

## Right- and left-hand skill: Failure of the right shift model

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Annett's right shift model of the distribution of skill asymmetry, and of the genetics of handedness, is examined in relation to several sets of data. It is found to be a less adequate description than is the more intuitively obvious 'symmetric bimodal' model, which is described in this paper.

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In two recent papers (Annett, 1983; Annett & Kilshaw, 1983), Annett has described results on the differences between the hands on a motor skill, which, it is suggested, support Annett's 'right shift model' of the inheritance of handedness (Annett, 1978*b*; 1980). In this paper I wish to reanalyse the data produced by Annett and suggest that they are actually more compatible with a conceptually simpler model, and I produce results on a number of other distributions which also support that simpler model.

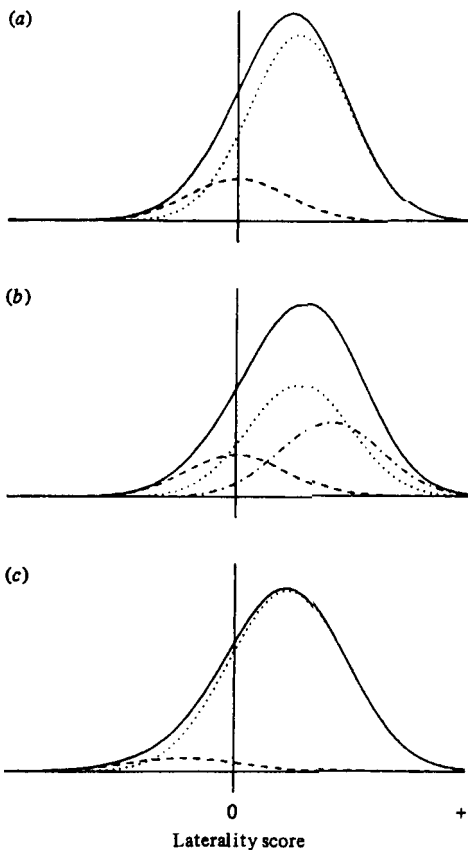
### Annett's right shift model of the inheritance of handedness

Annett's model seems to have its origins in the problem of the description and classification of handedness. In her 1972 paper, Annett considered the apparent discrepancy between skill asymmetries and writing hand asymmetries. Skill asymmetries tend to be approximately normally distributed, although with the mean shifted towards the right hand; Galton's (1884) data on grip-strength asymmetry are produced as support for this suggestion (data from Woo & Pearson, 1927), and Annett's own results on a peg-moving task are also quoted. By contrast, preferences for right- or left-hand usage, and in particular for writing, are shown to be J-shaped distributions; that is, the majority of the population are strongly right or left dominant, with an extremely small minority being truly ambidextrous. As a result of this apparent discrepancy, Annett suggests that hand preferences themselves are truly continuous; thus the conventional description of 'right-' or 'left-' handedness merely depends upon the arbitrary position of a threshold on the normal distribution of skill asymmetry, which is used to dichotomize the population. Annett (1972) also develops the idea that the differences between man (who shows both individual dominance and population dominance) and animals (who show individual dominance but not population dominance) is that in animals there is no shift of the skill asymmetry distribution towards the right, the normal distribution being centred at zero. (Individual dominance means that in an individual one hand is superior to the other; population dominance refers to the proportion of right-dominant individuals in the population.)

Annett (1972) also considers the problem of the inheritance of handedness, noting that her own earlier model (Annett, 1964) was inadequate due to its prediction that right- and left-handers would breed true, and that only the offspring of mixed-handers should show discontinuities between generations (p. 348). As a genetic model Annett proposes (p. 352) that those on the left-hand end of the skill distribution 'have less of the factor which induces the shift of the distribution to the right', and hence inheritance might be expected. Finally, it is suggested that in ontogeny 'the shift to the right and language development may both depend on a common factor and that this factor may be related to whatever induces the left cerebral hemisphere to serve speech in the majority of the human species' (p. 356).

Annett (1975*a*) suggested that 'in some individuals the right shift... factor is weak or absent, and in these cases the laterality of hand and speech depend only on chance' (p. 205).

In a second paper in that year, Annett (1975*b*) greatly extended the model. She was impressed by the data of Hoadley & Pearson (1929), who found for left-right differences in internal skull length that the 'distribution of differences... was unimodal, approximately normal with a mean slightly to the right of the point of symmetry... and a negative skew' (Annett, 1975*b*, p. 324). It was suggested therefore that skill asymmetry was distributed not as a single normal distribution but as a mixture distribution,  $\{p \cdot N[0, s] + (1-p) \cdot N[m, s]\}$ , in which a proportion  $p$  of the population lacked the right shift ( $rs^-$ ), and hence had a mean of zero, and the rest of the population had the right shift ( $rs^+$ ), and hence had a mean  $m$  of greater than zero (see Fig. 1*a*). (The function  $N[a, b]$  indicates a normal distribution of mean  $a$  and standard deviation  $b$ ). The  $rs^-$  distribution would effectively be hidden in the tail of the  $rs^+$  distribution, producing a superficial appearance of normality, but giving a negative skew to the distribution. A threshold  $x$  indicated the writing hand preference of individuals, those to the left using the left hand, etc. Two problems arose with the model: how to estimate the parameters ( $p$ ,  $m$ ,  $s$  and  $x$ ), and how the phenotypes  $rs^+$  and  $rs^-$  were



**Figure 1.** Various models of skill asymmetry: (a) the Annett two-component (dominant) right shift model; (b) the Annett three-component (additive) right shift model; (c) the 'symmetric bimodal' model described in the present paper. In (a) and (b) the parameters are the same as those suggested for males by Annett & Kilshaw (1983), and in (c) the parameters are those of the present paper for males. In each case the solid line is the sum of the dotted and dashed lines. In (a) the dashed line indicates the  $-/-$  distribution; the dotted line the  $-/+$  and  $+/+$  distributions; in (b) the dashed line indicates the  $-/-$  distribution; the dotted line the  $-/+$  distribution; the dashed and dotted line the  $+/+$  distribution; in (c) the dashed line indicates the distribution for left-handers; the dotted line the distribution for right-handers.

determined in individuals. Annett did not estimate the parameters *a posteriori* from the data alone, but instead chose to estimate some of them on *a priori* grounds by drawing on cerebral speech lateralization data. As a result, her models of handedness and speech dominance are closely interrelated, and if one fails the other may also fail. On the basis that 'those having right hemisphere speech are half of those who are  $rs^-$  in each handedness group' (p. 317), the proportion of  $rs^-$  individuals  $p$  is estimated at 0.184. From this it is concluded that 1.14 per cent of  $rs^+$  and 36.73 per cent of  $rs^-$  individuals are left-handed. As a consequence, if  $s$  is assumed arbitrarily to be unity, then  $m = 1.937$  and  $x = -0.339$ . Thus the parameters of the skill asymmetry data distribution are derived entirely from speech dominance results. At this stage the inheritance of  $rs^+$  and  $rs^-$  phenotypes had not been explicitly stated. A similar state of affairs can be found in Annett (1976). Annett (1978*a*) makes it clear, although there is talk of 'only one genetic influence on laterality' (p. 233), that the  $rs^-$  and  $rs^+$  factors are not genotypic but only phenotypic factors, which are assumed to be inherited. Annett (1978*b*) produces an explicit genetic model in which the  $rs^{--}$  genotype is phenotypically  $rs^-$ , whilst the  $rs^{++}$  and  $rs^{+-}$  genotypes are phenotypically  $rs^+$ . [In passing it should be noted that the model was called 'dominant' since the  $rs^+$  allele 'in single or double dose induces left-sided speech' (Annett, 1978*b*, p. 7), despite the usual convention whereby dominance or recessivity are defined in terms of the action of the less common of the two alleles; Annett's nomenclature is used in this paper.] By assuming that the incidence of the  $rs^-$  phenotype is 0.1854 (see above) then the frequency of the '-' allele must be 0.4306. From this model specific predictions may be made as to the pattern of handedness in families and in twin pairs. Annett sticks to the value of  $p$  of 0.1854, but in order to fit her model now proposes that  $m$  has a value of 2.3 for singletons and of 1.0 for twins; the occurrence of different phenotypic parameters in twins and singletons is genetically unusual. This estimation of parameters is therefore a hybrid—partly *a priori*, partly *a posteriori*. (Note also that although  $p$ ,  $m$  and  $s$  are nominally related to *skill* asymmetry, at no point are they ever actually applied to such a distribution.) The model would seem, therefore, to be equally identifiable if it discusses simply a latent, unmeasured variable, rather than making its association with skill explicit (although this point will be returned to later). Similarly Annett (1979) states explicitly in a figure similar to Fig. 1 of this paper that 'the horizontal axis represents differences between the hands in skill (measured, for example, by time for moving by each hand)' (p. 482), despite the fact that no further data on skill are reported, only on writing hand. The model is fitted as before except it is now found necessary to have different values of  $m$  for males (1.6) and females (2.2).

It is apparent thus far that although Annett has described a genetic model in which handedness varies continuously, as determined by skill asymmetry, almost no data have been presented which explicitly assess skill asymmetry and its distribution. Indeed, until the 1983 papers, the distribution of skill asymmetry, as assessed by the peg-moving task, had never been presented, despite its central theoretical role, only the uninformative means and variances being given.

An early explicit *genetic* prediction was that of Annett (1974) in which it was argued that left-handed parents are less likely to be right shifted and hence the children of two left-handed parents should also show little, if any, right shift. On a peg-moving task this was found to be the case, the mean peg-moving asymmetry of 45 children of L × L parents being not significantly different from zero. In the first 1983 paper (Annett, 1983) this observation was extended to 115 offspring of L × L parents, and the same result was found, the distribution of L–R times having a mean which did not differ significantly from zero.

In two further papers of 1983 (Annett & Kilshaw, 1983; Kilshaw & Annett, 1983) extensive data on the distribution of L–R times for a peg-moving task are presented.

Annett & Kilshaw (1983) also extended the genetic model, such that the heterozygotes ( $rs^{+-}$ ) have a different mean to the homozygotes—the heterozygote mean being midway between the two homozygotes. Thus the population should have a distribution  $\{q^2 \cdot N[0, s] + 2 \cdot q \cdot (1 - q) \cdot N[m/2, s] + (1 - q)^2 \cdot N[m, s]\}$ , where  $q = \sqrt{p}$ , and represents the frequency of the ‘-’ allele (see Fig. 1 *b*).

On the basis of goodness-of-fit testing Annett & Kilshaw concluded that the data are unable to differentiate conclusively between the two-component, dominant model of Annett (1978 *b*), and the three-component, additive model of Annett & Kilshaw (1983). Nevertheless the authors do state that:

A second possible hypothesis was that the distributions consist of two normal subdistributions, one of right-handed writers and one of left-handed writers, in the proportions and with the means and standard deviations observed. This hypothesis can be rejected at the 1 per cent level of confidence for both sexes (p. 276).

That question is analysed extensively later in this paper. It is also worth noting that once more the estimates of  $p$  have been derived *a priori*, whilst the estimates of  $m$  are *a posteriori* from the data themselves. For a standard value of  $s$  of 1 these data estimate  $m$  in the case of the dominant model to be 1.231 for males and 1.429 for females. Thus, by using different approaches, different estimates of  $m$  are found:  $m = 1.937$  when derived solely from dysphasia data (Annett, 1975 *b*);  $m = 2.3$  when derived from singletons and  $m = 1.0$  when derived from twins (Annett, 1978 *b*);  $m = 1.6$  and 2.2 for males and females when derived from a further genetic study (Annett, 1979); and  $m = 1.231$  and  $m = 1.429$  for the two sexes when derived directly from the asymmetry of a skill (Annett & Kilshaw, 1983). Clearly these estimates are not all consistent with one another, and it is not clear whether a single global estimate based on all sources of data would be acceptable.

In this paper I wish to concentrate entirely on the problem of the specific distribution of skill asymmetry, since that distribution is the core of the whole right shift model. If skill asymmetry is not of the distribution shown in either Fig. 1 (*a*) or (*b*) then the entire right shift genetic model is in serious difficulties.

