

Handedness on Tristan da Cunha: The Genetic Consequences of Social Isolation

I. C. McManus

University College London, UK

M. P. Bryden

University of Waterloo, Ontario, Canada

Provins (1990) has suggested that the apparently low incidence of left-handedness on the island of Tristan da Cunha is the result of social pressures such as deference to authority and group conformity, and that "any genetic factor determining left-handedness must be very weak". Here we use a large number of Monte Carlo simulations ($n = 10,825$) of the growth of the population of Tristan da Cunha from 1827 to 1961, to show that if the original population was randomly selected from a large population with a typical gene-frequency, then a combination of founder effects, genetic drift and evolutionary bottlenecks can readily explain the fairly low incidence of left-handedness that was found. Indeed in 15% of the simulations the *c*-allele, which is postulated to be responsible for left-handedness, has disappeared entirely, resulting in a population with no left-handers at all. The data from Tristan da Cunha are therefore entirely compatible with a genetic model of left-handedness.

Provins (1990) avait suggéré que l'incidence apparemment faible des gauchers sur l'île de Tristan da Cunha était le résultat de pressions sociales telles que la déférence envers l'autorité et le conformisme de groupe, et que "toute détermination génétique de la latéralité gauche devrait être très faible". Dans cette étude, nous avons utilisé un très grand nombre de simulations de Monte Carlo ($n = 10,825$) de la croissance de la population sur Tristan da Cunha, de 1827 à 1961, afin de démontrer que si la population originale était choisie au hasard à partir d'une population plus large possédant un facteur génétique typique, alors une combinaison d'effets des pères fondateurs, de la dérive génétique et de goulets d'étranglement évolutif pourrait facilement expliquer l'incidence relativement faible de gauchers qui a été trouvée. En fait, dans 15% des simulations, le "C-allele", lequel serait responsable de la latéralité gauche, aurait complètement disparu, ce qui aurait résulté en une population

Requests for reprints should be sent to Dr. I. C. McManus, Department of Psychology, University College London, Gower Street, London WC1E 6BT, U.K.

ICM was in receipt of a Commonwealth Research Fellowship at the Department of Psychology, University of Waterloo, Ontario, Canada, while this study was carried out. We thank Dr. K. A. Provins for his careful comments on refereeing the paper.

totalement dépourvue de gauchers. Les données sur Tristan da Cunha sont par conséquent parfaitement compatibles avec un modèle génétique de la latéralité gauche.

INTRODUCTION

The origins of left- and right-handedness are still controversial, although in recent years there has been a growing consensus that handedness is probably under genetic control, the most successful genetic models being those of Annett (1985) and McManus (1985). Nevertheless there has been a continuing series of publications (e.g. Dawson, 1972) which have argued that right-handedness arises as the result of a social pressure to conformity; the literature has been well reviewed by Harris (1990). A recent and very interesting example of the latter is the paper by Provins (1990), which analysed data from the remote, isolated population of Tristan da Cunha, a volcanic island in the South Atlantic, 2900kms from the nearest permanent mainland habitation, and 2400kms from the nearest island, St Helena. It has a complex history (Munch, 1971), and a specific ecology of its own (Wace & Holdgate, 1976).

In his study of the handedness of the Tristanites, Provins found a low incidence of left-handedness. The population was studied during their temporary exile in Britain during 1961–3, as the result of a volcanic eruption on the island that threatened their settlement. Handedness was assessed as part of a broader survey of physical activities, including games, sports and the playing of musical instruments. Handedness was assessed by asking about the hand used for eight unimanual tasks, as well as observing writing with a pencil on paper. Information was also obtained about the handedness of family members and other relatives. Interviews were conducted during the day, and as Provins says: "Many of the home visits were unsuccessful or resulted in only one or two family members being at home—often wives and sisters or mothers with children since the menfolk were out working or looking for jobs." The total sample of 76 individuals therefore comprised 20 males and 56 females. Of these 76 quasi-randomly selected individuals from the total population (1961), all wrote with their right hand, and only 2 (2.6%) could be classified as left-handed on the basis of other activities. On the basis of these data Provins (1990, p. 343), concluded that "any genetic factor determining left-handedness must be very weak and a preferred explanation of the findings is offered in terms of social pressures such as: (i) Deference to authority, and (ii) group conformity". While not doubting that Tristan da Cunha may well represent a community with high degrees of pressure to conformity (see e.g. Rawnsley & Loudon, 1964; Munch, 1971), we are not convinced that the low incidence of left-handedness is incompatible with a genetic explanation of handedness. Small isolated communities,

particularly those that have arisen from small numbers of founders, are well known in the genetic literature for their tendency to have atypical distributions of polymorphic genes (Cavalli-Sforza & Bodmer, 1971). In this paper we use a Monte Carlo simulation to investigate how the putative genes for handedness might have evolved in the isolated community of Tristan da Cunha, and we suggest that the relatively low incidence found by Provins is entirely compatible with handedness generally being under genetic control.

