2 R. A. FISHER ON (1) MENDELISM AND BIOMETRY (1911) AND (2) SOCIAL SELECTION (1912)

1. Mendelism and biometry[1]

Paper on 'Heredity' (comparing methods of Biometry and Mendelism) read by Mr. R.A. Fisher, Caius College, (Chairman of Committee), at second undergraduate meeting of the Cambridge University Eugenics Society in Mr. C.E. Shelley's rooms, C. New Court, Trinity College, on Friday, 10 November 1911, at 8.30 p.m.

In compiling this short paper I have not, needless to say, attempted to touch the whole subject; the inherited character controversy I have omitted altogether, as it may be considered as settled, from the practical point of view, in favour of Weismann; the further controversies which raged over Weismann's germ plasm theory may fairly be left to physiologists, if they think that the discussion was profitable.

I rather regret having made no mention of de Vries' mutation theory, or of Johannsen's remarkable work on pure lines; the latter I should certainly have included if I could have got at the original papers.

I have almost entirely devoted myself to the two lines of modern research which are of particular interest in Eugenics, that is to Biometrics and Mendelism; and perhaps experts and professionals will forgive the absence of more complicated details in both branches, if I explain that my object has been to give a fair view of the merits of the two methods, whose advocates have shown so little appreciation of the other school.

In speaking of heredity it has become usual to commence by pointing out that we can only speak of heredity in respect of variations, while variation itself is only a partial failure of heredity; but we are not now concerned with this apparent paradox; our problem is merely—given the parents, predict the children—and we are not even specially concerned with the physiological mechanism by which the latter are determined.

Prediction is a matter of probability; in the case of Mendelian heredity we can with certainty predict the possible types of children of given parents, and say that these will occur in the familiar Mendelian proportions; and if enough offspring can be obtained the numbers actually approximate to the ratios required by theory. The results of biometric research are much more vague, but are capable of a much wider application; the probable measurements of particular organs of the offspring can be calculated from those of the parents, and those of the general population, and we have to take a large number of families of similar parents from the same population before the accuracy of the prediction becomes apparent. A single family may differ as widely from the result predicted, as a single offspring in Mendelian inheritance may differ from the rest of its family. Mendelism concerns itself with natural pairs of unit characters, each of which may affect a number of organs and measurements which are inherited in the simple manner discovered by Mendel; biometry deals with artificial measurements, and applies to them statistical methods which are equally applicable to meteorological or economic data; the only assumption is that a large number of independent causes are acting at random; this explains why their results are only true of populations; in single instances there may be only a small number of independent variables.

I had better begin by outlining the view of inheritance which I have taken up, since I shall be continually using the ideas involved. On this theory the inherited nature of any living creature consists of a large number of Mendelian characters; from the moment the ovum is fertilized the creature is affected by its nurture or environment, so that different creatures with the same inherited nature will manifest every kind of variation from their true type; the independent causes are quite indistinguishable, and will affect the organism in innumerable ways. This variation due to nurture can only be treated by statistical methods; luckily in most cases it appears to be small, and still more luckily it is not inherited.

In case it is not superfluous I shall try to give a sketch of Mendelism. The simplest case is that of the blue Andalusian hen; for years breeders have known that these birds would not breed true; there were always black and speckled white chicks in the brood; if they had taken the trouble to count the number of each they would have found that half the brood was blue each time, a quarter were black and a quarter white. This is a simple case of segregation; the black and speckled white are pure breeds, homozygotes as they are called; when crossed all their offspring are heterozygous blue. Blue crossed with black gives a half blue and a half black; with speckled white a half are blue and a half speckled white. It does not matter what the ancestry of the birds was; the offspring can be predicted simply from the parents.

In most cases the heterozygote is indistinguishable in appearance from one of the pure types; this is then called the dominant, from the old notion that its inheritance was stronger and dominated the weaker or recessive type. A case of this occurs in Mendel's original work on garden peas; starting with short and tall varieties, Mendel found that the cross was tall, tallness being dominant, and was astonished to find that these tall heterozygotes gave one offspring in four of the short recessive type.