### The alternative hypotheses

There are two broad types of alternative hypothesis to that of the right shift model. The first says that the distribution of skill is not a mixture but is instead a single normal distribution, as Annett (1972) originally supposed. The second hypothesis says simply that since the common-sense view of handedness considers there to be two types, right and left (determined very reliably by the hand used for writing), then the distribution of skill consists of normal distributions centred around a right and a left mean, which may, but need not be, symmetrically arranged with respect to zero, i.e.  $\{p \cdot N[m_L, s] + (1 - p) \cdot N[m_R, s]\}$ , where  $m_R$  and  $m_L$  represent the means for right- and left-handers, where  $m_R$  is approximately equal to  $-m_L$ . These latter models I will broadly call ‘bimodal symmetric’.

### Model fitting and hypothesis testing

The best version of a model is that in which the estimated parameters allow the data to fit as closely as possible to prediction. The fitting of a model therefore requires that the best-fitting parameters be found, usually by an iterative process, since most models are not easily tractable analytically, particularly if they contain mixtures of normal distributions. A criterion for ‘goodness of fit’ is required, and an algorithm needed for finding best estimates. Having fitted the best versions of a series of models we need to know whether one model fits better than another. Since increasing the number of parameters can (but does not necessarily) improve the fit (up to the trivial limit where each datum has its own

parameter, and hence the fit is perfect), account must be taken of the number of parameters used. It is not necessary to show that the fit of a model is 'adequate' (i.e. would not be rejected by a conventional goodness-of-fit test) for the model to be acceptable, since there are many reasons why models may not fit, despite being 'correct' [e.g. a tendency to round numbers during data collection ('digit preference') may cause a failure of fitting at a local level whereas the model is making predictions about effects of an order of magnitude or two greater]. The important question concerns whether one model describes data significantly better than another.

Annett's method of model fitting is less than satisfactory for several reasons. The goodness-of-fit criterion was the Kolmogorov  $D$  statistic, which is the largest absolute difference between the observed and the predicted distributions of cumulative proportions. The  $D$  statistic has been described as 'insufficiently sensitive to departures in the tails of the distribution' (Cox & Hinckley, 1974, p. 69); however, it is precisely in the tails that mixture distributions will fail to be an adequate fit—one distribution often 'hiding' inside the tail of the other. Annett's algorithm for estimating parameters is almost certainly non-optimal, being *ad hoc*, and poorly described. More seriously, the significance testing is at fault. Annett's method is to find a minimum value of  $D$  for each model and then to compare the value for each model with critical values determined from standard significance tables. However, this method is not valid. Firstly, it allows no comparison *between* models themselves, only between each model and a perfect fit; hence it is not possible to test whether one model is a significantly better fit than another. Secondly, whilst the  $D$  statistic may be regarded as an adequate, if somewhat insensitive, criterion of goodness of fit, it cannot be used for significance testing of that fit against a perfect fit. As Conover (1980) has put it:

The Kolmogorov test is intended for use only when the hypothesised distribution function is completely specified, that is, when there are no unknown parameters that must be estimated from the sample. Otherwise the test becomes conservative. . . . The Kolmogorov test has been modified to allow it to be used in several situations where parameters are estimated from the data. Actually the test statistic remains unchanged, but different tables of critical values are used. These tables are no longer the same for all distributions; they change from one hypothesised distribution to another (p. 357).

Since Annett is estimating parameters from data the Kolmogorov tables are not adequate, and since they will become conservative they will suggest acceptance of hypotheses which should be rejected. A Lilliefors-type  $D$  statistic could be contemplated to overcome this problem (see Conover, 1980, p. 357), but would require calculating anew for each different model, since no tables have been published.

There are many better methods of fitting and testing than that described by Annett (see e.g. Everitt & Hand, 1981, for the statistical analysis of mixture distributions, and Adby & Dempster, 1974, for estimation methods). In this paper I will use a maximum likelihood method which I have described elsewhere in some detail (McManus, 1983*a*) and have used in a situation almost identical to the present one (McManus, 1982).

For a model with  $n_1$  free parameters to be estimated, the likelihood of the data is found given a set of initial estimates, by means of a quasi-Newton-Raphson method in which first and second differentials are estimated numerically at a particular set of estimates, and on the basis of which a new set of estimates is calculated, the process repeating until the maximum likelihood,  $L_1$ , is found. (For an account of the concept of likelihood see Edwards, 1972.) The inverse of the Hessian matrix at the maximum can be used to find the 95 per cent confidence intervals of the estimates. For a second model with  $n_2$  free parameters, the maximum likelihood,  $L_2$ , can be found. Models can be compared in two ways; if  $n_1 = n_2$ , then  $L_2/L_1$  gives a direct estimate of the relative likelihood of model 2

being an adequate description of the data, as compared with model 1; if  $n_2 > n_1$  then asymptotically  $-2 \cdot \log(L_2/L_1)$  gives a chi-square statistic with  $n_2 - n_1$  degrees of freedom.

It should be noted that a simple, conventional 'least squares' criterion of goodness of fit (the variance accounted for) is not appropriate in the present case since the dependent variable (the frequency of individuals in a particular category) is not normally distributed; neither is a conventional chi-squared goodness-of-fit test adequate due to small observed values in some cells (and merging of cells would result in a loss of sensitivity).

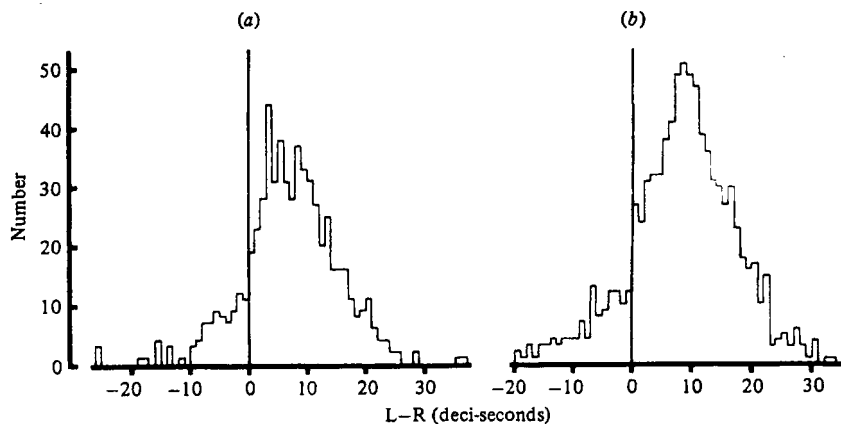
#### *A note on estimating Annett's models*

In fitting her models Annett has always assumed that the proportion of *rs*- individuals is 0.1854. This *a priori* restriction, derived from potentially error-prone dysphasia data, seems to be an unnecessary constraint upon her model. The model could fail to fit if this restriction is enforced but would perhaps fit with a different estimate of the probability. In this paper, therefore, models have been fitted with and without the restriction, in order to give the Annett models a maximum chance of fitting the data.

### Skill asymmetries

#### (i) *Annett's peg-moving task*

Subjects were asked to move a set of dowel pegs between a set of holes in a base-board (Annett, 1970). The time to carry out the task with the right and with the left hand was measured with a stop-watch to the nearest tenth of a second, and the difference, L-R, used as a measure of asymmetry, values being expressed in deci-seconds. Annett & Kilshaw (1983) give the actual distributions of scores in an appendix; only the 'combined main samples' were analysed in the present study, males ( $n = 617$ ) and females ( $n = 863$ ) being analysed separately. Figure 2 shows the distribution of the L-R scores and the simple question is: Do these distributions look more like those of Fig. 1(a), (b) or (c)?



**Figure 2.** Distribution of L-R scores (in deci-seconds) for Annett's peg-moving task (from Annett & Kilshaw, 1983: Appendix) for (a) males ( $n = 617$ ); and (b) females ( $n = 863$ ).

Table 1 shows the results of fitting a series of models to the male data and to the female data. Using Annett's estimate of  $p$ , her two-component and three-component models (models II and III) fit the data no better than a single normal distribution (model I) for the male subjects (relative likelihoods = 3.08 and 0.61 respectively). For female subjects the two-component (II), but not the three-component (III), model is a better fit than a single normal (relative likelihoods = 174.16 and 0.53 respectively). It should be noted here that

Table 1. Shows the estimates and the support (log. likelihood) for a series of models fitted to Annett's peg-moving task, for males and for females

Model	Free parameters	Number of parameters	Formula (L = Likelihood)	Males		Females	
				Parameter estimates	Support	Parameter estimates	Support
I Single normal	$m, s$	2	$L = N(m, s)$	$m = 5.86, s = 8.42$	-2246.237	$m = 7.95, s = 8.74$	-3095.700
II Annett-dominant ( $p$ constrained)	$m, s$	2	$L = 0.1854N(0, s) + 0.8146N(m, s)$	$m = 7.22, s = 7.90$	-2245.113	$m = 9.87, s = 7.75$	-3090.540
III Annett-additive ( $p$ constrained)	$m, s$	2	$L = 0.1854N(0, s) + 0.4904\tilde{N}(m/2, s) + 0.3242N(m, s)$	$m = 10.16, s = 7.65$	-2246.726	$m = 13.74, s = 7.33$	-3096.327
IV Annett-dominant ( $p$ unconstrained)	$m, s, p$	3	$L = p \cdot N(0, s) + (1-p) \cdot N(m, s)$	$m = 6.97, s = 7.98,$ $p = 0.1543$	-2245.054	$m = 9.84, s = 7.76,$ $p = 0.1824$	-3090.536
V Annett-additive ( $p$ unconstrained)	$m, s, q$	3	$L = q^2 \cdot N(0, s) + 2 \cdot q \cdot (1-q) \cdot N(m/2, s) + (1-q)^2 \cdot N(m, s)$	$m = 7.46, s = 8.11,$ $q = 0.2140$	-2245.884	$m = 10.68, s = 8.05,$ $q = 0.2522$	-3094.089
VI Bimodal symmetric	$m, s, p$	3	$L = p \cdot N(-m, s) + (1-p) \cdot N(m, s)$	$m = 6.89, s = 7.57,$ $p = 0.0695$	-2240.798	$m = 9.07, s = 7.57,$ $p = 0.0644$	-3084.285
VII Bimodal symmetric, different means	$m_1, m_2, s, p$	4	$L = p \cdot N(-m_1, s) + (1-p) \cdot N(m_2, s)$	$m_1 = 12.47, m_2 = 6.48,$ $s = 7.67, p = 0.0338$	-2239.378	$m_1 = 7.37, m_2 = 9.28,$ $s = 7.48, p = 0.0797$	-3083.931
VIII Bimodal symmetric, different variances	$m, s_1, s_2, p$	4	$L = p \cdot N(-m, s_1) + (1-p) \cdot N(m, s_2)$	$m = 6.68, s_1 = 9.67,$ $s_2 = 7.61, p = 0.0619$	-2239.736	$m = 9.19, s_1 = 7.75,$ $s_2 = 5.77, p = 0.0649$	-3082.690
IX Bimodal symmetric, different means, different variances	$m_1, m_2, s_1, s_2, p$	5	$L = p \cdot N(-m_1, s_1) + (1-p) \cdot N(m_2, s_2)$	$m_1 = 14.92, m_2 = 6.40,$ $s_1 = 6.06, s_2 = 7.73,$ $p = 0.0261$	-2239.178	$m_1 = 12.25, m_2 = 8.83,$ $s_1 = 4.38, s_2 = 7.76,$ $p = 0.0421$	-3081.583

because of inbuilt constraints the two-component and three-component models are not special cases of one another or of the simple normal distribution, and hence the multicomponent distributions may be a worse fit than the single normal distribution.

Allowing the proportion of  $rs^-$  individuals to vary from Annett's *a priori* estimate produces a better fit than a single normal distribution for the two-component model in females (model IV vs. model II:  $\chi^2 = 5.16$ , d.f. = 1,  $P < 0.05$ ) but not in males ( $\chi^2 = 2.37$ , d.f. = 1, n.s.). The estimated maximum likelihood proportion for males (0.1543) and females (0.1824) is in each case very close to Annett's *a priori* value. Similarly in females Annett's three-component model is a better fit when the gene frequency is unconstrained (model V) than when it is constrained (model III) in females ( $\chi^2 = 4.48$ , d.f. = 1,  $P < 0.05$ ; estimated proportions = 0.0636, 0.3772 and 0.5592) but not in males ( $\chi^2 = 1.68$ , d.f. = 1, n.s.). Thus far the analysis has suggested that Annett's three-component model is not an improvement over a single normal distribution, whereas the two-component model is an improvement, in females at least.