METHOD

Monte Carlo simulation was used to investigate the possible ways in which a gene for handedness might have evolved within a population constrained to be similar to that of Tristan da Cunha. The details of the simulation are as follows:

Population Dynamics

The population dynamics were simulated with the following rules:

1. The founder population comprised 7 pairs of unrelated individuals (7 male and 7 female). The males were aged: 20, 25, 30, 35, 40, 45 and 50, and the females: 15, 17, 19, 21, 23, 25 and 27.
2. Mating was at random, with the constraint that siblings could not marry, and individuals married only once during their lifetime.
3. Females married at or after the age of 16, having a 0.3 probability of marrying in each year after that age. Husbands were selected randomly from the unmarried male population over the age of 16, with men only being allowed to marry once. If no suitable husbands were available then women remained single.
4. Members of the population had a 50% chance of dying by the age of 65, calculated on the basis of a probability of 0.0106 of dying in any one year. After age 65 the probability of dying in any one year was 0.067.
5. The size of the total population was constrained to be as close as possible to that described by Roberts (1971) in his account of the demography of the island (see his Figure 1; p. 469). Specifically the population was assumed to grow linearly from 14 in 1827 to 103 in 1856; to drop to 35 in 1857 and then to grow linearly to 100 in 1885; to drop linearly to 60 in 1892, and then to grow linearly to 75 in 1905, after which the population grew linearly to 264 in 1961.
6. At times of net population growth the number of births in a particular year was calculated, as far as possible, to bring the expected population size to that expected on the linear model described in the previous paragraph, after taking deaths that year into account. It should be noted that this method of population growth automatically results in an appropriately declining level of fertility amongst females in later generations,

as has been described by Roberts (1971). The method also results in the almost logistic growth curve that seems to be required for the rapid population growth during the early years of the island's development (Birdsell, 1957).

7. Births occurred randomly amongst the eligible female population which consisted of those who were married and under the age of 45, who had not given birth in the current or the previous year, and who had a living husband.
8. Periods of population contraction occurred by two mechanisms. During slow contraction (less than 5 persons per year), population reduction occurred by random deaths within the entire population.
9. During rapid population contraction, loss was presumed to occur principally by emigration, in which case emigrants were selected by randomly choosing amongst all males over the age of 16, and including their wife and all children under the age of 16.
10. In years of population contraction, births continued to occur at the same rate as in the previous year in which contraction had not occurred.

