



Haldane and Fisher – scientific interactions

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Introduction

There is no scientific paper ‘Haldane and Fisher’—or ‘Fisher and Haldane’—but the two men did interact scientifically in a number of ways. They knew each other and led parallel academic lives. But they were acquaintances rather than friends, and totally different in character and in political sympathies. Both English (though Haldane’s ancestry was Scottish), they were educated at the most famous pair of the great English public schools, Haldane at Eton and Fisher at Harrow, followed by first-class degrees at the Universities of Oxford (Haldane) and Cambridge (Fisher). Haldane read mathematics followed by classics and philosophy, and Fisher mathematics throughout followed by a postgraduate year of physics. They differed little in age. Haldane was born on 5 November 1892 and Fisher on 17 February 1890. They were equally precocious in youth, and lived lives of equal length, dying at the age of 72 still firm of mind.

They were both much attracted to India. Fisher arrived at the end of 1937 at the invitation of P. C. Mahalanobis, the founder and Director of the Indian Statistical Institute, to attend the Indian Science Congress and the concurrent Statistical Congress. He accepted the Presidency of the latter. In honour of Fisher’s visit Mahalanobis published a biography of him in *Sāṅkhyā: The Indian Journal of Statistics*. He was warmly welcomed by Professor and Mrs Mahalanobis in their home and his advice was sought by many influential people right up to the Viceroy himself. He visited India again as soon as possible after the ending of World War II in 1945, and his affection for the Mahalanobis family was maintained throughout the rest of his life.

Haldane’s introduction to India was much earlier: ‘During World War I, I was wounded twice, in France and in Iraq, after which I spent sixteen months in India’. The experience left an indelible impression on him: ‘In 1918, I formed a resolution to return to India when it had achieved such a degree of self-government as would permit me to associate with Indians on a footing of equality’. Like Fisher, Haldane was invited to an Indian Science Congress, in 1952, and had similarly been invited to lecture at the Indian Statistical Institute by Mahalanobis. He emigrated to India in 1957.

Much has been written about both Haldane and Fisher, but here I am only concerned with their scientific overlap and interaction. A biography of Haldane by Ronald Clark appeared in 1968 and one of Fisher by his daughter Joan Fisher Box in 1978. Fisher was elected FRS in 1929 and his Royal Society biographical memoir appeared in 1963; the corresponding dates for Haldane are 1932 and 1966.

One of the last occasions on which Haldane and Fisher met was when the latter visited the Indian Statistical Institute again in March 1959. Haldane had this to say:

I am very glad to see Professor Fisher again. For a number of years we were colleagues at the University College London. Then he went away to Cambridge and I didn’t see as much of him as I could have wished. When we were at the University College, we were chronically in slight disagreement. But the disagreement was not so great as to prevent collaboration, and that, after all, is what matters. I produced some rather messy figures about alleged linkage in man, and Fisher tidied them up. Then I said, I believe I can trim that tidying up a little

bit more and so it went on. But although formally we were each quarrelling with the other, the net result, I think, was fairly constructive. I would also like to say that some of my juniors, including my wife, said that Professor Fisher was much kinder than I when they brought statistical problems. The reason, I think, is that I know very little statistics now, and in 1938, the time in question, I don't think I knew any at all. As Professor Fisher knew quite a lot, that gave him an unfair advantage and he won away the hearts of several of my juniors. But, I would like to say this. Although Professor Fisher may sometimes have been rather hard on his contemporaries or his seniors, he has, at least among those I know, a reputation of being extraordinarily kind to junior workers. And that, I think, is the reputation which matters, because the junior workers will be alive after all the others are safely disposed of and it is they who will hand out the tradition of what sort of a man Fisher was. It is, therefore, more from the point of view of my juniors than my own that I welcome Professor Fisher here. I have occasionally used his method, and much more commonly, he would say, misused them. He has occasionally used mine also. I do, most warmly, welcome him here and I hope that he will come back fairly frequently and stay, if I may say so, for a little longer than he did this time. I also hope that he will bring Mrs Fisher with him.