The alternative hypothesis is that a bimodal symmetric model is superior to the Annett models. Certainly a symmetric bimodal model (i.e. model VI,  $\{p \cdot N[-m, s] + (1-p) \cdot N[m, s]\}$ ) is a better fit than a single normal distribution (I) in both males ( $\chi^2 = 10.88$ , d.f. = 1,  $P < 0.001$ ) and females ( $\chi^2 = 22.83$ , d.f. = 1,  $P < 0.001$ ). The symmetric bimodal distribution is a better fit than Annett's two-component model (using the maximum likelihood estimate of the proportion of  $rs^-$  individuals, model IV) (relative likelihoods: males, 70.53; females, 518.53) or using Annett's *a priori* estimate of the proportion (model II) (males:  $\chi^2 = 8.63$ , d.f. = 1,  $P < 0.01$ ; females:  $\chi^2 = 12.51$ , d.f. = 1,  $P < 0.001$ ). The symmetric bimodal distribution (VI) is also a better fit than Annett's three-component model, whether one uses the maximum likelihood estimate of the proportion of  $rs^-$  (model V) (relative likelihood: males, 161.74; females, 18106.02) or the *a priori* estimates of  $rs^-$  (model III) (males:  $\chi^2 = 11.86$ , d.f. = 1,  $P < 0.001$ ; females:  $\chi^2 = 24.08$ , d.f. = 1,  $P < 0.001$ ). Fitting a series of bimodal symmetric models in which the means and/or the standard deviations differ between the right- and left-sided distributions (models VII, VIII and IX) does not show any evidence of a significant improvement in fit over the simple bimodal symmetric model (VI), and hence we may conclude that the distributional parameters do not differ between the two parts of the symmetric bimodal distribution.

We may thus conclude from this analysis that Annett's right shift models are not an adequate description of the data when compared with the reasonable alternative of a symmetric bimodal distribution. The latter model implies that the right-hand distribution should consist of right-handers and the left-hand distribution of left-handers. However the maximum likelihood estimates suggest proportions of 0.0643 for males and 0.0695 for females in the 'left' distribution. Annett & Kilshaw (1983) describe 8.1 per cent of males and 9.7 per cent of females as being left-handed writers. These values are, however, within the 95 per cent confidence limits for males (0.0369–0.1272) and females (0.0419–0.0976). It is thus possible that the two distributions correspond to the two writing hand groups; however, it is not possible to test this hypothesis directly since Annett does not cross-tabulate her peg-moving data by the writing hand of the subjects.

#### (ii) *Data from the National Child Development Study*

The analysis of the previous section suffers from two principal defects. Figure 2 is not convincingly mixed on inspection (despite the statistically convincing levels of significance of the symmetric bimodal model over the right shift model), and there is no indication of the writing hand of the individuals shown in Fig. 2. To circumvent these problems another data set is used. The National Child Development Study (NCDS), which commenced as the Perinatal Mortality Study (Butler & Bonham, 1963; Butler & Alberman, 1969;



National Child Development Study, 1969, 1972; Calnan & Richardson, 1976) examined all children born in the week 3–9 March 1958 in England, Wales and Scotland. A follow-up survey in 1969, when the children were aged about 11, asked the mothers to say which hand the child used for writing; these and other laterality data have been reported in detail elsewhere (McManus, 1981). Each child was also examined by their own doctor, who was asked to carry out two tests of motor skill asymmetry. In the first test the child was asked to put a dot in as many squares of a piece of graph paper as possible, in a one minute period, first with one hand, and then with the other. The number of dots made with each hand was counted, and a laterality score,  $100 \times (R - L) / (R + L)$ , was calculated. In the second task the time was measured for the subject using the right and the left hand separately to pick up 20 matches placed on a table; once more a laterality score,  $100 \times (L - R) / (L + R)$ , was calculated as an index of skill asymmetry. Figure 3 shows the

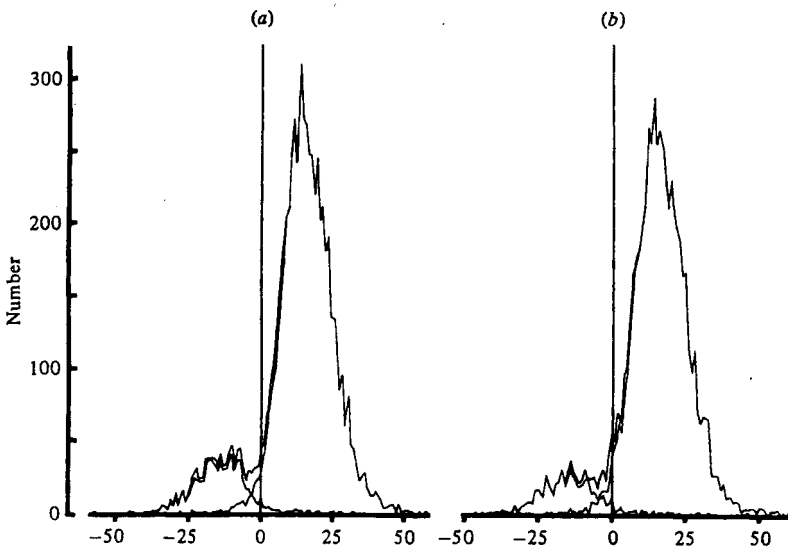


Figure 3. Distribution of asymmetry scores ( $100 \times (R - L) / (R + L)$ ) in the square-marking test from the NCDS for (a) males ( $n = 6548$ ) and (b) females ( $n = 6225$ ); within each overall distribution the scores of right- and left-handers are also indicated separately, the smaller distribution (to the left of 0) representing the left-handers.

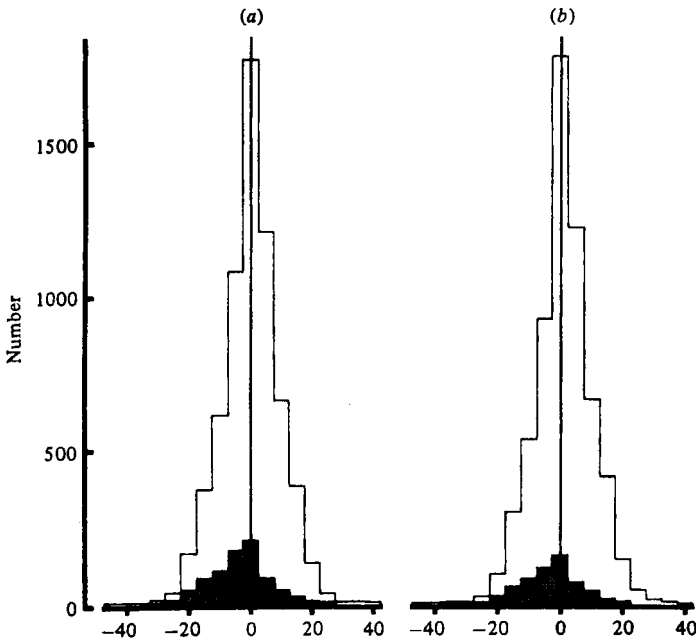
distribution of laterality scores of 12773 children on the square-marking task, by writing hand and sex. It is clear that there is a separate distribution in the left-hand tail which is comprised primarily of left-handers who, at a first approximation, have a mean as far to the left of zero as the right-handers are to the right of zero. The means and SDs of the laterality scores are summarized in Table 2(a). Formal goodness-of-fit testing of the whole distribution is not described, since it is clear, given the huge sample involved, that the data in Fig. 3 constitute a symmetric bimodal distribution, rather than an Annett-type right shift distribution, and that the primary determinant of the two modes is phenotypic writing hand. An interesting question concerns whether or not any of the right-handers form a separate distribution on the left-hand side of the scale or vice versa. Analysis within handedness groups suggests that 0.42 per cent (95 per cent limits: 0.25–0.70 per cent) of male right-handers and 0.26 per cent (0.14–0.51 per cent) of female right-handers originate in a separate distribution with left-hand superiority ( $\chi^2 = 54.47$ , d.f. = 1,  $P < 0.001$  and  $\chi^2 = 40.79$ , d.f. = 1,  $P < 0.001$  respectively in a test of a symmetric bimodal distribution

**Table 2.** Mean scores of the right and left hands, and the value of an asymmetry score (see text) for all subjects, right-handed writers, and left-handed writers for (a) the NCDS square-marking task, and (b) the NCDS match-moving task (standard deviations in parentheses)

	Right hand	Left hand	Asymmetry score	<i>n</i>
<i>(a) Squares marked in one minute</i>				
Males				
Total	87.16 (22.58)	68.89 (20.88)	+12.08 (13.62)	6548
Right-handers	90.03 (21.63)	65.91 (18.71)	+15.88 (9.22)	5642
Left-handers	68.19 (19.50)	89.68 (23.24)	-13.74 (10.28)	828
Females				
Total	91.66 (24.31)	70.18 (21.71)	+13.66 (13.24)	6225
Right-handers	94.00 (23.39)	67.93 (20.04)	+16.58 (9.46)	5564
Left-handers	69.38 (21.52)	91.23 (25.43)	-13.91 (12.39)	587
<i>(b) Time in s to pick up 20 matches</i>				
Males				
Total	44.69 (11.89)	44.77 (11.81)	+0.11 (9.02)	6534
Right-handers	44.40 (11.74)	44.97 (11.78)	+0.67 (8.80)	5631
Left-handers	46.58 (12.55)	43.32 (11.88)	-3.73 (9.55)	826
Females				
Total	43.28 (11.73)	44.00 (11.64)	+0.90 (8.94)	6213
Right-handers	42.97 (11.41)	44.06 (11.48)	+1.30 (8.68)	5553
Left-handers	46.22 (14.09)	43.55 (13.18)	-2.96 (10.32)	584

against a single normal distribution). 3.39 per cent (2.20–5.18 per cent) of left-handed males and 4.11 per cent (2.57–6.51 per cent) of left-handed females were from a separate distribution with right-hand superiority ( $\chi^2 = 72.34$ , d.f. = 1,  $P < 0.001$  and  $\chi^2 = 71.82$ , d.f. = 1,  $P < 0.001$  respectively, using the method as above). In none of these cases was there evidence for differences in parameters between the two halves of the symmetric bimodal distribution (i.e. contrasting models of type VI and IX in Table 1); chi-squared values (d.f. = 2) for male right-handers, male left-handers, female right-handers, and female left-handers were 5.28, 0.67, 1.38 and 5.50 respectively, none of which is significant. The origins of this bimodality are not clear; it is unlikely to represent simple coding or classification error, since the incidence so clearly differs in the right- and left-handers, and it possibly represents a 'pathological' group (see Bishop's, 1983, reanalysis of similar data; although also see my own doubts on the concept of pathological left-handedness, McManus, 1983c).

Table 2(b) summarizes results for the match-moving task. It is clear that the degree of asymmetry (mean = 0.50 per cent) is extremely low. More problematic is that the distributions of asymmetry scores within handedness groups are multimodal, with a particularly large spike exactly at zero. Examination of the raw data shows that this is due to recording biases in the data, some 45.95 per cent of the observations ending in a 5 or 0 (expected value = 20 per cent) and in 27.7 per cent of cases both the right- and the left-hand value end in 0 (expected value = 4 per cent). It is clear therefore that many of the doctors making the measurements have only recorded times to the nearest five seconds. In a skill where asymmetry is as small as the present one, this means that the distribution of asymmetry scores is dominated by recording biases, making further analysis difficult. The complete distribution of the asymmetry scores may be found in McManus (1979).



**Figure 4.** Distribution of asymmetry scores [ $100 \times (L - R)/(L + R)$ ] in the match task from the NCDS for (a) males ( $n = 6534$ ) and (b) females ( $n = 6213$ ); within each overall distribution the scores of right- and left-handers are indicated separately, the smaller shaded distribution (to the left of 0) represents the left-handers, and the larger unshaded distribution the right-handers. For clarity the combined distributions of right- and left-handers have not been shown.

Figure 4 shows the distribution of asymmetry scores after the raw scores have been rounded to the nearest 5 seconds, to compensate for recording biases. Asymmetry scores were calculated as  $100 \times (L - R)/(L + R)$ , and were themselves rounded to the nearest 5, since the 'granularity' of the raw scores meant that not all asymmetry scores were theoretically possible. It can be seen that the distributions for right-handers are shifted to the right, and for left-handers to the left, as would be expected under the bimodal symmetric model. However, significance tests for bimodality on the combined distribution of right- and left-handers were not significant. Given the small expected separation of the means relative to the large variability (separation = 0.463 SDs), then by extrapolating the results of McManus (1983*b*) it is clear that even given the very large sample size the statistical method has minimal power to detect bimodality.