Genetic Model

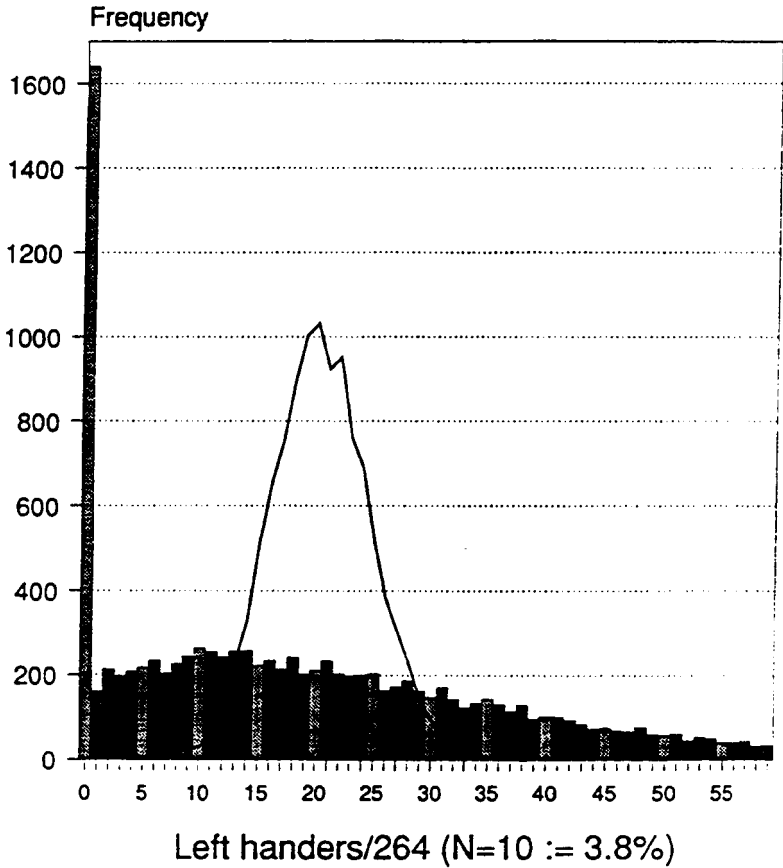
The genetic model of McManus (1985; 1991) was used for the prediction of left- or right-handedness in the population. There are two alleles, D (Dextral) and C (Chance), with the C allele having a frequency of 0.155 in the gene-pool. The probability of individuals being left-handed is 0 if they are of genotype DD; 0.25 if of genotype DC; and 0.5 if of genotype CC. The genotypes of the founder population were randomly selected from the typical population gene-pool, assuming a Hardy-Weinberg equilibrium. After the final generation of the model (i.e. in 1961) the number of left-handers (out of a population of 264) and the proportion of C alleles in the island's gene-pool were calculated and were the outcome measures of the simulation. It should be noted that although conceptually different, the genetic model of Annett (1985) makes almost identical predictions to the model of McManus (1985) for family calculations (McManus & Bryden, 1992), and therefore substantially similar results would be expected from it in simulations. The most important difference would be that since the RS+/+ genotype can result in a small proportion of individuals being left-handed (of the order of 1 in 200, according to the threshold), then even with a complete absence of the RS allele due to genetic drift, left-handers still occur in the population occasionally.

Statistical Model

The simulation was designed to investigate the separate effects of three sources of variance on the proportion of left-handers in the island

population: a) the particular family tree that had arisen from the members of the founder population (FAMILY TREE); b) within each particular family tree, the particular genotypes that were present in the founder population (FOUNDER); and c) the particular genetic recombinations occurring from the particular founder genotypes within a particular family tree (RECOMBINATION).

A total of 500 family trees were generated, and for each of these, five different sets of founder genotypes were generated, for each of which five



10825 replicates

Fig. 1. Number of left-handers on Tristan da Cunha. The shaded area shows the number of cases from 10,825 Monte Carlo simulations in which there were 0, 1, 2, etc., left-handed individuals found in a population of 264 individuals. Ten individuals therefore represent a population incidence of left-handedness of 3.8%. For clarity the histogram bars for 0, 5, 10, 15 etc., individuals are shown in lighter shading than for the other bars. The heavy solid line indicates the number of left-handed individuals found in 10,825 Monte Carlo simulations of 264 individuals taken from a very large randomly mating population.

different sets of recombinations were generated. A total of $500 \times 5 \times 5 = 12,500$ different genetic outcomes therefore resulted.

The simulation program was written in compiled FORTRAN and run on a Compaq LTE 386s/20 microcomputer; the simulation took about eight hours of computer time.

Outcome variables were the number of left-handers in the final population of 264 and the frequency of the C allele in the final population. Data were transformed by a logistic transformation with continuity correction before statistical analysis, which was by a nested analysis of variance.

RESULTS

Five hundred family trees were simulated; however of these 67 (13.4%) resulted in poor population growth (typically because of random fluctuations which resulted in low numbers of fertile females during bottlenecks in population growth), so that the final population target of 264 was not reached (and in the majority of cases the population became extinct or close to extinction). The remaining 433 valid family trees resulted in 10,825 genetic simulations. Figure 1 shows the percentage of left-handers found in the final population of 264 individuals; in 1641 simulations (15.2%) the population contained no left-handers, the modal number of left-handers in the non-zero cases was 10, representing 3.8% of the population, the 95% interval was from 0 to 62 left-handers (0% to 23.5% of the population), with the maximum number of left-handers being 107 (40.5% of the population). It is of importance to note that the mean incidence of left-handedness was 20.4 individuals (7.7%), (Standard deviation = 17.69; 6.70%) which is almost identical to that expected in the population from which the founders were drawn; however the variance of the distribution is far greater than