Perhaps the greatest simplification introduced by Mendel's discoveries is the fact that different pairs of characters or allelomorphs are inherited independently of one another. For instance, maize grains may be either white or yellow, yellow being dominant; they may also be either smooth or wrinkled; if a plant heterozygous in both characters be self-fertilized, all four types will appear, and the proportion of yellow grains to white will be the same, that is three to one among the smooth grains as among the

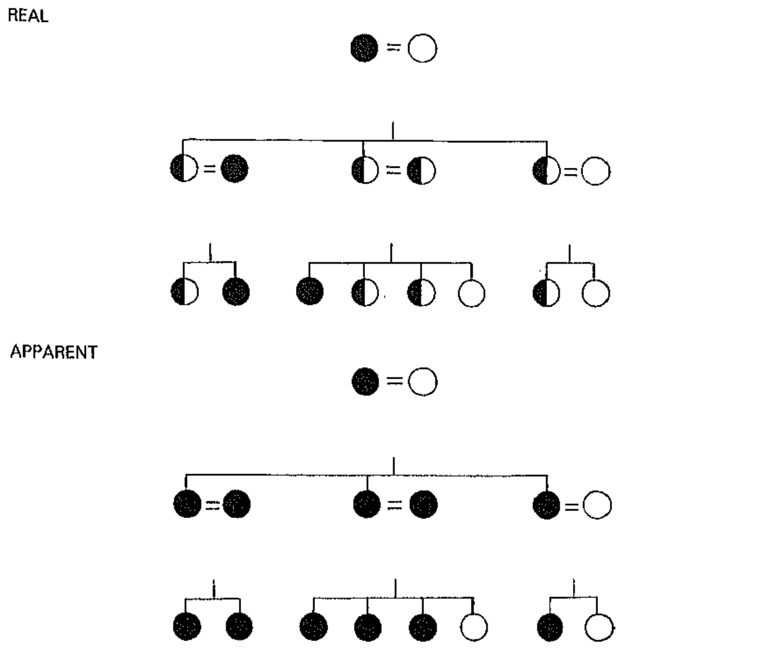

Fig. 1. Fisher's chart, showing 'real' and 'apparent' differences (corresponding to genotype and phenotype) for a pair of allelic genes with dominance.

wrinkled. Besides its admirable simplicity this segregation enables a breeder to create new pure strains; for instance, starting with a couple of grains, one white wrinkled and the other yellow smooth, you could in a few generations produce white smooth and yellow wrinkled grains which would breed true as long as they were wanted.

A number of Mendelian pairs have already been worked out in the case of men; among animals and plants new and valuable races have been created by combining different qualities. For instance, a valuable rust-proof wheat has been obtained by crossing the old rust-proof wheat which gave a poor yield with a wheat which yielded a good crop but was subject to rust. The first cross was heterozygous in both factors, but one-sixteenth of its offspring was pure-bred in both desirable qualities. Suppose we knew, for instance, 20 pairs of mental characters. These would combine in over a million pure mental types; each of these would naturally occur rather less frequently than once in a billion; or in a country like England about once in 20 000 generations;[2] it will give some idea of the excellence of the best of these types when we consider that the Englishmen from Shakespeare to

Darwin (or choose who you will) have occurred within ten generations; the thought of a race of men combining the illustrious qualities of these giants, and breeding true to them, is almost too overwhelming, but such a race will inevitably arise in whatever country first sees the inheritance of mental characters elucidated.

A large number of rare defects among men are now known to be Mendelian dominants; colour blindness, brachydactyly and the form of insanity known as chorea are among these; the inheritance of these is easily traced, since half the offspring of any affected person will be affected; the case of colour blindness is peculiar in being recessive in women.[3] These would all be stamped out in one generation by prohibiting affected persons from pairing. I venture to propound the hypothesis that there is a still larger number of recessive defects, by one or more of which almost everyone is affected; I suggest this first to explain the sporadic occurrence of defects in the children of healthy parents. Thus, if a recessive defect existed in one person in a thousand,[4] it would not become apparent unless two such persons were to mate, and then a quarter of their children would be affected; so that we should notice a sporadic defect affecting one in four millions.[5] Secondly, to explain the defects, which are well known to follow inbreeding; if there were a thousand such rare recessive defects in a mixed population, each member would on the average have one. A brother and sister each have a half chance of inheriting each of the defects of their parents; if they are mated the chance that they both have it is one-quarter, and the chance of each of their children showing the defect is one-sixteenth. If we knew the proportion of such children, who are in any way defective, we could calculate the average number of recessive defects in each healthy member of the population. With cousin marriage the danger is divided by four; each of the two common grandparents contributes its defects, but the chances of each occurring is only one in 64. For uncle and niece the danger is the same as for cousin marriages, having four common grandparents, being one-sixteenth for each of the recessive defects which we are supposed, on the average, to possess.*