### (iii) Grip-strength data from Galton's anthropometric laboratory

It was from Galton's data on asymmetry of manual strength (Woo & Pearson, 1927; Woo, 1928) that Annett (1972) derived her suggestion that handedness is a continuously distributed normal variable, and from which the right shift model developed. However, Annett (1975*b*) pointed out that the distribution 'has all [the relevant] characteristics, except a negative skew, and the absence of skew in this very large set of observations presents a new problem' (p. 325). That problem has not been satisfactorily resolved.

Galton, at his first Anthropometric Laboratory at the Health Exhibition of 1884, assessed the grip strength, in pounds, of 6992 individuals (sex apparently not stated). The mean strength of the right hand was 81.89 (SD = 11.18) pounds, and that of the left hand was 78.87 (SD = 11.40) pounds. Figure 5 shows the distribution of asymmetry scores

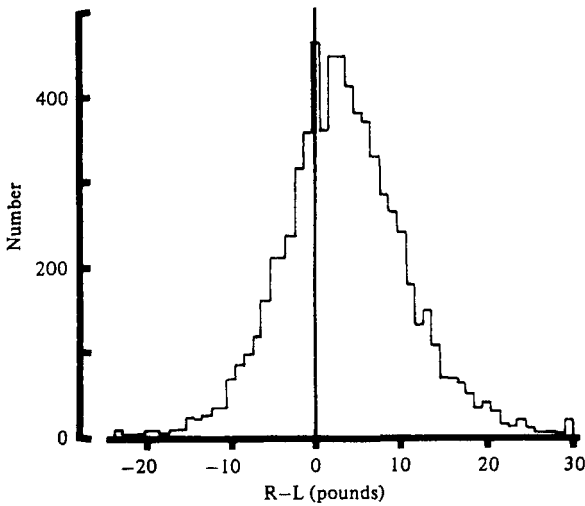


Figure 5. Distribution of asymmetry scores ( $R-L$ ) for Galton's grip-strength task ( $n = 6992$ ) (data from Woo & Pearson, 1927).

( $R-L$ ); the skew is  $+0.167$ , which is highly significant ( $P < 0.001$ ), and in the opposite direction to that predicted. The mean degree of asymmetry is  $+1.88$  per cent. Fitting of multimodal models to Fig. 5 suggests that whilst neither the Annett right shift models nor a symmetric bimodal distribution is superior to a single normal distribution, a trimodal distribution (with equal variances) is highly superior to a single normal distribution ( $\chi^2 = 179.55$ , d.f. = 4,  $P < 0.001$ ). However, fitting a quadrimodal distribution results in no further improvement to the fit. Examination of the estimates of the trimodal distribution shows that 91.47 per cent of the population have a mean of  $+2.73$  pounds, 6.23 per cent have a mean of  $+16.37$  pounds, and 2.29 per cent have a mean of  $-11.96$  pounds, the SD in each case being 6.05 pounds. It thus appears that there are two subdistributions with large asymmetries between hands, whilst the majority of the population shows almost no asymmetry. It would be tempting to suggest that the two minor distributions comprise individuals who, perhaps for reasons of employment, have hypertrophied musculature on one side, were it not for the fact that some 26.9 per cent of these individuals have a left-sided superiority, which is difficult to reconcile with the conventional estimates of the incidence of sinistrality. It must be concluded that Galton's data provide little comfort for any of the models described so far.

#### (iv) *The distribution of skull asymmetry*

Finally in this section it is worth mentioning the results of model fitting to Hoadley & Pearson's (1929) data on the internal length of skulls. On several occasions (Annett, 1975*b*, 1976; Annett & Kilshaw, 1983) it has been suggested that these results are compatible with the right shift theory. Elsewhere (McManus, 1982) I have demonstrated that these data are far more consistent with a symmetric bimodal distribution, than with an Annett right shift distribution.

#### **Handedness in the children of two left-handed parents**

Although Annett's model of skill asymmetry is supposedly a genetic model, the majority of evidence in its support is not strictly genetic, either because only single individuals have been studied, and hence chromosomal segregation has not occurred, or because if families

have been studied then only hand preference and not skill asymmetry has been assessed. The only exception is the data on the children of the two left-handed parents, which had been briefly reported earlier (Annett, 1974) and were extended by Annett (1983). A total of 115 children, both of whose parents were sinistral writers, were tested on the peg-board task. These children had a mean asymmetry score which was not significantly different from zero. This, it is suggested, was as the right shift theory would predict, since the majority of left-handed parents are likely to be of genotype  $rs^-$ , and thus their offspring should also be of genotype  $rs^-$ , and hence of phenotype  $rs^-$ . As a result of this prediction Annett (1983) demonstrates that the distribution does not differ significantly from a single normal distribution, or from a trimodal normal distribution in the proportions expected, given that 7 per cent of parents in the population are left-handed.

For the purposes of the present analysis I assume that the parents may be described in terms of the dominant version of the right shift theory (since earlier it was shown to be by far the better of the two models for describing the adult peg-moving data), and I derive parameters for adults from Annett's main sample, and for the children from Annett's birthday sample (Table 4 of Annett & Kilshaw, 1983). The latter is not perfect in view of the lack of precise age matching, but must suffice since that is all that is possible. If we accept that 8.3 per cent of fathers and 9.8 per cent of mothers in the population are likely to be left-handed (based on Kilshaw & Annett, 1983, Table 1) then the threshold for left-handedness in these populations will be  $-3.65$  deci-seconds, and  $-2.45$  deci-seconds for males and females. The proportions of the genotypes  $rs^-$ ,  $rs^{+-}$  and  $rs^{++}$  amongst left-handed parents will therefore be 0.641, 0.216 and 0.143 for fathers, and 0.687, 0.188 and 0.125 for mothers. We would therefore expect the proportions of the genotypes in the children to be 0.585, 0.360 and 0.055; that is, 58.5 per cent will be of the  $rs^-$  phenotype, and 41.5 per cent of the  $rs^+$  phenotype, and therefore the males should show a distribution of  $\{0.585N[0, 11.0] + 0.415N[8.5, 11.0]\}$  and the females should show one of  $\{0.585N[0, 9.0] + 0.415N[15, 9.0]\}$ , with means of 3.53 (SD = 11.77) and 6.22 (SD = 11.64) respectively. The children gave means of 2.5 (SD = 15.1;  $n = 58$ ) and 2.8 (SD = 13.4;  $n = 57$ ) respectively, neither value of which is significantly different either from zero or from the predicted mean.

It is therefore clear that Annett's earlier prediction of a mean of zero is erroneous, since 41.5 per cent of the children (under a dominant model) should manifest a right shift. Under the additive model the expected proportion of right shifted children (i.e.  $rs^{+-}$  phenotypes and  $rs^{++}$  phenotypes) is 35.9 per cent. This problem is recognized by Annett since in her model-fitting section (e.g. Annett & Kilshaw, 1983, Table 5(c) iii) mixture distributions with similar parameters are fitted. Therefore, the crucial question for the fitting of the model is whether the offsprings' distribution of asymmetry scores is a mixture in the expected proportions, or whether it is either a symmetric bimodal distribution (as implied earlier for the population as a whole) or is a single normal distribution. The simple answer to this question is that we do not know and cannot in all probability know, since the data set is not large enough to give an adequate power for distinguishing the hypotheses. Annett obtains  $D$  values which are non-significant for both a single normal distribution and an additive right shift model, with no discrimination between the two (the earlier strictures on this method of fitting must be borne in mind when interpreting the result). Using the maximum likelihood method described earlier, I was unable to find any evidence that any model has an improved fit over a single normal distribution. Knowing that 33.9 per cent of the children are left-handed writers, and assuming that they would all be of phenotype  $N[-m, s]$ , and that the right-handers would be of phenotype  $N[-m, s]$ , where  $m$  and  $s$  are approximately 10 and 12, then we would require a sample of at least 400 children in order to achieve a power of 0.5 of distinguishing a symmetric bimodal

distribution from a single normal distribution (McManus, 1983*b*). Explicit calculations for the power of distinguishing a right shift model from a single normal distribution are not available, but would almost certainly be less than that for a symmetric bimodal distribution vs. a single normal distribution, since the distance between the means of the two distributions is proportionately less.

It is therefore concluded that whilst the data of Annett (1983) are of interest, they have insufficient power to tell us the nature of the skill asymmetry distribution, or its genetic control.

### Discussion

In this paper I have discussed Annett's hypothesis that the distribution of motor skill asymmetry in the population is a mixture of two normal distributions—one centred at zero, and the other shifted to the right. Such a hypothesis has a strong counter-intuitive element, since a simple view of the distribution is that it would be what I have earlier called 'symmetric bimodal'. A detailed examination of the empirical distributions of skill asymmetry suggests that symmetric bimodal distributions are indeed a significantly better fit to the data than Annett's right shift models, and hence we must conclude, on the basis of the data available at present, that the right shift model is inadequate as a description of skill asymmetries. Two questions arise: How does the symmetric bimodal model explain the facts of skill asymmetry? and: What are the implications of the failure of the right shift model of skill asymmetry for the right shift model of the genetics of handedness and speech dominance?

The symmetric bimodal model takes as its basic assumption that each individual is either a right-hander or a left-hander. It is presumed that the best measure of an individual's category is his or her writing hand, since this measure has the strongest laterality score, and is probably the most reliable of laterality measures (with the usual provisos being made about individuals who have been forced to change their writing hand as a result of social pressure). This categorical asymmetry can result in other correlated asymmetries, according to the degree to which an otherwise symmetric system shares the (asymmetric) mechanisms of the writing hand (either centrally or peripherally). Thus any task can be partitioned into an asymmetric and a symmetric portion. As the degree of overlap with writing decreases, so the degree of lateralization of the task will decrease. It is assumed that the degree of lateralization for writing is broadly similar among individuals. However, individuals might differ in the degree to which they use the asymmetric parts of the system to carry out a particular task, and thus individual differences will arise. Furthermore, the amount of noise or error involved in measuring a task will also vary between tasks. The result is that, whilst we would predict that the population distribution for writing would be  $\{p \cdot N[A_L, 0] + (1-p) \cdot N[A_R, 0]\}$ , the population distribution of a task which shares only a proportion  $c$  of the handwriting processing system would be  $\{p \cdot N[cA_L, s] + (1-p) \cdot N[cA_R, s]\}$ , where  $s^2 = b^2 + w^2 + e^2$ ,  $b^2$  representing between individual variation,  $w^2$  representing within individual variation, and  $e^2$  representing errors of measurement. As  $c$  tends to zero and  $s$  increases then frank bimodality will be less and less visible, and the second distribution will become hidden in the tail of the first distribution; and it can be shown that if  $2s\sqrt{(1 + |\log(p) - \log(1-p)|)/2)}$  is greater than  $|c(A_L - A_R)|$  then only one mode will be visible in the distribution (Behboodan, 1970). It would seem that this conceptually simple model can explain all of the published data on the distributions of skill asymmetry (with the probable exception of Galton's data, which do not strictly concern a *skill* asymmetry, and for which a special interpretation is required). A clear implication of the model as presented above is that the best (or 'true') description of handedness is not in terms of a continuous skill asymmetry, but is rather in terms of a bimodal, probably categorical,

division of the populations into right- and left-handers, with the hand used for writing being the best criterion of that division.

