behavior of small particles postulated in the theory of quantum mechanics. As has been often noted, variations of individual atoms or small groups of atoms may in some instances create ultimate effects of great magnitude, notably but by no means exclusively exemplified by gene mutation. A molecular accident could, conceivably, affect slightly the stimulus threshold of a neuron, in consequence of which the path taken by a beetle in its wanderings through the medium may be modified, and perhaps deflected from an egg that otherwise would be eaten. In addition there may be innumerable events which, while in an ultimate sense determinate, are uncorrelated in any direct or systematic manner with conditions existing at the initiation of a culture, and are generally so complex as to defy predictability or detailed analysis. Such minor factors as the positions of the beetles at the initiation of a culture, or their tendency, perhaps because of a minor injury, to turn to the right or left on meeting an obstacle, would probably have no effect on the average on the outcome of competition, but in a particular culture might to a degree determine patterns of mating and predation. Events of this general kind, even though conceivably already predetermined at the initiation of individual cultures, could affect the numbers of individuals within each population in a manner susceptible to characterization and interpretation by stochastic models.

In actual experiments there must be indeterminacy with respect to influences of both kinds, those acting within populations and those affecting populations as units, although one may outweigh the other. Neyman, Park, and Scott,[6] in discussing stochastic models applicable to the competition experiments of Park and associates, considered the possibility that indeterminacy of outcome of a culture may exist so long as the ratio of the numbers of individuals of the two species remains within certain definite limits. Such a formulation implies indeterminacy due predominantly to internal factors of the type described in the preceding paragraph, that is, of individual populations themselves. In such case, the drift of the numerical ratio of individuals of the two species to one limit or the other is in any culture due to chance occurrences within it. But, on the other hand, should the genotypes of the founders of the population in actual fact constitute the major influence determining the outcome, such a shift in numerical ratio would be only the result of the competitive values already possessed by the initial genotypes.

In our experiments, within-species genetic variation was demonstrably of overriding importance, inasmuch as the ability of the species to win depended on the particular inbred lines used in a given trial, and the outcome was completely deterministic where genotypic variation was adequately restricted. As a corollary it can be concluded that chance phenomena within our individual populations were so feeble in their ultimate effects as to alter the outcome in few, if any, instances. Therefore it seems reasonable to suggest that in the experiments, differing from ours in some respects, of Park and his associates genotypic variability, which was not closely controlled, may also have been of major importance and responsible at least in part for the observed indeterminacy. Hardin[12] in discussing Park's results wrote: "With certain fixed values for the environmental parameters the experimenters have been unable to control conditions carefully enough to obtain an invariable result." He evidently presumed the influences affecting populations as a unit to be chiefly responsible for the indeterminism. Had Hardin not restricted himself to "conditions," but considered also the possibility of variation among individual genotypes, his conclusion would have been anticipatory of our experiments. It should be stated, however, that the existence of minor residual sources of uncontrolled variation within populations, no doubt, could, even where genotype and other influences affecting populations were very closely controlled, lead to indeterminacy in exceedingly closely matched competitions.

The view elaborated here lends great emphasis to the importance of the genotypes of founders of initially small isolates or Mendelian populations, as has been previously advocated by Mayr,[13] or, more generally, ascribes a significant role to genetic drift. Other indeterminate situations, directly related to genotype, also occur, as was clearly brought out in the *Drosophila pseudoobscura* experiments of Dobzhansky and associates[14-16] where drift, occasioned by the fact that only a small proportion of possible recombinants is represented in finite populations, was demonstrated. Our results also suggest that an assumption of indeterminism within experimental populations should not be taken lightly where genotypic variability has not been carefully controlled or not investigated to determine its adequacy to explain the observed results.

Summary.—Data are presented to indicate that indeterminacy of outcome of interspecific competition experiments may be largely a reflection of random selection of the genotypes of founder populations.

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*FINE STRUCTURE OF PHOTORECEPTORS IN THE HYDROMEDUSAN, POLYORCHIS PENICILLATUS**

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Sensitivity to light is found in most living systems from unicellular organisms to flowering plants on the one hand and to mammals on the other hand. Their photoreceptors, such as chloroplasts in plants and rods, cones, and rhabdomeres in animals have one feature in common, namely, extensive surfaces upon which a photopigment presumably is spread. There appear to be two basic types of animal photoreceptors: those of ciliary origin (i.e., a derivative of a flagellum or cilium) and those of nonciliary development. The rods and cones of vertebrate eyes are examples of the former; the rhabdomeres of arthropod visual organs illustrate the latter. Indeed, there is evidence that photoreceptors of ciliary origin may characterize the echinoderm line of metazoan evolution whereas the nonciliary type is generally found in the annelid line (see discussion for references). Which type is