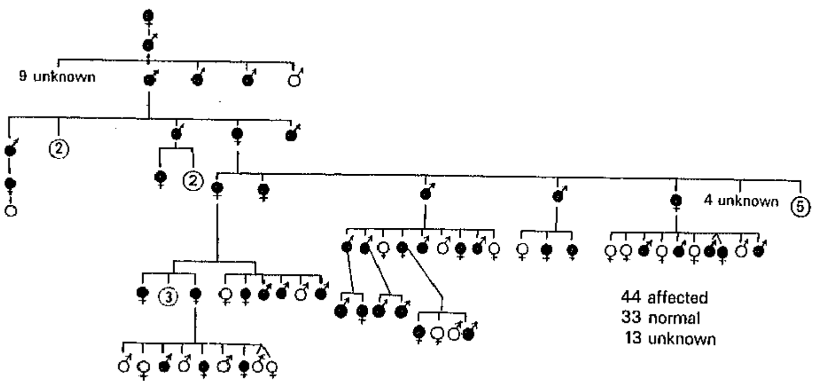

Fig. 2. Pedigree showing segregation for the autosomal dominant trait brachydactyly. (Condensed from Fig. 28 in W. Bateson (1909) *Mendel's principles of heredity*.)

Among animals and plants the number of allelomorphs known to scientists is rapidly increasing; they have been especially successful in solving problems of the inheritance of colour. The case of mulattos used formerly to be urged against the universal applicability of Mendel's method, but it is now known that crosses of black races with white do not result in a uniform blending of the colours, but that some half-breeds are quite black and others nearly white; it is probable that there are several factors involved, but as with other human characters it is unlikely that any difficult problems can be quickly cleared up, owing to the racial and economic difficulties of experimental breeding.

The theory of inheritance on which the biometricians based their researches was framed before the rediscovery of Mendel's laws; the spontaneous variations which are at any rate partially inherited are supposed to be capable of taking up any of an indefinite range of values for each organ; by taking a sufficient number of measurements, say of human stature, we can construct a frequency curve,† showing the number of individuals per million of population, whose heights lie within successive inches on the scale. If, as is the case with human stature, the measure is determined by a large number of small independent factors, the frequency curve will be of the important normal type, and can be completely specified by knowing the mean value, and the standard deviation, which is a most convenient measure of variability.

Among the beautiful and ingenious contrivances which biometricians have devised, perhaps next in importance comes the correlation table; and here we have a measure of inheritance itself. Suppose the million men, which we measured for the frequency curve, eventually become fathers. Consider the sons of all the men who occupy a given range, say from six feet to six feet one; they also will form a frequency curve; their mean is found to be taller than the general population, showing that there is a positive correlation; it will be shorter than their fathers were, showing a regression toward the mean of the population; actually their mean will be about halfway between these two values, and this is found to be true whichever group

*The theory I have here suggested requires that a strain free from defects may intermarry to any extent without harm; the successive dynasties of the Pharoahs, who habitually married their sisters, must have been such strains; marriage with half-sisters would in their case have been the more dangerous course.

†See Normal Curve

of fathers is chosen. The coefficient of correlation is then said to be about one-half. Coefficients of correlation have been worked out in a large number of cases, between all sorts of characters; the method may of course be applied to different organs of the same individual, and as such, will ascertain the numerical measure of the 'correlation' to which Darwin attached so much importance.

The value of biometrical work is largely due to the fact that the actual evolution of new species in the past is a question of populations, and must have taken place in the way indicated by statistical methods. The synthetic breeding required by Mendelism could never have taken place in a state of nature; the strains would never have become pure, until a slow and continuous selection had long acted on the whole population. Gradually the breed would improve in those qualities which were of importance; the work which a breeder could now do in three generations might take a hundred years for the slow haphazard elimination of nature to accomplish.