Initial contacts

It is not clear when Haldane and Fisher first met. Possibly at meetings of the Genetical Society, but they will surely have encountered each other in Cambridge from 1923 on. Fisher was a nonresident Fellow of Gonville and Caius College from 1920 to 1926 when he was Statistician to Rothamsted Experimental Station in Hertfordshire, and his visits to Cambridge are likely to have been quite frequent. Haldane moved from a Fellowship at New College in Oxford to be Sir William Dunn Reader in Biochemistry in Cambridge in 1923, with accommodation in Trinity College (adjacent to Caius, as it happens). They were both Fellows of the Cambridge Philosophical Society, a University society devoted to the presentation and discussion of papers in mathematics and the natural sciences. Haldane's series of eight papers 'A mathematical theory of natural and artificial selection' were all published in the *Transactions* or the *Proceedings* of the Society, parts I and II in 1924 and part III in 1926, at a time when Fisher might easily have attended meetings of the Society. Further parts followed later.

In 1930 Fisher published *The genetical theory of natural selection* which marked the beginning of a long period of recorded interaction with Haldane both in their scientific writing and their private correspondence. *The genetical theory* does not mention Haldane's papers, and when the two men attended the 6th International Congress of Genetics at Cornell, Ithaca, in 1932 Fisher explained that their approaches were 'somewhat sharply contrasted'. Haldane's was 'analytic and deductive. Genetic studies are regarded as revealing the mechanism connecting cause and effect, from a knowledge of which the workings of the machine can be deduced and the course of evolutionary change inferred. The other approach [Fisher's] is inductive and statistical'.

Haldane reviewed *The genetical theory* favourably in the *Eugenics Review*. It was one of those books which 'state a new point of view, and lay the foundations of new branches of science. ... It is extremely difficult and highly controversial. Nevertheless it lays down methods by which the problem of evolution, including the present evolution of man, can be discussed with a certain measure of precision. No serious future discussion either of evolution or eugenics can possibly ignore it'. At the time Haldane and Fisher were engaged in frequent correspondence on several topics, particularly the evolution of dominance, and it seems that Haldane's review had been returned by the editor of the *Eugenics Review*. Fisher urged Haldane to try again. 'I am sorry that your MS has disappeared. I should greatly have liked to read it.' Fortunately Haldane found it and Fisher sent it on to the editor. 'Naturally I found it extremely interesting, apart from its flattering aspect.' Earlier, when Haldane had made some comments in a letter to Fisher after a 'first reading' of the book, Fisher replied 'Many thanks for your letter; you can scarcely guess what a satisfaction it is that my book has found one very intelligent reader'.

Fisher certainly met Haldane in April 1930 because in a letter he refers to their talk 'about two factors that "maintain each other mutually in equilibrium"' in chapter IV of *The genetical theory*. Then in November Haldane writes to Fisher that he has 'got a paper on the 2-gene case [i.e. 2-locus]' and he sketches the diagram which would ultimately appear in number VIII of his series 'A mathematical theory of natural and artificial selection'. In the same letter he encloses a draft of number VII.

Haldane's book *The causes of evolution*, the result of lectures at the University College of Wales at Aberystwyth in January 1931, came out in 1932. No review by Fisher appeared until one was published by Professor Bennett in 1983. Possibly Fisher thought better of submitting it, for though it refers to 'this brilliant book' it is mostly a criticism of Haldane's discussion of the evolution of dominance, the major subject of their mutual exchanges—and disagreements—in the years around 1930. In the Introduction to his book Haldane wrote that he was 'much

indebted' to Fisher's 'brilliant book, "*The genetical theory of natural selection*"'. Each thought the other's book 'brilliant'.

The genetical theory contained a long chapter 'The evolution of dominance' in which Fisher proposed that 'wild allelomorphs must *become* dominant to their unsuccessful competitors' and that it occurred under natural selection 'by the selection of modifying factors', i.e. of genes at other loci that modify the expression of the heterozygote. Joan Box, in her biography of Fisher, devotes an even longer chapter to discussing the subject and the responses of Haldane and of Sewall Wright to Fisher's theory. Wright argued that the selective process envisaged by Fisher would simply be too slow: the selective intensities, being essentially second-order, would be swamped by other influences. In *The causes of evolution* Haldane wrote 'Fisher believes that the effect of this process has been to make most genes which frequently mutate recessive. Wright and I have criticized this theory, and I doubt if it can stand in its original form. Nevertheless it undoubtedly has some truth in it, and there can be little doubt that mutation pressure has been a cause of evolution, if perhaps a less important one that Fisher believes'. There are further remarks in the appendix to *The causes of evolution*.