TABLE 1

Nested analyses of variance for the two dependent variables of the logistic transform of the proportion of left-handers and the proportion of C-alleles in the gene-pool

<i>Dependent variable</i>		<i>Proportion of C alleles in gene-pool</i>		<i>Proportion of left-handers</i>	
<i>Source</i>	<i>df</i>	<i>Sum of Squares</i>	<i>Mean Square</i>	<i>Sum of Squares</i>	<i>Mean Square</i>
Family Tree	432	106.36	0.2463	24.04	0.0556
Founders within Family Trees	1731	425.44	0.2458	96.96	0.0560
Recombinations within Founders within Family Trees	8226	228.84	0.0278	55.70	0.0068
Total	10824	867.07	0.0801	200.74	0.0185

would be expected if the samples were drawn from a randomly mating large population. Figure 2 shows the proportion of C alleles found in the gene-pool of the 264 individuals (i.e. 528 alleles); in 1490 simulations (13.8%) the gene-pool contained no C alleles, the modal frequency for the non-zero cases was 10%, the overall range was from 0 to 79%, and the 95% confidence interval was from 0 to 47%. The mean incidence of the C allele (15.46%, $SD = 13.13\%$) was almost unchanged from that in the original population, although the effects of genetic drift, etc., have been to increase the *variance* of the gene-frequencies in the simulations.

Table 1 shows the analysis of variance for the overall frequency of left-handedness and for the frequency of the C allele in the gene-pool. The two analyses produce almost identical results. In each case the amount of variance attributable to family trees and to founders within family trees was almost identical, with only a very tiny amount of variance due to recombinations within founders within family trees.

DISCUSSION

Small, genetically closed communities are different from the larger, more outbred communities which typify the populations on which most psychological studies are carried out. In particular small populations tend to be inbred (thus it has been estimated that the average inbreeding coefficient in Tristan da Cunha in 1961 was 0.040, which is equivalent to two-thirds of the similarity of the offspring of a first-cousin marriage [Jenkins, Beighton, & Steinberg, 1985]). The small size of the gene-pool, in an effect that is exacerbated by inbreeding, means that genetic drift is greater than in larger populations, so that rarer alleles are more likely to be lost from the gene-pool by simple chance fluctuations, but are also more likely to be fixed by a similar mechanism; the result is that the mean frequency of a gene remains identical across many replications. The effects of genetic drift are well observed in the present simulations, in which nearly 14% of simulations had lost the C allele entirely from the gene-pool by the year 1961. Small populations also show a strong "founder effect", whereby all alleles found in the population must have originated from the small number of alleles found in the original founders (14 individuals in the present simulation). These effects are subsequently magnified by "evolutionary bottlenecks" in which the population shrinks to small numbers, thereby reducing the genetic variance yet further (and two such incidents are known to have occurred on Tristan; the mass emigration of 1857, and the boating disaster of 1885, which was also followed by an emigration). In the present simulations the particular choice of founders was an important source of genetic variance, as also was the particular family tree of individuals who happened to survive. More surprisingly the pattern of recombinations within a family tree had relatively

little impact on the outcome. The important role of founders can be seen by considering the situation in which all of the individuals carry the D allele only; since the D allele occurs in 84.5% of the normal gene-pool, the chance of obtaining 14 individuals who are all of DD genotype is 0.89%, and in these cases it is inevitable that all individuals would be right-handed. That particular case could not of course have occurred on Tristan da Cunha since left-handers are subsequently known to appear in the population. That founder effects and genetic drift are important for the genetics of Tristan da Cunha have been adequately confirmed in other studies which have shown that at least nine blood polymorphisms show no variation on the island (Jenkins, Beighton, & Steinberg, 1985), and that the normally common A₂ allele of the ABO blood group system does not exist on the island. The high frequency of the Gd^A allele confirms the important role of the founders, who originated from St Helena, and also certainly transmitted this and other "African" alleles; and indeed they can be traced back to particular individuals (Jenkins, Beighton, & Steinberg, 1985). The theoretical consequences of founder effects and drift for the Tristan da Cunha population have been discussed in greater detail by Thomas and Thompson (1984), who show that only 64% of the original alleles contributed by founders are still present in the population. That figure is very compatible with the present simulations since it would suggest that the predicted frequency of C alleles should be reduced from a normal 0.155 to 0.099, a value similar to the mode shown in Fig. 2.