It has been shown by Karl Pearson, on whose mathematical work the whole science of biometrics has been based, that a number of pairs of Mendelian allelomorphs scattered at random in a population would serve as the independent arbitrary causes which biometricians require. On this basis he has worked out the coefficient of correlation between parent and child, and finds that it should be one-third if dominance is complete, and one-half if there is no dominance, i.e. if the heterozygote lies mid-way between the pure races. The coefficient found experimentally is usually about one-half, which seems to indicate that the factors which determine the principal measurable quantities are to be regarded as exhibiting no dominance. At first sight this may seem a curious discrepancy from the ordinary Mendelian results, in which dominance is an almost universal phenomenon; but it must be remembered that the majority of these results refer to colour inheritance, which is apparently determined by the presence or absence of some enzyme or ferment, capable of producing the colour; the heterozygote also contains the enzyme, possibly only as a half dose, but this is sufficient to determine that the pigment is produced. It would not be at all surprising if allelomorphs relating to structure showed imperfect dominance, or no dominance at all.[6]

One of the great beauties of biometrical work is the certainty of the results obtained; biometricians avoid all the difficulties of abstract theories, they deal only with observations; and even if their observations are full of small errors, and they probably are, they appear to be able to squeeze the truth out of the most inferior data. The probable error can in every case be calculated, and though possible error is unlimited, the probability of large errors can be shown to be very small. I was recently impressed by the potency of the theory of probabilities in this respect; if you put a kettle over a fire it will probably boil, but it is not a certainty; it may freeze; it is true

that the odds against such an event are very large; but it remains a possibility, or so my 'theory of gases' tells me.

It is interesting that Mendel's original results all fell within the limits of probable error; if his experiments were repeated the odds against getting such good results is about 16 to one. It may have been just luck; or it may be that the worthy German abbot, in his ignorance of probable error, unconsciously placed doubtful plants on the side which favoured his hypothesis.[7]

The interest of biometrical work for eugenists lies in the fact that Francis Galton employed this method, the only one then open to him, to show that human characters are as strongly inherited as those of animals, and mental characters as much as physical. Karl Pearson has collected data of school-children and has established the fact that all the mental characters for which he has data are as strongly inherited as are physical measurements. In his *Hereditary genius* Galton treats of mental and moral characters on the assumption, now seen to be fully justified, that intellectual and moral excellence follow the normal curve, or what is known as Quetelet's law; he arranges men in 14 classes, seven above and seven below the average, lettering them from the centre from A to G. Little 'f' and little 'g' are insane or idiotic, little 'd' and 'e' are stupid and often feeble-minded; thence we rise to the bulk of the population lying from c,b,a,A,B, to C, which is the level of the ordinary foreman of a jury. D and E are able, resourceful men to whom most of the prizes in life fall. F and G, Galton described as eminent; they contain about 1 in 4000 of the population. They are the men to whom all advances in thought are due, they produce all the best literature, give us leading scientists, doctors, lawyers, and administrators: in *Hereditary genius* Galton shows how strongly such talents are inherited; and it is of the utmost importance to select such men from whatever class they may be born in, to enable them to rise in the world, to encourage them to marry women of their own intellectual class, and above all to see that their birth-rate is higher than that of the general population. Most of them rise inevitably to a comfortable position; it is natural that they should marry into families of high if not conspicuous ability; but at present, there is no doubt that the birth-rate of the most valuable classes is considerably lower than that of the population in general, and conspicuously lower than that of the lowest mental and moral class of the population.

Biometrics then can effect a slow but sure improvement in the mental and physical status of the population; it can ensure a constant supply to meet the growing demand for men of high ability. The work will be slower and less complete than the almost miraculous effects of Mendelian synthesis; but, on the other hand, it can dispense with experimental breeding, and only requires that the mental powers should be closely examined in a uniform environment, for instance, of the elementary schools, and that special facilities should be given to children of marked ability. Much has been done of late years to enable able children to rise in their social position. Still we may as well remember that such work is worse than useless while the birth-rate is lower in the classes to which they rise, than in those from which they spring.

2. Social selection

Paper on 'Evolution and Society' read by Mr R.A. Fisher, Caius College, (Chairman of Committee), at sixth undergraduate meeting of the Cambridge University Eugenics Society in Mr W.B.G. Batten's rooms, S. Tree Court, Caius College, on Wednesday, 13 March 1912, at 8.30 p.m.