The MRC Committee on Human Genetics, 1932

From 1932 the contact between Haldane and Fisher, which hitherto had been mainly on paper, became much more in person. As a result of an initiative by C. C. Hurst, the Medical Research Council set up a Committee on Human Genetics to advise it. Haldane was asked to be its chairman, and the other members were Julia Bell, E. A. Cockayne, Fisher, Lancelot Hogben, L. S. Penrose and J. A. Fraser Roberts. Personal contact between Haldane and Fisher now became more frequent. Writing about Haldane to Leonard Darwin just after the first meeting of the Committee Fisher said 'I am on quite civil terms at present; he is Chairman of a Committee on Human Genetics of the Medical Research Council, of which Hogben and self are other members. ... I have had to slang him [Haldane] to some extent in *Proc. Camb. Phil. Soc.* where he has written rather foolishly on some points in theoretical statistics, but I do not think he will take offence. I am heartily glad at his election to the Royal [Society], for he is shoulder above most geneticists in this country; but he is oddly unreliable, chiefly, I think, because he never knows where he is an amateur and where an expert'.

Haldane had written a somewhat confused and long-winded paper 'A note on inverse probability' in which he had erroneously supposed that Fisher's method of maximum likelihood was based on 'the tacit assumption' of a Bayesian prior distribution for the unknown parameter. This not unnaturally irritated Fisher, who responded

quickly and sharply. The paper is interesting to geneticists because it contains the first example of using Bayesian methodology in linkage, and interesting to Bayesian statisticians for an early example of 'Bayes factors'.

Professors at University College London, 1933

In 1933 both men were appointed to professorships at University College London. Henceforth their contact would be almost daily. In the upheaval following Karl Pearson's retirement a Professorship of Genetics was created for Haldane while Fisher was elected to the Galton Professorship of Eugenics after having been invited to apply for it. He wrote to Haldane 'I ought to thank you first for the great part that you have undoubtedly played in putting the invitation in my way'. Haldane replied 'Please do not thank me in connection with your appointment. When asked my advice I mentioned a number of arguments against you, some of which were new to members of the committee. It was the merest regard for truth, and not any personal regard which I may feel for you, which forced me to add that you were the only possible candidate for the post'.

The University College years saw the emergence of statistical methods for the estimation of genetic linkage in man. In 1931, Hogben in his book *Genetic principles in social science* had been quick to draw attention to the pioneering work of Felix Bernstein in Germany. Hogben, Professor of Social Biology at the London School of Economics, followed this up in 1933 with another book, *Nature and nurture*, in which he gave an extended account of Bernstein's methods, and then in 1934 with a pair of papers in the *Proceedings of the Royal Society, Series B*, 'The detection of linkage in human families'. Haldane immediately joined in with a paper covering 40 pages of the *Annals of Eugenics*, whose editorship Fisher had inherited with his Galton chair. Fisher had had to 'tidy up' 'some rather messy figures about alleged linkage in man' (as Haldane reported in his 1959 speech given in my Introduction above). David Jones, who attended Fisher's Cambridge lectures on Human Heredity in 1956, tells me that 'He then went on to linkage, starting with Bernstein 1931, complimenting Haldane for a good try, and then [to] his own efforts to "keep Haldane on the rails"'. Fisher published his paper immediately following Haldane's, using his own methods of statistical inference which he had developed over the previous dozen years.

In 1935 Fisher continued to extend Haldane's work and introduced his 'u'-statistics, functions of the data with preferable statistical properties to those used by Bernstein and Haldane. They were later studied by D. J. Finney and N. T. J. Bailey but finally eclipsed by the advent of alternative methods of estimation based directly on the likelihood function and, ultimately, the new computers. These stemmed from a fundamental paper by Julia Bell and Haldane in 1937, but by then Fisher had turned his

attention more towards the theory of the estimation of linkage in the mouse, his experimental animal of preference.