The failure of the right shift model of skill asymmetry is difficult for the right shift model of the genetics of handedness. Consider just the dominant version of that genetic model. It states that there are two phenotypic distributions,  $P_1$  and  $P_2$ , which are distributed as  $p \cdot N[0, s]$  and  $(1-p) \cdot N[r, s]$ , where  $p$  is the proportion of individuals of genotype  $-/-$ ,  $r$  is the phenotypic degree of right shift of the genotypes  $-/+$  and  $+/+$ , and  $s$  is the standard deviation of each distribution. The crucial question concerns the nature of  $P_1$  and  $P_2$ . As suggested earlier, Annett has implied that  $P_1$  and  $P_2$  are distributions of observed skill asymmetry. However, that suggestion is incompatible with the data. The only obvious alternative for the right shift model is to suggest that  $P_1$  and  $P_2$  are phenotypic distributions of a latent, unmeasurable variable which maps on to actual skill asymmetry to produce a symmetric bimodal distribution (perhaps as a result of non-genetic learned influences in early life). Such a model can then be fitted to conventional family data (in which individuals are simply described as right- or left-handed), as Annett (1978*b*) has done. Let  $A[a, b, c]$  indicate the area under a normal distribution  $N[b, c]$  from minus infinity to  $a$ . Annett fits her genetic model to typical family data, in which the population incidence of left-handedness is  $L$ , by finding the threshold  $x$  such that  $L = p \cdot A[x, 0, s] + (1-p) \cdot A[x, r, s]$ ; given  $x$  then the expected proportion of left-handed offspring may readily be found for particular mating combinations. Consider a variant of Annett's model in which the phenotypic distributions of  $P_1$  and  $P_2$  are  $p \cdot N[k, s]$  and  $(1-p) \cdot N[r+k, s]$ ; i.e. the distributions  $P_1$  and  $P_2$  are translated along the abscissa by a constant  $k$ . The value of the threshold  $x'$  is found by solving the equation  $L = p \cdot A[x', k, s] + (1-p) \cdot A[x', r+k, s]$ ; and hence  $x' = x+k$ . The fitting of the model is therefore completely independent of  $k$ , and thus the absolute positions of  $P_1$  and  $P_2$  cannot be determined from conventional family data (and neither could the absolute positions be determined even if data of the peg-moving type were available in families, since these show no absolute mapping on to the latent variable). It is also worth noting that if  $k = -r/2$  then  $P_1$  and  $P_2$  together show a symmetric bimodal distribution. The conclusion is clear. Given Annett's method of fitting her model to genetic data, it is impossible to gain information about the *absolute* position of the latent variables  $P_1$  and  $P_2$  (and in general it is probably the case that one may never be able to obtain absolute information about latent variables). Without such knowledge, however, the central theoretical advance of the right shift model is empty, and perhaps needlessly complex. The model might be salvaged by insisting that  $x$  must always be precisely zero (i.e. by insisting on a non-arbitrary anchoring point for  $P_1$  and  $P_2$ ) but then the model simply does not fit the family data. Finally, it must be noted, as has been mentioned earlier, that the distribution of manifest skull asymmetry is also incompatible with Annett's postulated right shift distribution, and in such a case it is difficult to see how social pressure, or any other artifact, could seriously distort the translation of a latent distribution into a manifest distribution. A simpler genetic model of handedness which is compatible with the symmetric bimodal model of handedness phenotypes and does not require the presence of latent variables has been described elsewhere (McManus, 1979, 1983*d*, 1984), and has also been applied to the genetics of hand clasping and arm folding (McManus & Mascie-Taylor, 1979).

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## Which theory fails? A reply to McManus

Marian Annett

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The claim that the right shift (RS) theory fails is examined and rejected on several grounds. First, it is uncertain that the symmetric bimodal (SB) theory can generate predictions that are clearly distinct from those of the RS theory. Second, the interpretation of the empirical data depends on an analysis of the skills required for the task and of the samples tested; the latter were not drawn from the general population. Third, the aim of seeking algorithmic solutions is inappropriate as an alternative to the original aim (Annett & Kilshaw, 1983) of testing whether previously successful heuristic solutions could be rejected. Fourth, the common-sense classification into left- and right-handers, although undoubtedly the starting point of all analyses of laterality, including that of the RS theory, has led to little progress in the search for the causes and consequences of lateral asymmetries. The classification can lead to sterile arguments about the 'true' incidence of left-handedness, of which examples are to be found in McManus's paper. Finally, elaborate statistical techniques may assist but cannot supplant the careful evaluation of evidence. The RS theory is falsifiable, but not on the grounds suggested by McManus.

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The symmetric bimodal (SB) model assumes that there are right-handed writers and left-handed writers, and when individuals who have years of practice in using writing implements with their preferred hand are asked to make pencil marks on paper, the mean difference between hands will be bimodal, with modes roughly symmetric about 0. Who could doubt such assumptions? These are facts which need no intuition to discern. The interesting questions about laterality arise when one tries to look behind and beyond these facts to ask what caused the distribution and what predictions follow from it. On these questions, the vast laterality literature, based as it is on the common-sense paradigm, has little of interest to say. The right shift (RS) theory, making a small change in the usual paradigm, has offered suggestions about how asymmetries of hand and brain could be related. What McManus has done is to attempt to construct a theory which is founded on the common-sense classification into right-handers and left-handers, and at the same time incorporates most of the assumptions of the RS theory.

McManus invites a comparison between the RS and SB models for fit with distributions of L-R skill, obtained for a peg-moving task. The value of this exercise depends first on whether it is possible to distinguish the predictions of the two models and second on whether the task and the samples, on which the empirical data depend, offer an appropriate test of the predictions.

### Distinguishing between two theories

Figure 1 illustrates the main features of the two theories in order to show the critical points of difference. The main innovation of the RS theory (Annett, 1972) was to suggest that there is only one systematic influence on human laterality, a factor (later attributed to a gene,  $rs^+$ , Annett, 1978*b*), which facilitates the development of speech in the left hemisphere, and incidentally gives a slight advantage to the right hand. In the absence of this factor, there are only chance biases to either side. The  $rs^-$  gene(s) is thought to be indifferent to laterality; having no known effects, it would not make sense to speak of it as 'dominant' (see McManus 1985, p. 3), though it can be regarded as acting as a recessive. Figure 1*Ai* shows the normal chance distribution with mean of 0 postulated for humans lacking the  $rs^+$  gene, and also for other species. This distribution is sufficient to account

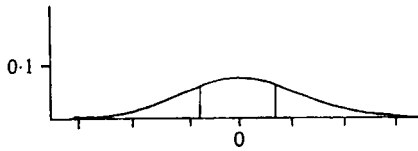
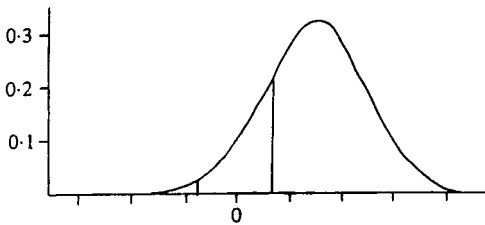
for the hand and paw preferences of primates and other mammals, where animals are equally likely to develop preferences for either side and some 50 per cent show mixed-hand preferences. A distribution approximating Fig. 1*Ai* was found for the peg-moving performance of children of two left-handed ( $L \times L$ ) parents (Annett, 1974, 1983). The chance distribution is thought to arise from accidental differences arising during the development of the two sides of the body in all complex bilateral organisms. It is the main source of variability of L-R differences (Annett, 1978*a*) irrespective of whether systematic biases of the distribution are present or absent.

The SB theory (Fig. 1*Bi*) resembles the RS theory in hypothesizing that there is a subgroup of the population in which laterality depends on chance, and whose L-R mean is 0. This group, some 15 per cent of the population according to McManus's (1984) genetic theory, includes those who inherit a double dose of a gene for chance (CC genotypes) and 50 per cent of heterozygotes (DC genotypes). This implies that in 50 per cent of the latter, the C gene is expected to 'dominate' and actively determine chance. No suggestions are offered as to what selection pressures could lead to the evolution of a gene whose effects would arise in its absence as well as in its presence. The critical point of difference, for the present purpose, is that the SB model assumes that the 'chance' subgroup of the population would differentiate into two distinct subgroups, right-handers and left-handers. This would arise by a process analogous to canalization in embryological development; growth may proceed along any of several alternative pathways but, having progressed along a particular path, could not return to take an alternative route. For handedness, this implies that an individual potentially able to write with either hand would come to prefer to use one hand with increasing practice, and would find it difficult to relearn to write with the other hand. There can be little doubt that such a mechanism applies to learning to write. The problem addressed by the RS theory, but not by the SB theory, is that processes of canalization are probably operative for other aspects of skilled performance, not only writing, *and the hand chosen may differ between tasks*. While it is true that few people write with either hand (perhaps less than 0.5 per cent), some 30 per cent of the population use different hands for different tasks, the mixed-handers in Fig. 1*A*.

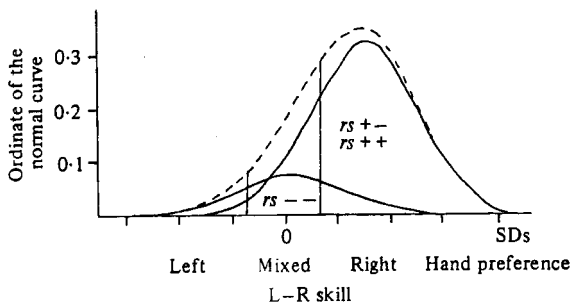
Figure 1*Aii* shows that the  $rs^+$  gene does not determine right-handedness, but merely moves the chance distribution along the abscissa such that the mean is to the right of 0; that is, the gene increases the probability of greater skill in the right hand than the left hand, but it does not invariably outweigh strong chance biases to the left hand. The SB model postulates a gene for directional asymmetry (D), which determines right-handedness, especially for writing. As far as we know, writing was invented only a few thousand years ago, so questions can be asked about how such a gene evolved. On the SB theory, all DD genotypes should be right-handed writers and all should have L-R skills favouring the right hand (in the absence of developmental pathology, and without the 'noise' due to errors of measurement). The total distributions are shown in Fig. 1*iii*. Both theories assume a major group with mean to the right of 0 and a minor group with a mean of 0. The distinctive postulate of the SB theory is that the minor group differentiates into two clearly separate subgroups, identifiable as left-handers and right-handers.

The theories can be compared for their assumptions about the relations between hand preference and skill. For the SB theory, the relationship should be perfect, those to the left of 0 being left-handed writers and those to the right of 0 right-handed writers. On the RS model, incidences of left- and mixed-handedness are assumed to depend on thresholds which may be strict or generous, and so cut the distributions at points which vary over a wide range (as indicated in Fig. 1*A*). The socio-cultural pressures of a dextral society are expected to ensure that the incidence of left-handed writing is always less than the proportion of individuals with L-R skills favouring the left hand; that is, the threshold for

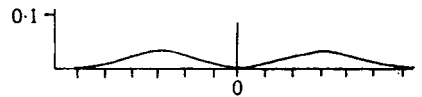
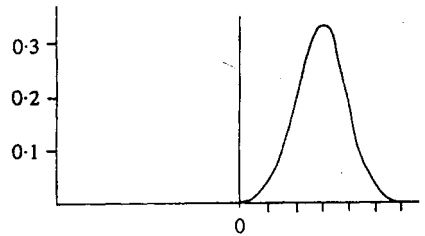
## A. Right shift theory

(i) Chance ( $rs- -$  genotypes)(ii) Bias to dexterity ( $rs^{++}, rs^{+}$  genotypes)

(iii) Total distributions (---)



## B. Symmetric bimodal theory

(i) (CC and  $\frac{1}{2}$ DC genotypes)(ii) (DD and  $\frac{1}{2}$ DC genotypes)

(iii)

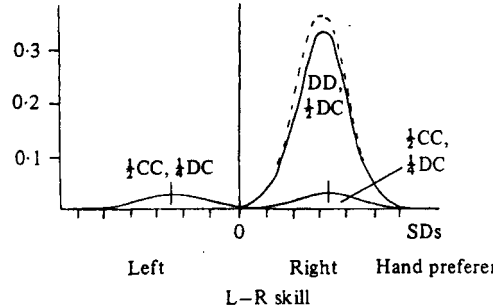


Figure 1. Distributions of L-R skill hypothesized by the theories.

writing is expected to be to the left of 0. Systematic relationships between degrees of left- and mixed-hand preference and degrees of L-R skill, as required for the threshold concept, have been found in several samples (Annett, 1976a, 1984). The SB model rejects the threshold concept, as it must if left- and right-handers are clearly distinct, by canalization. The SB model also assumes there is a 'true' incidence of left-handedness, estimated to be about 7.75 per cent of the population (McManus, 1984). However, in order to handle empirical data, where incidences vary from the 'true' value, the SB model assumes that, when incidences are smaller, some true right-handers are manifesting as left-handers and, when incidences are higher, true right-handers are manifesting as left-handers. That is, incidences are treated 'as if' a threshold were operative.