One of the most interesting things about Darwin's explanation of the origin of species is that scarcely anything need be assumed about the actual nature of species, as evidence that natural selection occurs; the same process is in progress with respect to languages, religions, habits, and customs, rocks, beliefs, chemical elements, nations, and everything else to which the terms stable and unstable can be applied. The only things required of a species are the capacities of variation and inheritance and although in examining and analysing these two capacities we may come across the most complicated properties in fact, and the most delicate distinctions in theory, yet the only thing necessary for natural selection is that those which are suitable to survive shall survive, and those which are unsuitable, unstable we may call them, shall cease.

Instances are familiar enough; there is a parasitic worm which infests the gullets of parrots; the worm tickles the parrot's throat, the parrot coughs over its food, and other parrots become infected; the worm, I imagine, had no intention of making the parrot cough, but the fact that it does so is a vital point gained in its struggle for existence. The habit of playing bridge survives in a very similar way; the habitual player finds himself driven quite involuntarily to infect others with a similar passion. The game of bridge cannot be said to have any desire to recruit fresh adherents, but I have no doubt that cards would never have come into use at all, if they could only have been used for solitary games of patience.

When dealing with the matter in such a very general manner as is illustrated above, we may use the idea of an organism in a very wide sense; a habit like smoking may be said to be parasitic on an individual, or on a class, or on a nation in which it has become habitual; on the other hand, the hosts which support an institution like family prayers are the household, the family, or the religious sect which encourages the institution. In speaking of parasites too, it is clear that these parasitic institutions are not necessarily evil; this is true even of animals; for instance, I believe the human stomach could not digest cellulose were it not for the action of a colony of bacteria,

which performs the necessary katabolism. Besides this, parasitism is not a sufficient term to apply to the general relations of organisms; indeed we may say that every form of symbiosis found in the animal kingdom, is paralleled, usually with greater complexity, and more perfect development, in human society. The terminology too in the latter case is so much more varied and complete that it is at first difficult to see that all the modern social problems, for instance of centralization or decentralization, of personal freedom or regimentation, of differentiation of the sexes and specialization of the classes, have been faced under other conditions in the animal kingdom, and solved in Nature's provisional, tentative way by the simple, pragmatic method of trial and error. And it is worth noting that the solution which commends itself to Nature, and which is of interest to us, as that which will be adopted by the future, is characterized not by the greatest happiness, or by the most magnificant realization of human ideals, of this age or of any other, or by any other such considerations, but solely by its stability and power of survival.

An instinct from the external point of view is a tendency to perform some definite act or series of actions under the stimulus of a suitable train of circumstances; the term is rightly restricted to those acts which have some purpose by which the animal benefits directly, or indirectly in furthering some symbiotic alliance. From the psychological point of view it is a motive or desire depending on the idea that the man's state is more desirable, more pleasant, more happy if the instinct is obeyed than if it is not. Pleasure is Nature's bribe to persuade a conscious mind to obey its instincts. The terms pleasure, happiness, contentment refer to states which differ in their durations, and differ in their activity; it is as well to emphasize the similarity of their origin as due to the need of persuading a free will to conform to the courses which selection has shown to be best.

Now if our object were the greatest human happiness, would we succeed by producing a race whose instincts exactly coincided with their economic needs? It will help us to answer this question if we observe that the more complicated an instinct is, and the more difficult to perform, the greater is the pleasure derived from it. Indeed it is necessary than an animal's interest should be centred on those objects which are hardest to obtain; the greater effort requires the greater reward. Among carnivorous mammals the great problem is to obtain food, and their highest pleasure seems to be in hunting and eating; among men selection seems to have acted most ruthlessly by failure to obtain a woman, especially during the immense periods over which female infanticide, often combined with polygamy, seem to have prevailed, and the result is that half our poets devote their labours to the pleasures of love. This consideration by itself suggests that our pleasures will be of a tepid nature if ever our instincts become easy to obey, but we have another side light on the problem. The very existence, real or apparent, of Free Will implies a multiplicity of possible courses, a conflict of instincts; if ever the instincts become so perfectly adapted to economic needs that the wisest course is inevitably followed, we should have no choice, no need for motives, and rewards, and penalties, nothing but an automatic reflex action.