In 1935 Fisher addressed the International Congress on Life Assurance Medicine in London on ‘Linkage studies and the prognosis of hereditary ailments’. In a brief lecture he explained to his audience how a knowledge of the linkage between a pair of genetic factors, especially when it was close, would be of value in those cases in which one of the pair, such as might determine a blood group, was linked with a factor determining a disease. ‘It is therefore of great importance that these linkage groups should be sorted out, in order that common and readily recognisable factors may be used to trace the inheritance and predict the occurrence of other factors of greater individual importance, such as those producing insanity, various forms of mental deficiency, and other transmissible diseases’. (Here, of course, ‘transmissible’ is not used in its sense of a spreading infection but with reference to genetic transmission from parent to offspring.)

This passage, of such relevance to the modern discussion of the problems posed to insurance by the possibilities for prognosis from genetic information, raises the question of who first thought that linkage between a marker locus and a disease locus might have value in prognosis, Fisher’s paper having carried no references. In a lecture to the Eugenics Society a few months earlier Fisher had explained the idea, citing Huntington’s chorea as an example of a disease and the blood groups and the ability to taste PTC as examples of ‘harmless traits’ that were inherited. Again, there were no references. But might not Haldane have been involved in the genesis of such an idea? And indeed we find it in his Norman Lockyer Lecture ‘Human biology and politics’ delivered at the end of 1934, Huntington’s chorea again being the example. So possibly the idea emerged during conversations between Haldane and Fisher in the UCL Senior Common Room where they presumably encountered each other from time to time. In fact in *Possible worlds: the future of biology* (1927) Haldane had floated the idea in connection with the prediction ‘of such characters as musical ability, obesity, and bad temper’ in a new-born baby from marker loci linked to any genetic factors influencing such traits, rather than diseases. Eighty years later we may observe that precious little is known about genetic influences on ‘musical ability, obesity, and bad temper’ except that musical ability seems to be more common in certain families. The same can be said of mathematical ability, also one of Haldane’s examples.

In another of the essays in *Possible worlds*—‘Darwinism today’—Haldane gave an example of what came to be called ‘inclusive fitness’. ‘Of two female deer, the one which habitually abandons its young on the approach of a beast of prey is likely to outlive one which defends them; but as the latter will leave more offspring, her type survives even if she loses her life’. In 1955 he was to repeat the idea in a *New Biology* article (to be mentioned below), this time

with the example of saving a drowning child. Twenty years later John Maynard Smith recalled Haldane once ‘calculating on the back of an envelope for some minutes’—in about 1955—and announcing ‘that he was prepared to lay down his life for eight cousins or two brothers’. This led to bad feeling between Maynard Smith and W. D. Hamilton, who had used very similar wording in his pioneering work on inclusive fitness, but this is of no relevance to relations between Haldane and Fisher. What is relevant is that Fisher, aged 23, had published the idea in 1914: ‘A is the eldest son, and stays at home; his brother B goes to the wars; then so long as A has some eight children, it does not matter, genetically, if B gets killed, or dies childless, there will be nephews to fill his place’. (I suppose Fisher had in mind four boys and four girls and was considering only masculine attributes.) In truth, the idea is a very simple one, following immediately from Mendelian inheritance. Both Fisher in 1930 and Haldane in 1932 made use of it in their books, and it would have been a very natural topic of conversation between them in the University College common room.

World War II 1939–1945

The stories of the battles fought by both Haldane and Fisher with the authorities at University College following the outbreak of World War II in 1939 have been amply rehearsed in both biographies, but they are only tangentially part of an account of their scientific interaction. Fisher and the remnants of his Department were evacuated to Rothamsted Experimental Station, his former employer before he moved to University College. Since he and his family had continued to live in Harpenden, adjacent to Rothamsted, this was a fortunate arrangement. Haldane, meanwhile, faced the same problem for what remained of his own Department, and Fisher ‘persuaded Haldane to ask for an office at Rothamsted, with his assistant, Helen Spurway’. His request was granted. ‘Haldane joined in the usual Rothamsted social affairs ... booming round the place with an affable unconventional *bonhomie*, and arguing interminably with R. A. Fisher on every subject under the sun’.