This comparison of the two models finds no obvious difference with regard to L-R skill, except that for the SB theory there should be a dip in the distribution at about 0, due to canalization. This apparent difference evaporates if the comparison depends on any single task which has been practised using one side, such as writing. Dart throwers, tennis players, bowlers, and many others would be likely to show a bimodal distribution of differences between the hands in skill, if the comparison depended on one practised skill.

What is each theory saying about the skills assumed to *underlie* these manifest skills? The distributions representing the RS theory in Fig. 1 were intended to refer to some underlying substrate of relative difference between the hands in skill, from which hand preferences for particular actions arise through various developmental experiences. The

distributions representing the SB theory are specifically related by McManus to the writing hand. What does the SB theory have to say about tasks other than writing?

The symmetric bimodal model takes as its basic assumption that each individual is either a right-hander or a left-hander. . . This categorical asymmetry can result in other correlated asymmetries according to the degree to which *an otherwise symmetric system shares the (asymmetric) mechanism of the writing hand (either centrally or peripherally)* (McManus, 1985, p. 14, my italics).

If McManus means what is said here, that the system is basically symmetric except when asymmetries become manifest for writing, then the *SB theory is the RS theory*. There is no substantial point of disagreement.

What does the SB model expect for a task like peg moving, whose relationship with writing is not precisely known and can be assumed to be correlated but imperfect? McManus's Fig. 1 *c*, shows two normal distributions with means shifted by about 1 SD to either side of 0. There is considerable overlap between the distributions, about 16 per cent of each handedness group having superior skills with the *other* hand. The proportion of right-handers with superior left-hand skill greatly exceeds the proportion of left-handers in the total population. The distribution looks quite unlike that of children for the NCDS survey using a pencil (McManus's Fig. 3). The latter does look like the representation of the SB model in my Fig. 1 *B*. Ambiguity about the nature of the distribution is evident in the text when it is asked 'whether or not any of the right-handers form a separate distribution on the left-hand side of the scale or vice versa' (McManus, 1985, p. 9). Having postulated a fundamental division at 0, McManus has created a difficulty about the right-handers and left-handers who fall on the 'wrong side' of the divide. However, McManus's Figs 1 *c* and 3 differ markedly as to whether there should be a division of the sample at about 0.

This analysis finds the SB model unclear as to expectations for peg-moving data. It is also unclear whether the distributions would be relevant to the 'true' categories of left-handers and right-handers. If there are no true categories, but only asymmetries differentiating out of a basic symmetry, then the RS and SB theories are alike in the predictions they would make about L-R distributions.

### **Empirical data**

What kind of empirical data offers a test of the theoretical expectations reviewed above? This question must be considered in relation to the tasks used and also in relation to the samples tested. A single well-practised task is inappropriate since habit is likely to have led to 'canalization'. For most of the tasks psychologists have employed to investigate the hand skills of self-classified right- and left-handers, correlations between preference and skill have been so poor as to lead to a widely accepted conclusion that these variables are unrelated (reviewed by Porac & Coren, 1981). What is to be made of these observations? Do we say that the 'essence of laterality' is manifest in writing only or do we say that psychologists have not been very good at analysing the relevant skills? The data for picking up matches and pressing dynamometers appear to be of doubtful value for questions of relationships between preference and skill and these aspects of McManus's paper will not be considered here.

What is the status of the peg-moving task as a measure of L-R asymmetries? The fact that this task prompted me to think of laterality as continuously distributed does not necessarily imply that it offers a perfect embodiment of the hypothesized underlying distributions. The question of the nature of the difference between the hands in skill, as measured by peg moving, has been investigated experimentally (Annett *et al.*, 1979) and

further work needs to be done. It may even turn out that aspects of the skills involved in the task are differentiated between right- and left-handers. However, no break between right- and left-handers at 0 is evident in the observed distributions (Fig. 2).

With regard to the samples tested, it is axiomatic for statistical inferences about population distributions that samples should be representative of the population. Giving out vast quantities of questionnaires and being content to analyse some 25 per cent returns is inadequate for the investigation of lateral asymmetry in the population, and yet it is the most common method adopted (Porac & Coren, 1981; McManus, 1984). Elaborate statistical analyses of samples which are *not representative of the population sampled* can tell us nothing about population distributions.

In order to avoid distortions through volunteer effects, every opportunity was taken to collect *complete* samples from whole class groups of students or schoolchildren. These samples were reanalysed, tested for homogeneity and combined where appropriate to give normative data (Annett & Kilshaw, 1983; Kilshaw & Annett, 1983). All real samples have 'quirks' which were fully discussed in the original papers and in the reanalyses. There were more left-handers than expected in some of the age groups of schoolchildren. The combined main samples depended heavily on students in higher education. More than 50 per cent of these were OU students attending summer schools. This last sample was not as 'complete' as the others and it was unusual in having a relatively low incidence of left-handed writers in males (6.5 per cent) and a relatively high incidence in females (10.3 per cent). McManus ignores all the qualifications which must be made about the samples, and uses them to search for algorithmic solutions to questions about population distributions.

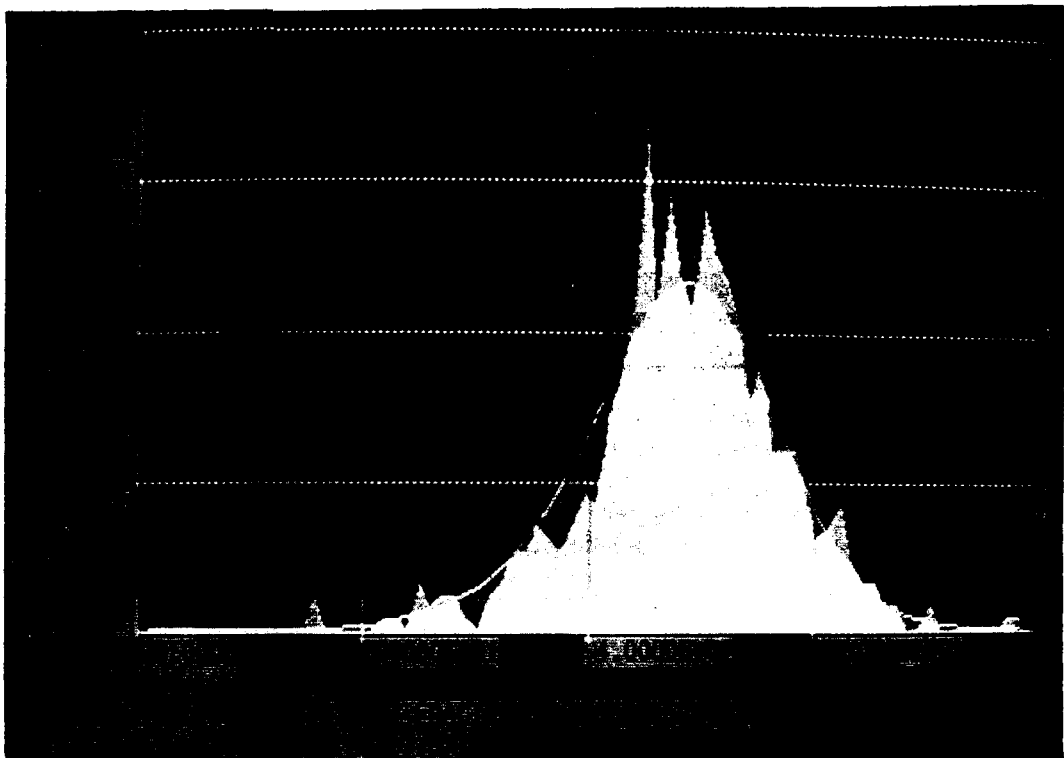
Aside from possible inadequacies of the data, there are specific reasons for believing that the combined main samples are *not* representative of the general population. I have suggested that there might be a balanced polymorphism for the  $rs^+$  gene with heterozygote advantage (Annett, 1984; Annett & Kilshaw, 1984). That is, among students in higher education the middle of the continuum of L-R skill is likely to be overrepresented in comparison with the left and right extremes.

### Algorithms and heuristics

The gist of McManus's strictures about the use of the Kolmogorov-Smirnov  $D$  statistic for tests of the L-R distribution is that it offers an inappropriate algorithm for selecting parameters. This is to misconstrue the purpose of the exercise. Annett & Kilshaw (1983, p. 272) wrote,

In some future analysis, it may be possible to determine the optimal parameters of the distribution to fit findings for dysphasia, family handedness and the population L-R distribution. Here, the aim is the more limited one of assessing how far the parameters derived from an analysis of dysphasia (Annett, 1975) and applied successfully to the prediction of handedness in families (Annett, 1978*b*, 1979) can predict the distribution of L-R times in large samples.

I was not interested in new algorithms but in whether the already tried heuristics would work again. My aim was, and is, to give a description of hand preference which can account for cerebral dominance for speech. The success of the heuristic of deriving parameters of the RS model from the dysphasia series for application to the family handedness series, was one of the most satisfying discoveries I could hope to make. To imply, as does McManus, that the derivation was second best to an analysis of L-R distributions is to miss the point completely. Testing the fit of *these same parameters* to empirical L-R distributions was another check on the parameters, but the L-R data was not elevated to the role of infallible criterion; I was too aware of its shortcomings, as



**Figure 2.** Computer graphic display of the empirical L-R data for males and the curve predicted as the sum of three distributions, with the means, proportions (fractions) and standard deviations shown below the display. The values used here are those derived algorithmically for the SB model (McManus, 1984*a*, Table 1, Model VI). (Kolmogorov =  $D$  statistic;  $40 = 0.0$  or  $L = R$ )

mentioned above. In using the K-S statistic as a measure of goodness of fit, I was not trying to prove the model, but rather asking the more traditional question of whether the model could be disproved, as I believe the account makes clear (Annett & Kilshaw, 1983, p. 276).

There was an aspect of the model which could not be known in advance for empirical data, the means and SDs of the right shifted distributions. These were derived from the data, heuristically rather than algorithmically. It was asked whether I would like the computer program to be set to run systematically through all possible values of the parameters to discover the optimal ones (the algorithmic solution) and I declined the offer. Instead, the computer graphics were used to plot the data and superimpose the curves obtained for the various input values. Figure 2 gives an example using the L-R data for males and the curve predicted from McManus's values for the SB model (McManus, 1985, Table 1, VI). This visible curve fitting was an extremely useful heuristic. The main point is that within a wide range of means and SDs of the right shifted subdistributions, the RS model could not be rejected when the proportion and mean of the  $rs^-$  subgroup were constrained as demanded by the model. However, the  $D$  value found for the curve obtaining maximum support, according to McManus's model, is *not* a good fit to the actual data. It exceeds the 5 per cent rejection level.

Figure 3 shows, for the same data, the fit of the heuristically derived values for the additive version of the RS model (shown in McManus's Fig. 1*b*) as published by Annett

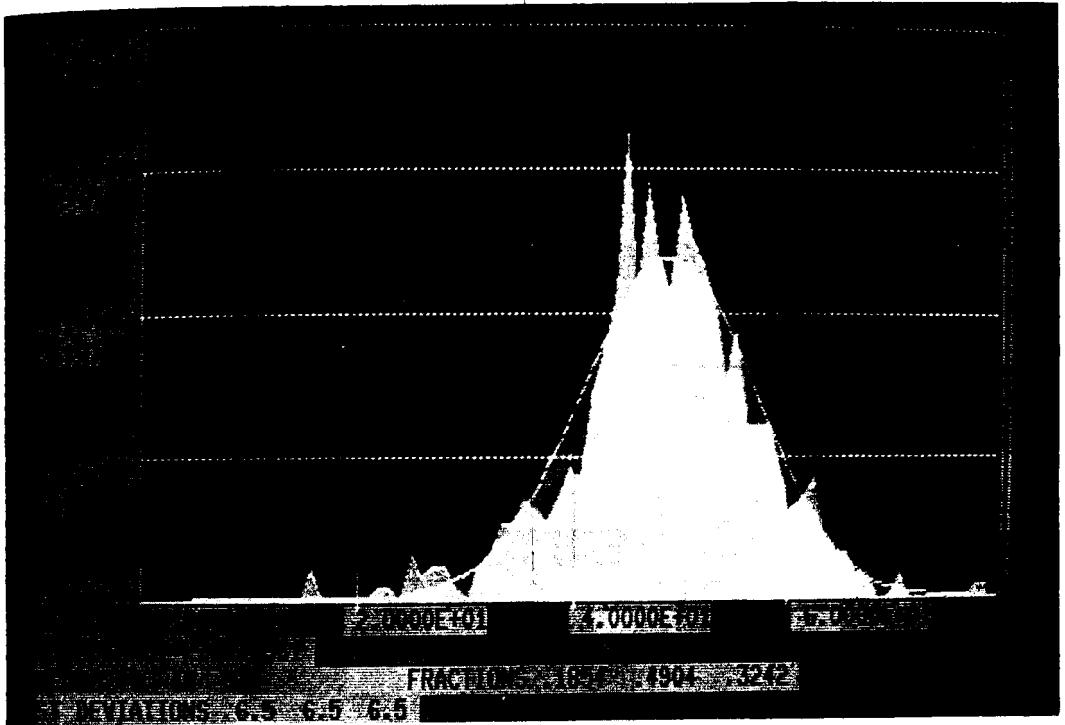


Figure 3. As for Fig. 2 but using the values derived heuristically for the RS model (Annett & Kilshaw, 1983, Table 4a iv).

