

An opinion on this question must await evidence regarding the response of the individual fibers. Our investigation is still continuing in the effort to analyze in more detail the nature of the response obtained, and thus to secure evidence which may give an empirical answer to this and other questions concerning the action of the nerve, and which may then decide as well the dependent problem of auditory theory.

<sup>1</sup> *J. Physiol.*, 1926, **61**, 49-72, 151-171, 465-483; **62**, 33-51; 1927, **63**, 378-414.

<sup>2</sup> See A. Forbes and A. Gregg, *Amer. J. Physiol.*, 1915, **39**, 229 ff.; G. Wilkinson and A. A. Gray, *The Mechanism of the Cochlea*, 1924, 175 ff.

<sup>3</sup> As represented, e. g., by E. G. Boring, *Amer. J. Psychol.*, 1926, **37**, 157-188.

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### MUTATIONS AND ALLELOMORPHISM IN THE GROUSE LOCUSTS (TETTIGIDAE, ORTHOPTERA)<sup>1</sup>

BY ROBERT K. NABOURS

KANSAS AGRICULTURAL EXPERIMENT STATION AND DEPARTMENT OF GENETICS,  
CARNEGIE INSTITUTION

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Five species of the grouse locusts (*Tettigidae*) have been submitted more or less to breeding analyses, as follows: *Paratettix texanus*, more than twenty-three dominant and three recessive, elementary, color patterns; *Apotettix eurycephalus*, twelve dominant, primary patterns and the "normal recessive," or "wild type;" *Telmatettix aztecus*, four dominant and the one recessive; *Tettigidea parvipennis pennata*, six dominant patterns, and *Acrydium arenosum*, more than twenty-five dominant patterns and the one recessive. Symbols, or letters, have been arbitrarily assigned to the several factors for elementary patterns upon their verification. Example, *B*, *F* and *I* represent the factors for the whiteness, yellow stripe and black spot, respectively, *P. texanus*, and *M*, *O*, *Z*, *G* stand, severally, for the factors for prominent patterns in *A. eurycephalus*.<sup>2,6,7</sup>

The so-called "normal recessive," or "wild type" pattern, +/+ is common to, and very much the same, in all the species so far examined. The color patterns considered are on the pronota and posterior femora, and appear to be due mainly to the distribution of various colored pigments in the hypodermal cells. The colors are also probably influenced somewhat by the topography of the surfaces and other features of light absorption and reflection. A much more complete study is needed of the chemical, embryological and morphological features of these marvelous, primary and hybrid emergent patterns.

Twenty-six primary patterns, including the "wild type," +/+, and

several of the hybrid complexes of *P. texanus* have been illustrated. Of these, twenty-one are so closely linked, or approach multiple allelomorphism to such an extent, that none has crossed over with any other. One, Hm, actually crossed over with members of this group five times in over 7000 pairings. Another,  $\Theta$ , is loosely linked with the members of the group, showing about 47 per cent and 25 per cent of crossing over in the females and males, respectively. The other two,  $\Phi$  and sf, recessives, apparently belong to other, separate, pairs of chromosomes. Illustrations of specimens of *A. eurycephalus* and *T. parvipennis pennata* have also been published.<sup>2,6</sup>

The only mutant known to have occurred among all the grouse locusts bred in the laboratory was the *Sm* (old *IS*) of *P. texanus*. The first individual bearing this new pattern appeared in a mating,  $I/S \times B/S$  (ref. 5, p. 48, mating 472, 1917). The tentative explanation then advanced, in which the factor *I* was involved, has long since been abandoned. It is now thought that a gene, extremely close up with the gene for *S* in the male, in that mating, mutated into a factor for the pattern *M*. Several years subsequently, *M* was discovered in nature and introduced into the laboratory. It was soon observed that the hybrid emergent of the patterns *S* and *M* appeared to be precisely the same as the mutant pattern *Sm*.

There is now reason for believing that this mutation (*M*) has occurred in the laboratory at least two other times. The appearance of *Sm* (old *IS*) again (ref. 5, p. 50, mating 507, 1917) was probably due to a similar mutation of the same gene in connection with one of the *Cs*, or the *S* in the male of the mating (this specimen did not live to reproduce). The other case was reported in my first paper (ref. 4, p. 155, mating (*e*)). Deducing from the evidence of a sketch and notes made during its life, and from memory (it also died before reproducing), I am now confident that the extraneous color attending the pattern of this individual (*B/E*) had no connection with the factor for *I*, but was due to an *M* mutation on the chromosome bearing *B*, or the one carrying *E*. The appearance of the *M* pattern, especially in hybrid combination with *S*, *B*, *E*, etc., gives the impression of what at first was crudely and inaccurately considered a "diluted," or "dispersed" *I* pattern.

The extremely close linkage, possibly some of them multiple allelomorphs, of these more than twenty-one factors for dominant color patterns in *P. texanus*, and the absence, or rarity, of factors for such striking characteristics in the remainder of this pair, the other five pairs and the sex chromosomes, indicate a peculiar tendency for conspicuous color mutations to occur in just one region of the one pair. There are other unit-behaving patterns than the *Sm*, particularly *Cof* and *Jof*, each of which appears to be due at least to two factors. These characters, which have individually so far behaved as units, are apparently the same as *C*

and *J*, respectively, with the addition of the conspicuous, orange of the middle and hind femora. They are probably due to close-up mutations of orange femora (*of*), instead of *M* as in the case of *Sm*, though not necessarily involving the same gene. It is likely that this orange femora pattern will sometime be found alone in nature, or in connection with other factors, or it may occur as a mutant in the laboratory.