Small populations do not only show the loss of relatively common alleles, but can also, due to founder effects and genetic drift, show *higher* frequencies of alleles than is typical in larger populations (the effects of inbreeding and drift overriding what are presumably the selective disadvantages which normally keep the gene-frequency low). In the simulations this is apparent from the 2.5% of cases in which the C allele is present at a frequency of more than 47%, and in which the rate of left-handedness is more than 23.5%. Similar effects can explain the known occurrence on Tristan of high rates of genetically transmitted conditions such as retinitis pigmentosa (Eickhoff & Reighton, 1985) and asthma (Turner, 1989).

The present simulations, like any simulations of real phenomena, are relatively crude; in particular it would in principle be possible to simulate the founder and recombination effects within the particular tree which constitutes the actual historical pedigree of the population; however to our knowledge the genealogy has not been published in its entirety, although portions have been reproduced (Jenkins, Beighton, & Steinberg, 1985; Thomas & Thompson, 1984). These portions make it clear that the early populations had a complex pedigree in which some women had children by several successive husbands. The present analysis has not taken that complexity into account. Nevertheless it is unlikely to have a substantial influence on the final

conclusions. The precise number of founders is itself complicated; Thomas and Thompson (1984) refer to 16 founders, of whom 11 constitute "the early core", and comprised eight men and three women. Our use of seven male founders is in part justified by the occurrence of only seven surnames on the island. It is unlikely that this particular assumption substantially affects the conclusions of the simulation.

Given the results of the Monte Carlo simulation we may now consider the conclusions of Provins (1990) in more detail. Provins suggests that the incidence of left-handedness on Tristan da Cunha is low, and explains its low

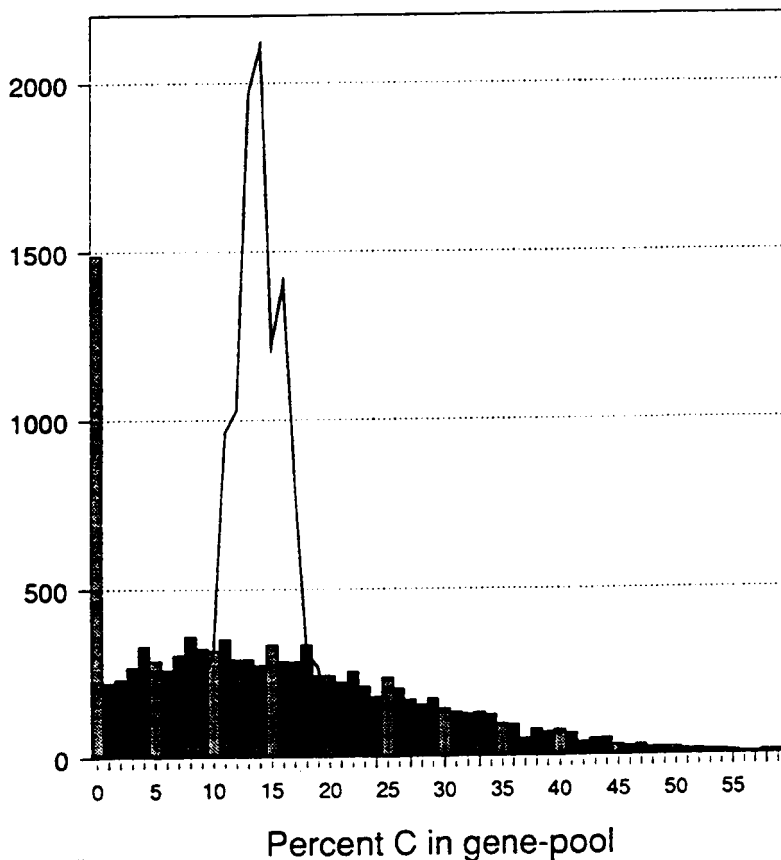


Fig. 2. Frequency of C allele on Tristan da Cunha. The shaded area shows the percentage of Monte Carlo simulations in which the proportion of C alleles in the population of 264 individuals was 0, 1, 2, 3% etc. The solid line indicates a Monte Carlo simulation for a similar situation in which the individuals are taken from a very large, randomly mating population. It should be noted that division by 264 does not result in equal numbers of integers occurring in different histogram bins, and hence the various intervals show some fluctuations due to this factor.