& Kilshaw (1983, Table 4a iv). This fit cannot be rejected statistically. Undoubtedly even better fits could be obtained by further fine tuning of the parameters, but I chose to work with specified restrictions (Annett & Kilshaw, 1983, p. 273). For example, it was discovered early in the curve fitting that improved fits could be obtained if the variance of the  $rs^-$  distribution were allowed to be larger than that of the  $rs^+ rs^{++}$  distribution(s). As there was no prior theoretical justification for allowing this difference in variance (as opposed to several *post hoc* interpretations that might be thought of) I considered it better to retain, for the present, the common variance assumption.

Table 1 compares, for the males, the algorithmic solutions (of McManus's Table 1) with the heuristic solutions derived for the RS theory, or the observed values. The latter have been recalculated for this purpose, and corrected to an additional decimal place. Table 2 gives the corresponding analyses for female data. In each case the  $D$  value of the K-S statistic gives a measure of fit. Whatever objections there may be to the use of the K-S statistic as a tool in searching for parameters, the objections do not apply here as all values are given. The analyses for males show that the algorithmic solution fails in every case to provide a good fit to the data whereas the heuristics based on the RS theory are more successful.

With regard to tests against observed parameters, the single normal curve can be rejected for males. For left-handers and right-handers, Annett & Kilshaw (1983) reported that the distributions could not be described as the sum of the two handedness groups; this calculation was based on the incidence of left-handed writing in the total sample (8.2 per cent). As mentioned above, there were sex differences in some subsamples in the direction contrary to expectation. Incidences in male subsamples ranged from 6.3 to 13.6 per cent

**Table 1.** Males: Kolmogorov-Smirnov tests of the fit of the models listed by McManus (1985, Table 1) to empirical L-R data. For the Annett (RS) models, the  $rs$  mean is 0, and the  $p$  values as deduced for the three genotypes. Other values are as derived algorithmically, heuristically, or observed

Model	McManus algorithms			Annett heuristics (italics) or observed values				
	Prop.	Mean	SD	D(K-S)	Prop.	Mean	SD	D(K-S)
I. Single normal	1	5.86	8.42	0.0802*	1	6.42	8.37	0.0562*
II. Annett-dominant ( $p$ constrained)	0.1854	0	7.9	0.0756*	0.1854	0	6.5	0.0257
	0.8146	7.22	7.9		0.8146	8	6.5	
III. Annett-additive ( $p$ constrained)	0.1854	0	7.65	0.0837*	0.1854	0	6.5	
	0.4904	5.08	7.65		0.4904	6	6.5	0.0277
	0.3242	10.16	7.65		0.3242	12	6.5	
IV. Annett-dominant ( $p$ unconstrained)	0.1543	0	7.98	0.0751*				
	0.8146	6.97	7.98					
V. Annett-additive ( $p$ unconstrained)	0.2140	0	8.11					
	0.4972	3.73	8.11	0.1623*				
	0.2888	7.46	8.11					
VI. Bimodal symmetric	0.0695	-6.89	7.57	0.0598*	0.0810	-6.12	7.76	0.0401
	0.9305	6.89	7.57		0.9190	7.52	7.48	
VII. Bimodal symmetric different means	0.0338	-12.47	7.67	0.0599*				
	0.9662	6.48	7.67					
VIII. Bimodal symmetric different variances	0.0619	-6.68	9.67	0.0601*				
	0.9381	6.68	7.61					
IX. Bimodal symmetric different means different variances	0.0261	-14.92	6.06	0.0601*				
	0.9739	6.40	7.73					

\*  $D$  exceeds the 20 per cent rejection limit (0.0431 for  $n = 617$ ).



Table 2. Females: Kolmogorov-Smirnov tests (as for Table 1)

Model	McManus algorithms			Annett heuristics (italics) or observed values				
	Prop.	Mean	SD	D (K-S)	Prop.	Mean	SD	D (K-S)
I. Single normal	1	7.95	8.74	0.0395*	1	7.96	8.76	0.0394*
II. Annett-dominant ( <i>p</i> constrained)	0.1854 0.8146	0 9.87	7.75 7.75	0.0252	0.1854 0.8146	0 10.00	7.0 7.0	0.0247
III. Annett-additive ( <i>p</i> constrained)	0.1854 0.4904 0.3242	0 6.87 13.74	7.33 7.33 7.33	0.0451*	0.1854 0.4904 0.3242	0 7 14	6.5 6.5 6.5	0.0289
IV. Annett-dominant ( <i>p</i> unconstrained)	0.1824 0.8176	0 9.84	7.76 7.76	0.0249				
V. Annett-additive ( <i>p</i> unconstrained)	0.2522 0.5000 0.2478	0 5.34 10.68	8.05 8.05 8.05	0.1573*				
VI. Bimodal symmetric	0.0644 0.9356	-9.07 9.07	7.57 7.57	0.0235				
VII. Bimodal symmetric different means	0.0797 0.9203	-7.37 9.28	7.48 7.48	0.0267	Left-handers Right-handers	-5.73 9.44	7.51 7.53	0.0278
VIII. Bimodal symmetric different variances	0.0649 0.9351	-9.19 9.19	7.75 5.77	0.0577*				
IX. Bimodal symmetric different means different variances	0.0421 0.9579	-12.25 8.83	4.38 7.76	0.0229				

\* *D* exceeds the 20 per cent rejection limit (0.0364 for  $n = 863$ ).

and in female samples from 7.0 to 10.3 per cent. Hence, the total incidence for sexes combined was considered the most appropriate for the K-S tests. However, when the calculations are repeated using the actual proportions, means and standard deviations, to a greater accuracy than before, for each sex separately and including those who reported forced change of writing hand as left-handers, the  $D$  value cannot be rejected. The fit is less good for males than for the heuristic RS solution, but as McManus reminds us, K-S values should not be compared in this way.

For females there are good fits for almost all models. Even the single normal hypothesis is only just rejectable. The female samples were very much more homogeneous than the male samples (Annett & Kilshaw, 1983). This homogeneity probably accounts for the comparative success of the algorithmic method in finding values of mean and SD close to those observed (for the single normal, model I) and also for the agreement between the algorithmic and heuristic solutions for the RS models (II and III). The SB algorithms for models VI and IX give good fits overall, but the proportions and means of the minor subgroup differ considerably from those of observed left-handers.

McManus draws attention to the various estimations I have made of the means of the right shifted subdistribution and considers whether the estimates are *a priori* or *a posteriori*. How would it be possible to deduce such a value *a priori*? It can only be estimated from empirical data and since all such data are imperfect, it would be odd if all estimates were in perfect accord. However, my consistency in application has been greater than McManus credits. The estimate of about 1.9z for the dominant version of the model was derived directly from incidences of left-handedness in dysphasic patients inferred to be RS<sup>-</sup> and RS<sup>+</sup> (Annett, 1975, Table VI) and this estimate was the basis for the main calculations for handedness in families (Annett, 1978*b*). When sexes were distinguished for parents and children, the values of 1.6z for males and 2.2z for females were professed to be guesstimates based on the mean 1.9z (Annett, 1979). Good fits were found for all the family data available except for that of Ramaley (1913), which gave a chi-square value which could be rejected at the 5 per cent level of confidence. A slightly larger value of shift, 2.3z, was found to give a better fit to Ramaley's data, and also a remarkably good fit for the combined samples of Chamberlain (1928), Rife (1940) and Annett (1973), totalling 10654 children. At present, I am not inclined to make much of this observation since analyses of new studies of handedness in families (Carter-Saltzman, 1980; McGee & Cozad, 1980; Leiber & Axelrod, 1981; Ashton, 1982; Spiegler & Yeni-Komshian, 1983) lead me to believe that there may have been systematic distortions in the report of parental left-handedness in some of the older studies. Further progress has been made (Annett, 1984) in estimating the relative shifts in males and females, to match observed sex differences in incidences of left-handedness.

The algorithmic and the heuristic analyses (Tables 1 and 2) confirm that the right shifted means for females are invariably larger than those of males. There seems little doubt that the bias to dextrality is stronger in females. McManus says 'it is not clear whether a single global estimate based on all sources of data would be acceptable'. To my mind it would be quite unacceptable because it would ignore the obvious possibility that the same gene can find differing levels of expression in different groups. It is an intrinsic part of the RS theory that the gene is expressed more strongly in females than males, in the singleborn than in twins, and in normals than in those with developmental handicaps. Bearing in mind the possibility that the gene influences development during some sensitive period of brain growth, degree of expression can be expected to differ between these groups. To suggest that the whole theory is invalidated because a smaller shift is required for twins than the singleborn is to ignore the several other differences, in birth weight and in rate of language

development, which are consistent with the hypothesis of lesser expression of the  $rs^+$  gene in twins. The SB model makes no provision for differences due to sex or twinning.

### Left-handers and right-handers

What has the literature on laterality to say about left-handers as a category? Apart from a strong association between hand and foot preferences, and a weak association between hand and eye preference, very little can be said. There is *one* generalization which can be made about groups of left-handers, as follows. For any task on which groups of right-handers show a typical directional bias, groups of left-handers show a reduced bias in the same direction as right-handers. Whenever significant differences are reported between handedness groups, the significance depends on a reduction of the bias found in right-handers. No significant biases *opposite* to those of right-handers have been found in groups of sinistrals larger than about  $n = 12$ . That is, there is no single violation of the expectation of the RS theory, to my knowledge, that any minor subgroup which lacks RS is roughly symmetrical about a mean of 0.

The great advantage of the RS hypothesis that the mean of any minor subgroup in the population is 0 is that it would predict the vast quantity of 'negative' data in a laterality literature still searching for the essence of sinistrality. The lack of bias to either side in the minor subgroup is especially clear for the physical asymmetries of skull and cerebral circulation described by LeMay and her colleagues (LeMay, 1977; Galaburda *et al.*, 1978). It is evident in the physical brain asymmetries and the handedness of patients known to have *right or bilateral speech* (Ratcliff *et al.*, 1980). What stronger evidence of lack of bias in the atypical case could be found? McManus's model fitting to the Hoadley & Pearson (1929) skull data is no counterweight to this substantial evidence for the RS theory. As for the L-R data above, the Hoadley & Pearson data are fully compatible with the RS model but McManus finds a slightly higher support value for the SB model.

It is when McManus tries to discredit the RS theory by juggling with estimates of incidence of left-handedness that the barren nature of the two-category classification is exposed. If there are two distinct categories, why are there such large differences in estimates of left-handedness in the population? By assuming that incidences depend on a threshold which can vary over a wide range, the RS theory is both released from sterile arguments as to the 'true' incidence of sinistrality, and is then able to show how certain myths about cerebral speech have arisen from shifts of criteria of sinistrality (Annett, 1976*b*). McManus eschews the threshold concept, as said above, but he is obliged to treat real data *as if* a threshold were varying (McManus, 1984). The RS theory can predict the distribution of handedness in families when parental incidences range from 4 to 24 per cent, and filial incidences range from 5 to 40 per cent. But the figures are not interchangeable. The predictions differ for each level of incidence, as one would expect for thresholds which cut a stable underlying distribution at different points. For McManus to claim that the incidences of left-handedness found in my combined main samples are the 'true' incidences for parents and in the birthday samples the 'true' incidences for offspring is a transparent manoeuvre. I certainly would not claim that my own data offer the 'true' incidence any more than I would allow Levy's (1977) claim that Rife's data offered the one true set of incidences for family studies (Annett, 1978*a*). Estimates of children's handedness in families are very sensitive to variations in the incidences for parents, but this could not be known for the  $L \times L$  parents, who were volunteers from the general (as opposed to academic) population. The special features of the combined main samples and the birthday samples have been mentioned above. To use them as a basis for predictions about  $L \times L$  families is to beg many questions.