Of scientific interaction at Rothamsted there is no evidence from their publications. Haldane must have been away a good deal, busy with work on physiological problems for the Royal Navy and other war-time assignments, as well as with expressing his Marxist views in various political publications. The latter soon involved him in the Lysenko controversy, fully described in his biography. In 1948 he, S. C. Harland, Cyril Darlington and Fisher were to take part in a BBC programme about the ‘Lysenko affair’, each recording his opinion separately and for publication in *The Listener* (see accompanying article by [deJong-Lambert 2017](#)). These were political questions on which we may be sure that Haldane and Fisher had

divergent views. However, they are outside this account of their scientific interaction.

Fisher, by contrast, stayed quietly at Rothamsted, frustrated by the lack of official willingness to engage his talents in war work. His publications in 1942 centred on combinatorial problems involving Latin squares in factorial experiments, papers which displayed his great skill in combinatorial questions of the sort then taxing the secret code-breakers at Bletchley Park, just a 25-mile bicycle ride up the Roman Road of Watling Street.

D. J. Finney was at Rothamsted during the war and I have asked him about relations between Fisher and Haldane then. ‘My recollection of Fisher and Haldane at Rothamsted is that they continued on amicable terms—often talking together during the tea recess, but united in indignation at UCL having thrown them out “for the duration”’. Professor Finney celebrated his 100th birthday on 3 January this year.

Post-War

In 1943 Fisher was elected Arthur Balfour Professor of Genetics at Cambridge in succession to R. C. Punnett. It has been suggested that Haldane had eyed the professorship, as well he might have done, but Fisher had the stronger Cambridge connections. Though Haldane had been Reader in Biochemistry his controversial behaviour in a divorce case, resulting in his being deprived of the office and reinstated on appeal, may not have been forgotten. Fisher, a former Fellow of Caius, had been an Elector to the Professorship, but had resigned when it became vacant thus making himself eligible. In the event the University took the initiative. The Chair had been vacant since 1940, and Fisher was told that it would be now be advertised if he agreed to stand. He held it until his retirement in 1957.

Fisher had probably hoped that with the move he would become the Editor of the *Journal of Genetics*, a Cambridge University Press journal edited by Punnett alone since Bateson’s death. In 1941 Haldane had been asked to approach Punnett on behalf of the Genetical Society, of which Fisher was then President, with a view to it being associated with the Society in future. Punnett was unwilling, but when the suggestion was about to be repeated in 1943 Haldane stepped in, going directly to Punnett and buying the *Journal* for his wife (see accompanying article by Rao 2017). With the *Annals of Eugenics* staying at University College, though also published by Cambridge University Press, Fisher found himself without editorial functions. To fill the gap, in 1947 C. D. Darlington, Director of the John Innes Institute, and Fisher founded and for 10 years edited a new journal *Heredity*. Originally published by Oliver and Boyd, long-standing publishers of Fisher’s books, it is now the property of the Genetical Society (renamed the Genetics Society).

Haldane and Fisher both attended the International Congress of Genetics in Stockholm in 1948, and in September 1949 they were both in Milan for a meeting on human genetics of the Italian Society of Genetics. Haldane gave a long paper ‘Natural selection in man’ and Fisher a rather short one on ‘Marker genes in human genetics’. Haldane made a brief point afterwards to which Fisher responded.

In 1953 Fisher gave the Croonian Lecture of the Royal Society, choosing as his subject ‘Population genetics’, and probably Haldane would have been in the audience. In any event, in 1955 Haldane used the same title for a chapter in the April number of *New Biology* (a biennial Penguin paperback) in which he expressed himself in the context of his own mathematical approach. But he concluded ‘Sir Ronald Fisher has recently delivered a lecture to the Royal Society on this subject which hardly overlaps this article at all. The subject is a very large one, and one can only deal with a few aspects of it in an article of this length’, thereby acknowledging the difference between what in 1932 Fisher had called Haldane’s ‘analytic and deductive’ approach and his own ‘inductive and statistical’ one.