value in terms of deference to authority and group conformity. Study of his data suggests that the incidence is not in fact particularly low, since of the 76 subjects studied, two seem on the basis of their general pattern of hand usage (excluding writing) to be left-handed, giving an incidence in those studied of 2.6%. Additionally eight out of 70 of those subjects reported that one parent was left-handed, and excluding overlaps this gives a parental incidence of $6/140 = 4.3\%$; combining these estimates suggests that around 3.7% of the Tristan population may be left-handed. Although on the low side, this value is far from atypical for studies of left-handedness, as is seen in the meta-analysis of Seddon and McManus (1991). Indeed in that study the overall incidence, based on studies of over 250,000 subjects, was only 7.78%, a proportion that is just significantly different from an estimate of 3.7% based on 216 subjects (Chi-square = 4.60; *Idf*, $P < 0.05$) but not from an estimate of 2.6% based on 76 subjects (Chi-square = 2.98, *Idf*, *NS*). However neither of these estimates take into account the statement of Provins that despite large family sizes (average = 5.4 siblings), only two left-handed siblings were reported, and they had already been identified in the study. These data are slightly difficult to interpret, since if each of the 76 subjects reported on 5.4 independent siblings, the population would need to consist of at least 410 individuals. There were inevitably many overlaps between the family members reported by different individuals (Provins, personal communication, 1992), and it is therefore conceivable that these reports on siblings, particularly when drawn from a population with a wide range of age, account for the entire population of 264 individuals, thereby making the true estimate of handedness in the living population $2/264 = 0.76\%$. If so, then that value is significantly less than 7.78% (Chi-square = 18.14, $P < 0.001$). It is also possible, as has been pointed out to us (Provins, personal communication, 1992) that since in the original report (Provins, 1990, p. 346) two sisters each reported a left-handed brother who nevertheless turned out to be predominantly right-handed, that individuals' reports of handedness in parents may also be biased towards left-handedness. However at this point the value of the Monte Carlo simulations becomes apparent, since examination of the distribution shown in Fig. 1 shows that the likelihood of obtaining two or less left-handers in an inbred island population of 264 is 18.6%, which is not statistically significant. And indeed it becomes apparent that even if *none* of the islanders were left-handed then that would not be statistically significant since in 15.2% of the simulations no left-handers were found, despite left-handedness depending entirely on genetic factors in those simulations. This situation of course contrasts with a similar sized population being drawn from a very large, randomly mating population (see Fig. 1), in which there were *no* cases in 10,825 Monte Carlo simulations in which as few as two left-handers

occurred; indeed the smallest number of left-handers was seven, and that occurred but once.

It is clear from the present analysis that the data of Provins are compatible with a conventional genetic model of handedness, in which drift, founder effects and evolutionary bottlenecks have resulted in an atypical distribution of allelic frequencies in a small, inbred population. This does not of course disprove Provins' suggestion that social factors may also be of importance in determining some aspects of handedness. In particular we note that although two individuals were left-handed on a broad assessment of a range of skills, they nonetheless wrote with their right hand. This is indeed suggestive of a degree of social pressure to conformity in a conspicuous social behaviour. The situation is perhaps similar to that reported in studies from Africa in which it was reported originally that left-handedness had a very low incidence (Verhaegen & Ntumba, 1964); subsequent studies confirmed that on initial inspection there was indeed a low incidence of left-handedness, but that detailed investigation of performance showed this was only for skills such as writing which were subjected to continuing social reinforcement of right-handedness (Brain, 1977); left-handedness for skills not subjected to social pressure was far more frequent. The "true" or "natural" incidence of left-handedness may then be seen as much closer to that of Western populations in which such pressures are typically absent. A similar situation may well also be present in Tristan da Cunha.

The present study has implications for any investigation of the incidence of left-handedness in remote, perhaps relatively primitive, societies, which are socially and culturally isolated from Western influences, since in most cases the populations involved are relatively small, and therefore likely to be subject to similar genetic restrictions to those of Tristan da Cunha. Studies such as those of the Tucano Indians in the Amazon (Ardila et al., 1989), in which the incidence of left-handedness is apparently very low, may be an example in point, although the same problem will also apply to other studies such as the data of Connolly and Bishop in the Highlands of New Guinea (Connolly & Bishop, 1992) in which the incidence of left-handedness is remarkably similar to that found in Western cultures.