Although we may agree that this economist's paradise with its utilitarian instincts would be a thoroughly undesirable arrangement, it remains to be considered whether or not it is an inevitable one. A society of amoebae in some dim pre-Laurentian age, might well be imagined as discussing how undesirable it would be if free-swimming protozoa with all their faculties intact, contractile, irritable, capable of absorbing food, and of reproduction by division, should ever bind themselves together to form a many-celled animal, should degrade or lose one or more of their faculties in specialization for some particular function, should lose their free motion, and live out a sterile life cramped in a wall of cells as inert as themselves. They might have argued thus and yet overlooked the fact that if these organized societies were more efficient in the struggle for existence than disorganized units, they would certainly come into existence and increase in organization and perfection by competition with one another, until their cellular structure were barely recognizable. And further, that associated with these societies would arise a mind, not associated with one cell or another but with the whole society, beside which the mind of an amoeba would be, as it is, utterly indiscernible.

This process of co-ordination, of integration of units into societies has been carried a step further among the social insects; here, at any rate, the great problem of reproduction has been solved in precisely the same manner as in the self-fertilizing hermaphrodites of the animal kingdom. Queens and drones are produced which by their union cause an immense increase in the number of insects and finally [lead] to the production of a fresh hive. In these respects an ant hive is very similar to, for instance, a fresh water polyp. The subjection of the ants on the one hand, and the cells on the other, to the needs of the whole, has in both cases been established by intercommunal competition. The complicated and highly perfected instincts of the workers have been produced by the natural selection of those hives in which these instincts were well developed. There is no conflict between the interests of the family and the nation, which in human society constitutes the central problem in eugenics; where those individuals who are of most use to the state, and who will sacrifice themselves most readily for the common good, are often prevented by that very sacrifice from procreating their valuable kind. Among social insects the instinct of self-sacrifice may be completely developed, since the only chance of reproduction lies in the survival of the hive.

Human societies are not so far developed as those of insects, and are very far from the complete cell-socialism of the animal body; still it is obvious that the best organized will survive, those in which every class is well cared for, and correspondingly every class performs its functions regularly and without interruption; the nations in which moreover there exist highly skilled and efficient specialized members will reach a higher degree of organization than those in which the members are unskilled although efficient in a general way. The great problem is how far will the individual come to act as a mere part of the social machine, with his instincts perfectly adapted to his life of social service.

We may admit that efficiency in the petty duties prescribed for him by the state is an economic factor which may determine the usefulness of the ordinary man in times of peace; and it is possible that as armies become more elaborately organized, no higher qualities will be required of him in time of war. Although here history is against our argument in showing several instances of enormous, wealthy, highly organized nations having broken themselves in trying to subdue some small, poor, high-spirited race, to whom such social organization would smack too much of servility, and who valued their personal liberty more than wealth. If, however, this is not so in the specialized armies of the future, we can only look for the qualities which men admire to some small ruling caste who may limit the energies of the great national machine. And here too the question arises, 'Will this great organized nation, so like an animal organism in its mode of origin, acquire a Mind, not residing in this man or in that man, but in the whole community of men?' It is possible that some such instinctive groping after the idea of common obedience constitutes the social value of Theism, and it certainly is related to the Catholic notion of the corporate unity of the Church. If this is the fact, that a Mind will come and take control of an organism as soon as it is sufficiently organized to obey, as one animal, just as minds have taken possession of those colonies of cells which we call men, then there will be no need of a ruling caste, with phenomenal intelligence, but all men will act instinctively as parts of the vital mechanism of a Greater Being.

There is another point of view from which we may follow the same analogy; the original free-swimming cell was composed entirely of different forms of that strange substance called protoplasm, which is, practically speaking, live matter; in the animal and vegetable bodies, although they are made of cells, all sorts of other materials of organic origin come into use in the structure; much dead matter is deposited as carbonate and phosphate of lime in our bones, the wood fibres in trees are principally dead cellulose, and a hundred more cases might be cited, but still the body is built out of cells and their products, and cells have to devote themselves to special purposes, such as nerves, or to secreting the material needed in building. In a hive of insects quite foreign matter is utilized in building the combs for honey, and for other purposes; showing that living matter has extended its dominion to substances outside living organisms. Finally, among men all manner of inorganic material has been added to the dominion of the life-force, so that we have houses of stone instead of cell-walls of cellulose, wires of insulated copper instead of living nerves. Indeed it is the lack of communication which seems the great bar to a communal mind among insects; if their sense impressions could be received at a central exchange, there would be a co-ordination in the movements of the hive which would resemble, at any rate, the working of a single intelligence. But it should be noted that this external material besides aiding co-ordination, to some extent renders degradation unnecessary. As an organic substitute for the telegraph we might have to post men, like the Earl of Queensbury's cricketers, along the route, to throw the message one to another. Men bred and specialized for this purpose might be contented, but they would not be men.

