LEFT-HANDEDNESS IN TWINS: GENES OR ENVIRONMENT?

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ABSTRACT

Twin family data can cast light on the longstanding problem about the influences of genes and environment on the etiology of left-handedness.

Therefore, hand preference was assessed in 1700 adolescent twin pairs and their parents. Left-handedness (LH) appeared not significantly enhanced among twins compared to the general population. In addition the following observations were made: (1) Significant more LH in first born twins than in second born twins. (2) Significant higher left-handedness association in MZmm pairs compared to DZmm pairs and not or may be marginally so in MZff versus DZff pairs.

These results, combined with the observations that (a) left-handed fathers increase the probability of LH in sons but not in daughters; (b) LH in mothers increases LH prevalence in both sons and daughters to the same degree; and (c) very low birth weight, corrected for the effect of gestational age, increases LH prevalence in first born twins only, make an environmental explanation more likely. The possibility that exposure to prenatal male hormones – to which low birth weight and high birth stress children are more vulnerable – might be a crucial condition for the etiology of LH, is discussed.

INTRODUCTION

Recently, Davis and Annett (1994) presented data that confirmed earlier observations of a higher prevalence of left handedness in twins compared to singleborn subjects as well as a higher left-handedness prevalence in males than in females. The undisputable merit of Davis and Annett's data is that the observations on both twins and singletons come from the same data set where subjects could be either twin or singleton.

The authors consider these findings as a "robust and substantial empirical support for the RS theory of handedness" (page 110). RS refers to "right shift" which is the label for the theoretical model, developed by Annett in 1978 and revised in 1985, for the explanation of the phenomenon of differential hand preference in humans. The model says that handedness depends on chance and that therefore on the level of a population 50% of all individuals will be right handed (RH) and 50% left handed (LH), just as is the case in mammals. In humans however, this 50-50 chance distribution is shifted towards the right if a particular gene is present (rs +) and not if that gene is absent (rs −). The model assumes that deviation from chance in the direction of left hemisphere advantage is transmitted by two alleles (either rs + or rs −) at a single locus,

and that rs −/− produces the 50-50% chance distribution and both rs +/− and rs +/+ a weaker and stronger shift towards the right respectively. Annett then *inferred* rs + and rs − gene frequencies from cerebral lateralization data with respect to language, obtained in dysphasia patients, the underlying assumption being that in fact the rs + gene is a gene for left hemisphere speech, leading to a disadvantage to the left hand. The calculated gene frequencies enabled Annett to estimate degrees of shift in rs +/+ and rs +/− individuals relative to rs −/− persons (set at zero per definition). Using these population genetical parameters, the model appears to describe the phenotypical differences between individuals in a normal population (e.g. Annett, 1985). Degrees of shift values are obtained by Annett on language lateralization data from dysphasia patients and (successfully) applied to handedness in normal individuals.

The empirical fact that in both males and twins LH prevalence is higher than in both females and singleborn Ss, is accomodated by assuming that rs + gene expression is lower in males and twins than in females and singletons respectively, which in turn could be associated with differential (brain) maturation (Annett, 1985). I.e., under the assumption of differential gene expression twin handedness data appear to fit the model too. Irrespective of the scientific value of the RS model in general, it could be argued that Davis and Annett (1994) reverse logic rules by considering their enhanced LH prevalence figures in twins relative to singletons as empirical support for the RS theory. The authors have only made clear that deviating handedness prevalences in twins are not incompatible with the RS model.

An important question that has to be answered is: Is it necessary to assume a brain laterality gene (labelled rs +) owned by the person whoms phenotype (hand preference) we study, when one (Rife, 1950, for example) finds that families that include an RL pair of twins are more likely to have another singleborn left-hander in the family than families with RR twins? Annett (1985, page 59) concludes from that fact: "Whatever the effect of twin birth itself, the chance of left-handedness in twins is *affected* by the presence of left-handed relatives".

However, when a particular physical or behavioral feature (such as left-handedness) "runs in families", then this can be ascribed to either shared genes or shared environments or both. Further, one should realize that maternal genes – transmitted to the offspring or not – may create an environmental condition for the fetus. Therefore, a genetic disposition (rs + or any other label) is not necessarily a gene (or more) owned by the phenotype. Looking at twin data, as Davis and Annett did, one should not confine oneself to raw prevalence figures, because twin data contain more information that is relevant for the genes-environment dispute, such as effects of birth order (within a twin pair) and LH prevalence in parents of twins.

When a genetic explanation of left-handedness is most likely, then one would expect to find in twins:

— Higher concordance in MZ than in DZ twin pairs (done by several investigators and resulting in equal or slightly reduced concordance in DZ pairs relative to MZ pairs);

— LH prevalence equal in first and second born twins;
— Handedness prevalence in parents of twins equal to that in their twin offspring;
— No effect on handedness prevalence of zygosity.