In conclusion we should perhaps point out there is an implicit paradox in studies which examine questions concerning the separate roles of genes and environment by looking at small, remote cultures or societies. If these societies are sufficiently remote then they are necessarily small, but if that is the case they probably are subject to such severe genetic restrictions as to mean that the sample size of individuals is not large enough to allow any meaningful comparison of hypotheses—as in the Tristan da Cunha study, in which even *no* left-handers is compatible with a genetic model (as also would have been an incidence of 23.5%). The paradox arises because if the sample size had been large enough for adequate statistical analysis then the

population would probably not have been sufficiently isolated, socially or genetically, to allow adequate conclusions about its social processes.

Manuscript first received November 1991

Revised manuscript accepted June 1992

REFERENCES

- Annett, M. (1985). *Left, right, hand and brain: The right shift theory*. Hove, UK: Lawrence Erlbaum Associated Ltd.
- Ardila, A., Ardila, O., Bryden, M. P., Ostrosky, F., Rosselli, M., & Steenhuis, R. E. (1989). Effects of cultural background and education on handedness. *Neuropsychologia*, 27, 893-897.
- Birdsell, J. B. (1957). Some population problems involving Pleistocene man. *Cold Spring Harbour Symposia on Quantitative Biology*, 22, 47-69.
- Brain, J. L. (1977). Handedness in Tanzania: The physiological aspect. *Anthropos*, 72, 180-192.
- Cavalli-Sforza, L. L., & Bodmer, W. F. (1971). *The genetics of human populations*. San Francisco: W. H. Freeman.
- Connolly, K., & Bishop, D. V. M. (1992). The measurement of handedness: A cross-cultural comparison of samples from England and Papua New Guinea. *Neuropsychologia*, 30, 13-26.
- Dawson, J. L. M. B. (1972). Temne Arunta hand-eye dominance and cognitive style. *International Journal of Psychology*, 7, 219-233.
- Eickhoff, S., & Reighton, P. (1985). Genetic disorders on the island of St Helena. *South African Medical Journal*, 68, 475-478.
- Harris, L. J. (1990). Cultural influences on handedness: Historical and contemporary theory and evidence. In S. Coren (Ed.), *Left-handedness: Behavioral implications and anomalies* (pp. 195-258). Amsterdam: North-Holland.
- Jenkins, T., Beighton, P., & Steinberg, A. G. (1985). Serogenetic studies on the inhabitants of Tristan da Cunha. *Annals of Human Biology*, 12, 363-371.
- McManus, I. C. (1985). Handedness, language dominance and aphasia: A genetic model. *Psychological Medicine*, (Monograph Suppl. 8).
- McManus, I. C. (1991). The inheritance of left-handedness. *Biological asymmetry and handedness (Ciba foundation symposium, 162, 251-281)*. Chichester, UK: John Wiley.
- McManus, I. C. & Bryden, M. P. (1992). The genetics of handedness, cerebral dominance and lateralization. In F. Boller, J. Grafman, I. Rapin, & S. J. Segalowitz (Eds.), *Handbook of Neuropsychology: Sec. 10., Vol. 6. Developmental neuropsychology* (pp. 115-144). Amsterdam: Elsevier.
- Munch, P. A. (1971). *Crisis in Utopia: The ordeal of Tristan da Cunha*. New York: Thomas Y. Crowell.
- Provins, K. A. (1990). Handedness and conformity in a small isolated community. *International Journal of Psychology*, 25, 343-350.
- Rawnsley, K., & Loudon, J. B. (1964). Epidemiology of mental disorder in a closed community. *British Journal of Psychiatry*, 110, 830-839.
- Roberts, D. F. (1971). The demography of Tristan da Cunha. *Population Studies*, 25, 465-479.
- Seddon, B. & McManus, I. C. (1991). *The incidence of left-handedness: A meta-analysis*. Unpublished manuscript.
- Thomas, A., & Thompson, E. A. (1984). Gene survival in isolated populations: The number of distinct genes on Tristan da Cunha. *Annals of Human Biology*, 11, 101-111.

- Turner, K. J. (1989). Epidemiology of the allergic response. *Ciba Foundation Symposium*, 147, 205–222.
- Verhaegen, P. & Ntumba, A. (1964). Note on the frequency of left-handedness in African children. *Journal of Educational Psychology*, 55, 89–90.
- Wace, N. M., & Holdgate, M. W. (1976). *Man and nature in the Tristan da Cunha islands*. Morges, Switzerland: International Union for Conservation of Nature and Natural Resources.