After all we may still hope that the magnificent qualities and capabilities of the best type of man will render specialization unnecessary. And that the small spirited nations were right in believing that liberty was better than regimentation.

Notes

1. An uncorrected copy of this paper was incorporated in Norton, B. and Pearson, E.S. (1976). A note on the background to and refereeing of R.A. Fisher's 1918 paper 'The correlation between relatives on the supposition of Mendelian inheritance'. *Notes Rec. R. Soc. Lond.* **31**, 151-62. Fisher's copy of the paper, given here, includes his original footnotes, diagrams, and corrections of typographical errors.
2. With 20 gene pairs there are 2^{20} = 1 048 576 different pure or homozygous genotypes. The frequencies of these genotypes in a population must depend on the gene frequencies and the system of mating, but Fisher does not mention this aspect of the problem. His typescript gives the frequency of each of these genotypes as rather less that 1 in a *million*, but on his copy Fisher has written in *billion* to replace million. Once in a billion (10^{12}) would seem to be roughly equivalent to once in 33 000 generations, if we take 30 years for the length of a generation and about 1 000 000 births per annum. Although the same frequency of 1 in 10^{12} would also be appropriate for an F_2 progeny with 20 independent gene pairs, it scarcely seems possible that Fisher was thinking of this example somewhat loosely as an extension from the synthetic cross involving two factors in wheat which he had just considered. Later on he writes, 'the synthetic breeding required by Mendelism could never have taken place in a state of nature'.
3. The influence of W. Bateson's book, *Mendel's principles of heredity*, is clearly evident. Fisher's reference to colour blindness as 'peculiar in being recessive in women' agrees with Bateson's description—although by 1911 E.B. Wilson had, in fact, suggested that the genes responsible for the common defects of colour vision were on the X chromosome. Like Bateson, Fisher does not mention linkage. Also in conformity with Bateson, he uses *allelomorph* but not *gene*, *genotype*, or *phenotype*—terms which were introduced by Johannsen in 1909. However, Fig. 1 shows that Fisher was making the same basic distinction as Johannsen between genotype ('real') and phenotype ('apparent'), a distinction of great importance in understanding the action of selection.

4. i.e. in the heterozygous state.
5. In other words, if the frequency of the recessive gene is $q = 1/2000$, then the frequency of affected persons is $q^2 = (1/2000)^2$ or one in four million. It is perhaps surprising that Fisher does not introduce the concept of gene frequency here. Though he was apparently unaware of G.H. Hardy's 1908 paper giving the relationships between the equilibrium genotypic frequences in a random mating population, one can scarcely doubt that Fisher would have found it easy in 1911 to derive the general law of binomial square genotypic frequencies and also to introduce the concept of gene frequency.
6. Pearson, assuming complete dominance, had argued that Mendelism could not account for the observed correlations between relatives for measurable quantities, whereas Yule had suggested that it could—if incomplete dominance were taken into account. Fisher is here concerned to offer some reasons why dominance might be complete for colour inheritance but incomplete for genes affecting structural characters. The interesting suggestion that dominance in colour inheritance is 'apparently determined by the presence or absence of some enzyme or pigment capable of producing the colour' perhaps arose from Fisher reading in *Mendel's principles of heredity* about Garrod's work with alcaptonuria which, Bateson says (p. 233), 'must be regarded as due to the absence of a certain ferment'. Fisher later showed (*CP* **9**) how assortative mating would increase the correlations, which Pearson had found to be too low with complete dominance, and that for a quantitative character such as height, dominance made an important contribution.
7. Fisher (*CP* 144, 1936), after a detailed study of Mendel's work, concluded, 'the data of most, if not all of the experiments, have been falsified so as to agree closely with Mendel's expectations'. Clearly, by 1911, Fisher was already aware of the exceptionally close agreement of Mendel's data and expectations.

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