With regard to the impossibility of gaining 'information about the *absolute* position of the latent variables P1 and P2', the only absolute I have suggested is that when RS is absent the mean is 0. This is a very simple hypothesis, a null hypothesis, which other theories must disprove. I see no value in theoretical arguments about the possible effects of adding a constant to the 'latent variable'. There are excellent reasons for believing that there are stable underlying distributions of the kind postulated by the RS theory. The stability is demonstrated in the way the observed incidences move together when the distributions are cut according to different but linked criteria. It was precisely because the proportions of mixed-handed humans (30 per cent) and non-humans (50 per cent) were as expected for the same thresholds on the continuum, when a normal curve is shifted from a mean of 0 to a mean greater than 0, which suggested the RS theory (see the alignment of thresholds in Fig. 1A). Similarly the proportions of consistent left-handers and of mixed-handers in a sample of dyslexics were just as expected for a distribution shifted less far to the right than that of controls, given the *same thresholds* in both samples (Annett, 1984; Annett & Kilshaw, 1984). Expectations for the handedness of children with 0, 1, and 2 left-handed parents match in all cases where the same data can be examined for a severe and/or generous criterion of sinistrality, even when both levels of criterion are examined in both generations. Since in all calculations I have kept the mean of the minor distribution anchored at 0, I think we can be fairly confident that there are no constants, additional to those attributable to the action of the  $rs^+$  gene, shifting the distribution to and fro.

### The falsifiability of the RS theory

The RS theory will be failed when a substantial group of left-handers is found to have right-hemisphere speech, or alternatively, when a substantial group of right-hemisphere speakers is found to be left-handed, at a level significantly larger than the 50 per cent predicted by the theory (or up to 75 per cent for generous criteria such as left- and mixed-handedness). It will also be failed when appropriate gene markers are discovered if any genes giving specific biases in the atypical direction are found.

When Annett & Kilshaw (1983) used the L-R data to test the predictions of the RS model, they were in all cases asking the traditional statistical question of whether the model could be rejected. It could not be rejected. Has McManus shown that the RS model can be rejected? Certainly not. His claim is that the RS model fails because a slightly higher support value was found for distributions which might theoretically be interpretable as left-handers and right-handers (although they were not in fact so interpretable) than for the distributions expected by the RS theory.

Is it reasonable to suggest that a model which has proved powerful in unifying hitherto disparate and puzzling data could be failed on such slender grounds?

'Though by the likelihood axiom the support will inform us fully of the contribution to our judgement that the data can make, we shall also be influenced by the simplicity of the hypotheses, by their relevance to other situations, and by a multitude of subtle considerations that defy explicit statement. *The scientist must be the judge of his own hypotheses, not the statistician*' (Edwards, 1972, p. 34, my italics).

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## On testing the right shift theory: A reply to Annett

I. C. McManus

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Annett's criticisms of McManus' (1985) critique of the application of the right shift theory to population distributions of skill asymmetry are themselves criticized.

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Annett's reply to my paper (McManus, 1985) is wide-ranging and might well be confusing to many readers since it refers extensively to a second paper of mine, as yet not in print (McManus, 1984), in which I consider a new genetic model of handedness and cerebral lateralization. However that second paper is strictly irrelevant to the questions raised by the present one which is self-contained, and considers only the observed distributions of skill asymmetries, and only makes references to the symmetric bimodal (SB) model as a *phenotypic* model. McManus (1985) makes no references to the 'true' incidence of left-handedness (Annett, 1985, p. 18\*), or to genetic models (p. 19) or to the DD genotype (p. 19), and indeed has no need to do so, being solely concerned with the phenotypic description of asymmetry within the population.

### The symmetric bimodal model

The symmetric bimodal theory is partly misunderstood by Annett, and a few clarifications might be helpful. The SB theory does indeed incorporate some of the assumptions of the right shift (RS) theory (p. 17). However there is one crucial feature of the RS model which is not incorporated: that there is a subgroup in the population whose skill is normally distributed with a mean of zero. There is indeed in the genetic model (McManus, 1984) a subgroup with mean of zero, but it is explicitly not normally distributed. The SB theory of phenotypes does not assume that there should be a perfect relation between hand preference and skill (p. 18); this will be the case only if a task involves just the handwriting processing system (painting or drawing might well be examples). Most tasks will also involve a lower level symmetric processing system to a greater or lesser degree, thereby resulting in diminishing correlations between skill and preference, and also accounting for the absence of a 'dip in the distribution at about 0' (p. 19) for many skills. The shape of the distribution depends on the parameters, and hence it is hardly surprising that the data from the NCDS (McManus, 1985, Fig. 3) look different from those of Fig. 1 of McManus (1985), which used the parameters best fitting to Annett & Kilshaw's (1983) data. There is no 'ambiguity about the nature of the distribution' (p. 20), nor is it 'unclear as to expectations' (p. 20); there are simply some parameters which are task specific and thus undefined. The *form* of the distributions is totally defined.

A final point of misunderstanding is when Annett suggests that 'If... the system is basically symmetric except when asymmetries become manifest for writing, then the *SB theory is the RS theory*. There is no substantial point of disagreement' (p. 20; Annett's italics). When there is no population performance asymmetry, then indeed the theories are identical, both predicting a single normal distribution centred at zero. This is the only occasion on which their predictions agree; in all other non-trivial situations the disagreement remains substantive.

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\* All page references are to Annett (1985) unless otherwise stated.

### Empirical data

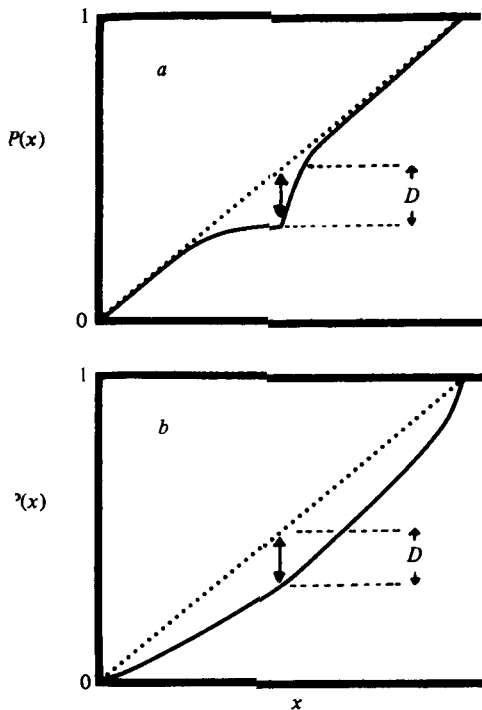
The square-marking dataset from the NCDS seem adequately to fulfil all of Annett's criteria; it is very large, highly representative of the entire population, is not well practised and shows a reasonable correlation between skill and preference. Surprisingly it is barely mentioned in Annett's reply. As far as the data of Annett & Kilshaw (1983) are concerned I find it remarkable that the author feels that 'it is not equal to the demands McManus makes of it' (pp. 11–12). If so, it is surely not equal to any demands and perhaps should never have been published. If data are seen as suitable for support of one theory then they must also be regarded as suitable for testing that theory against any other theory.

### Model fitting

Annett differentiates heuristic from algorithmic methods of model fitting. I frankly find that difference obscure and irrelevant. In Annett's usage 'heuristic' appears to mean that a method happens to work, whereas 'algorithmic' seems to suggest statistical nit-picking, a distinction that does not seem to be useful. I would describe my approach as well within the mainstream of statistical analysis, and hence essentially *classical statistical modelling* of stochastic data. If Annett's method is something else then I find its logic difficult to comprehend, particularly given that Annett & Kilshaw (1983, p. 272) say that their parameters 'are derived heuristically... by varying the means and then the standard deviations to discover the best fits'.

As far as model fitting is concerned, there is the problem of the criterion of goodness of fit. In principle there is an infinite number of potentially arbitrary criteria of fit. Annett has chosen, and chooses again, to use the Kolmogorov statistic, the problems of which may readily be shown.  $D$  is the maximum absolute difference between the cumulative distributions of the observed and expected distributions. Consider Fig. 1. Figures 1a and b have the same value of  $D$ , and hence by the Kolmogorov criterion are equally good fits of data to predictions, a result which is inconsistent with any common-sense interpretation of fit. The likelihood criterion which I have used in my model fitting is generally accepted as one of the most useful criteria of fit since it utilizes all of the information available in the data to its maximum extent; any other criterion must reject some information at the expense of other, and therefore is less sensitive and occasionally frankly erroneous. By a likelihood criterion model 1a is a better fit than model 1b, which, I would suggest, is as required of any generally reasonable criterion of fit. The maximum-likelihood method of parameter estimation is usually well behaved, the only important exception being that it can be seriously misled by outliers (of which there is no evidence in Annett's data or the NCDS samples).

Annett suggests in her Tables 1 and 2 that using a Kolmogorov criterion then 'the algorithmic solution fails in every case to provide a good fit to the data whereas the heuristics based on the RS theory are more successful' (p. 23). The objections to Annett's fitting methods have been given previously and need not be repeated again. All that needs to be said is that the success of models simply cannot be compared in this way, and that even if they could then it would always be possible to find some criterion of fit for which Annett's results would be found. The likelihood criterion is the only generally fair test of fit, and then the differences are in the opposite direction to that found by the Kolmogorov method. The differences are also capable of formal statistical testing, when conventional significance levels are readily attained in favour of the SB model. The reader is also reminded that whilst the fitting of Annett's data by the two models may be construed as an area of reasonable controversy, this is hardly so for the NCDS square-marking data, where almost any criterion (including that of 'eye-balling') will come down in favour of the SB model.



**Figure 1.** Hypothetical cumulative probability distribution of data (dotted line) and two models (solid lines, *a* and *b*), each of which by the Kolmogorov *D* criterion is an equally good fit to the data.

### The status of the RS theory

Annett's RS theory is an empirical theory and hence must be tested in its ability to make novel predictions about data which are as yet uncollected. The novelty must be in the form of the data, not their mere statistical independence of previous samples (most theories making it for granted that similar studies should yield similar results, and that the specific theory alone can hardly be credited with the general regularity of the universe). The claim that 'the RS theory will be failed when a substantial group of left-handers is found to have right-hemisphere speech, or alternatively, when a substantial group of right-hemisphere speakers is found to be left-handed' (p. 28) is almost incredible. The RS theory set out to explain the already well-established facts about handedness and language dominance. It cannot claim that those data, and similar ones yet to be collected, are themselves a criterion of falsification of the model. One might as well say that the model will only be disproven when the sun has been demonstrated to go round the earth, or the moon to be made of green cheese. A model can always be produced which in retrospect will explain all extant data, as long as sufficient free parameters are allowed. The suggestion that 'it is an intrinsic part of the RS theory that the gene is expressed more strongly in females than males, in the single-born than in twins, and in normals than in those with developmental handicaps' (p. 26) is not strictly correct. These are not *intrinsic* to the theory, but rather are *ad hoc* modifications of the theory to explain otherwise awkward data. Indeed a further *ad hoc* addition might even have been caught in the process of creation: 'among students in higher education the middle of the continuum of L-R skill is likely to be overrepresented in comparison with the left and right extremes' (p. 21). Sufficient free



parameters will always allow models to be fitted in retrospect. It is in their ability to *predict* data as yet uncollected, and in their willingness to be rejected by those data, that models are regarded as scientific rather than pseudo-scientific (Popper, 1972*a*). Ideally there should be no quibbling over 'a slightly higher support value' (p. 28) or 'slender grounds' (p. 28), although a certain dogmatism may be useful 'to defend a theory against criticism, or it would succumb too easily, and before it had been able to make its contributions to the growth of knowledge' (Popper, 1972*b*, p. 30). The degree of testability of a hypothesis is proportional to the *improbability* of the predictions that it makes. Thus far Annett's theory has made one prediction which is highly improbable, and thus very testable, and the prediction has apparently been refuted. It is not clear at present that the theory is capable of making other empirical predictions which make it adequately testable.

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