Presumably several others of the respective patterns that have appeared to be units may actually be such hybrid emergents of two or more dominant patterns, the respective genes for which are on the one chromosome, but too closely associated to allow of crossing-over. However, other possibilities are recognized, one being the lack of the tendency to crossing-over in the possibly considerable region of the chromosomes along which these factors may be ranged. The genetic evidence, and the considerable cytological contributions of Robertson<sup>8</sup> (and in *MSS*) and Harman<sup>9</sup> appear consistently to support the ordinary conception of the linear hypothesis.

It is entirely probable that some of the dominant patterns which have invariably behaved as units, each hitherto attributed to the effects of a single gene, are severally, actually hybrid emergents of two, or more, extremely closely linked genes, one, or more, or all of which, singly would be recessive. It may not be stated with confidence that any one is not of this order. It is possibly a general feature of dominant characteristics that they consist of hybrid emergents of two or more recessive genes in such closely linked clusters that crossing-over, if any, is extremely infrequent. Several of the brilliant, unit-behaving, color patterns of the grouse locusts may be due, respectively, to more or less long series of recessive genes which have mutated in groups, and others, such as *Sm*, *Cof* and *Jof* may, in turn, consist of closely linked aggregations of certain of these.

The above statements concerning mainly *P. texanus* apply equally as well to the other species studied, except that linkage among several of the factors in *A. eurycephalus* is somewhat less close. In *A. arenosum* the factors appear to be extremely loosely linked, or even arranged in several linkage groups. No sex-linked characteristics have been found in any of them.

In *P. texanus*, such factors as *J* and *K* show no crossing-over, while in *A. eurycephalus* the factors for the similar patterns *Y* and *K* cross-over to the extent of 5 or 6 per cent. In *A. arenosum*, the linkage of the factors for patterns of like appearance is still more loose, or they are possibly in separate linkage groups. Even if it still be supposed that these species have recently separated from a common stock, this lack of analogous position of factors for apparently similar patterns could be accounted for by assuming that translocations had occurred among the chromosomes.

The comparative effects of the same gene in single and double doses may be excellently illustrated by the use of these patterns. For example, an individual of the composition *Y/T*, in *A. eurycephalus*, shows the white

spot of the  $Y$  distinctly tinged with the mahogany of the  $T$ ;  $YT/Y$  has the spot very white with only a trace of the mahogany; while  $YT/T$  shows the spot much obscured by the pigment of  $T$  (ref. 6, Illustrations). Several other combinations indicate the same thing, as  $O/OT$  which is markedly whiter than  $OT/T$  and both are distinguishable from  $O/T$  or  $OT/OT$ .

<sup>1</sup> Paper 113, Zoölogy Department, Kansas Agric. College.

<sup>2</sup> Bellamy, A. W. "Multiple Allelomorphism and Inheritance of Color Patterns in *Tettigidea*." *J. Gen.*, 7, 1, 55-70 (1917).

<sup>3</sup> Harman, Mary T. "Spermatogenesis in *Paratettix*." *Biol. Bull.*, 29, 262-277 (1915).

<sup>4</sup> Nabours, Robert K. "Studies of Inheritance in Orthoptera 1." *J. Gen.*, 3, 141-170 (1914).

<sup>5</sup> Nabours, Robert K. "Studies of Inheritance in Orthoptera 2 and 3." *J. Gen.*, 7, 1-54 (1917).

<sup>6</sup> Nabours, Robert K. "The Genetics of the *Tettigidae*." *Bibliographia Genetica*, 5, 27-104 (1929).

<sup>7</sup> Nabours, Robert K., and Iva Larson. "Inheritance of Color Patterns in the Grouse Locust *Acrydium arenosum*." *An. Rec.*, 44, 4, pp. 288-289 (1929).

<sup>8</sup> Robertson, W. R. B. "Chromosome Studies 3 and I." *J. Morph.*, 26, 109-141, (1915) and 27, 179-280 (1916).

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## THE ELECTROMAGNETIC FIELD EXTERIOR TO A SYSTEM OF PERFECTLY REFLECTING SURFACES

BY F. H. MURRAY

DEPARTMENT OF DEVELOPMENT AND RESEARCH, AMERICAN TELEPHONE AND TELEGRAPH COMPANY

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In several papers,<sup>1,2</sup> Weyl has investigated the problem of "Hohlraumstrahlung" by making use of the properties of a certain vector solution of Laplace's equation, which is represented as a sum of potentials of a single and a double layer. The corresponding properties of a vector solution of the wave equation in three dimensions are employed here to determine the reflected field which results when a given electromagnetic field is modified by the presence of a system of perfectly reflecting surfaces. The problem is reduced to the solution of a system of integral equations of Fredholm type, in which the integration is extended over the reflecting surfaces. It is shown that a unique solution exists.

1. Let the system of reflecting surfaces  $S_1, S_2, \dots, S_n$  be denoted by  $S$ ; it will be assumed that if an arbitrary point  $(x_0, y_0, z_0)$  on  $S$  is given, a transformation of the coördinate axes can be made such that all points of  $S$  in some neighborhood of this point can be represented in the form