Haldane remained at University College until his departure for India, also in 1957, but the contacts between the two men had become limited and their interests had diverged. Fisher continued with the experiments with mice that he had started in London, creating stocks designed for the investigation of linkage. This might have interested Haldane for two reasons, but there seems to have been no interaction. First was the historical fact that Haldane, his sister Naomi Mitchison and A. D. Sprunt had been among the first to establish the existence of the phenomenon of linkage in the mouse. It had been discovered originally in plants, by Bateson and Punnett, but here was a mammalian example. The publication of Haldane, Sprunt and Mitchison in December 1919 was held up by Haldane’s military service and indeed did not appear until after Sprunt’s death on active service, by which time W. E. Castle and Sewall Wright had, in August, published evidence for linkage in the rat.

The second reason was that Fisher, pursuing his experiments on linkage in the mouse, became interested in the phenomenon of interference, for which Haldane had discussed the mapping function (linking recombination value and map distance) on the simplest model for crossingover in 1919. This work had been extended by the Indian D. D. Kosambi in 1944 and by others, and then by Fisher and his Cambridge colleagues. But Haldane does not seem to have commented on the progress in these topics, which had so interested him originally.

Epilogue

I think that as a student I saw Haldane and Fisher together at meetings of the Genetical Society, but the last time I saw them together, and perhaps the last time they saw

each other, was at the Second International Conference of Human Genetics in Rome in 1961. I do not know if they spoke to each other, but I recall standing talking to Fisher and Peter Parsons, also from Cambridge, when Peter remarked ‘Look, there’s Haldane’, who was standing a little way off by himself, ‘Shall we go and talk to him?’ I do not recall Fisher’s response, but we didn’t. Fisher died in 1962.

In 1963 Haldane attended the Eleventh International Congress of Genetics at The Hague. I heard him give his long review ‘The implications of human genetics for human society’. He later attended the paper ‘Analysis of human evolution’ by L. L. Cavalli-Sforza and me, and asked a question in the discussion. Cavalli-Sforza answered him, but added that perhaps I would like to add a word, which I did. It is the only ‘conversation’ I ever had with Haldane. He was required to submit his question in writing and I possess what he wrote. He died in 1964.

Note on sources

This account of the scientific relations of Haldane and Fisher is neither a scientific paper nor a researched contribution to the history of science. It is based on secondary sources and my own recollections and impressions formed over many years. Of the secondary sources the two biographies are the most important: *J. B. S.: the life and work of J. B. S. Haldane* by Ronald Clark, London 1968 and *R. A. Fisher: the life of a scientist* by Joan Fisher Box, New York 1978. Both books contain comprehensive bibliographies for their subjects. Quotations from Fisher’s correspondence

come from *Natural selection, heredity, and eugenics*, edited by J. H. Bennett, Oxford 1983. Haldane’s speech of welcome to Fisher in 1959 is reproduced from *J. B. S. Haldane: a tribute* Indian Statistical Institute, Calcutta, 1992 (the Haldane centenary). I have made use of four of my own historical papers: The early history of the statistical estimation of linkage, *Annals of Human Genetics* **60**, 1996, 237–249; Darwin and Mendel united: the contributions of Fisher, Haldane and Wright up to 1932, in *Encyclopedia of Genetics*, edited by E. C. R. Reeve, London 2001; Mendelism and Man 1918–1939, in *A Century of Mendelism in human genetics*, edited by M. Keynes, A. W. F. Edwards and R. Peel, Boca Raton, Florida 2004; and Linkage methods in human genetics before the computer, *Human Genetics* **118**, 2005, 515–530. In the absence of footnotes I shall be glad to answer any queries as to other sources.

I should also like to draw attention to ‘J. B. S. Haldane and R. A. Fisher’s draft life of Karl Pearson’ by Sahotra Sarkar in *Notes and records of the Royal Society of London* **49**, 1995, 119–124, for an interesting account of a matter involving Haldane and Fisher but without direct interaction and therefore not described here. The paper also amplifies the suggestion that Haldane had hoped for the Cambridge Professorship of Genetics in 1943.

References

- deJong-Lambert 2017 J. B. S. Haldane and ЛЫСЕНКОВЩИНА (*Lysenkovschina*). *J. Genet.* **96**, (<https://doi.org/10.1007/s12041-017-0843-2>).
- Rao V. 2017 J. B. S. Haldane and Journal of Genetics. *J. Genet.* **96**, (<https://doi.org/10.1007/s12041-017-0841-4>).