An environmental explanation – via either cultural transmission as advocated by Tambs and Berg (1987), or via some biological mechanism such as exposure to birth or pregnancy difficulties (e.g. Coren, 1992) – is more likely when opposite observations would be made.

We have studied handedness in a large sample of twins and their parents and assessed the above mentioned characteristics. In addition, we have investigated the association between birth weight of the twins and LH-prevalence.

MATERIALS AND METHOD

Subjects

In 1989, families with a twin pair were recruited by asking all 720 city councels in The Netherlands for addresses of twins aged 12-22 years. A positive response was obtained from 252 city councels who supplied a total of 3859 addresses. 177 addresses were available from other sources. After contacting these families by letter, 2375 families replied that they were willing to participate. Finally, 1700 families returned a mailed questionnaire.

Mean age of the twins was 17.8 years (SD=2.28). Zygosity was determined by questionnaire with items about physical similarity and frequency of confusion of the twins by family and strangers (e.g. Goldsmith, 1991). In a group of 131 same-sex adolescent twin pairs – participating in another study — agreement between zygosity based on this questionnaire method and zygosity based on bloodgroup polymorphisms and DNA fingerprinting was 95%. The total sample of twin pairs consisted of 275 monozygotic male pairs (MZmm), 360 monozygotic female pairs (MZff), 258 dizygotic male pairs (DZmm), 322 dizygotic female pairs (DZff) and 485 pairs of opposite sex (DZos).

Questionnaire

Questionnaires asking about zygosity, health, alcohol and tobacco use, personality and hand preference were mailed to all families. The questionnaire for the twins and the parents contained the same self-report questions. In addition parents answered several questions about their twins, such as birth weight, birth order and health and behavior during early development. The present report deals with the hand preference and birth weight data. Results about the other data will be reported elsewhere. Hand preference was assessed in both parents and twins with one two-choice question:

"Do you consider yourself predominantly right-handed or predominantly left-handed?"

The same question was used in a large Dutch population survey on hand preference by the Central Bureau of Statistics in 1986 (Van den Brekel, 1986). If relevant, the present figures will be compared with those of Van den Brekel.

RESULTS

A total of 1700 families returned the questionnaires. Not always all four family members had filled out the questionnaire, the father being the most frequent lacking person. More precisely: questionnaires or part of them (especially with regard to hand preference) from 270 fathers, 102 mothers and

38 twins were missing. Parental hand preference data were complete (i.e. available for both father and mother) for 1388 couples. For 42 parental couples only the paternal data and for 210 couples only the maternal data were known. For 1663 twin pairs (3326 subjects) hand preference data were available for both the first and second born twin of the pair. There remained thus $3400 - 3326 - 38 = 36$ single twin subjects for whom no hand preference data of their co-twin were available. This latter group of 36 has been included in statistical calculations only when the twin-*pair* aspect was irrelevant.

Hand Preference in Twins

Of all 3326 twin subjects (i.e. from all complete pairs) 471 said to be left-handed (LH). This is 14.16%, which is not significantly different from a comparable age group (15-19 years) in the general Dutch population, where out of 618 subjects 78 (12.6%) reported to be LH ($\chi^2(1, N = 3944) = 0.91$, p = .34). When the present twin LH frequency is tested against the 6-8 years group in the 1986 Dutch population survey study (this is about the age our twin subjects had in 1986), the twin figures appear to be significantly neither: 471/3326 ($= 14.16\%$) versus 36/338 ($= 10.65\%$) ($\chi^2(1, N = 3664) = 2.88$, p = .09).

Birth Order, Zygosity and Sex

Table I presents all LH figures for each zygosity type, for boys and girls as well as for first and second born twins.

Since by necessity the data are collected in pairs of children, that is as twins, we have investigated whether the six twin groups differ with respect to (the co-occurrence of) LH in first and second born. Table II presents the numbers of twin pairs, cross-classified by LH in first born and LH in second born for each twin group.

From the data of Table II the following three coefficients have been computed for each group separately:

— The odds of LH prevalence in twins, e.g. for MZmm twins this yields $(2*15 + 31 + 20)/(2*203 + 31 + 20) = 0.18$ (cf. Landis and Koch, 1977).

— The marginal odds ratio of LH prevalence in first born twins compared

TABLE I

Proportions of Left-handers among Twins as a Function of Zygosity, Sex and Birth Order

Zygosity	Numer of persons	Number of LH	% LH all	% LH first born	% LH second born	% LH boys	% LH girls	Total
MZmm	538	81	15.06	17.10	13.01	15.06	—	All MZ:
MZff	706	91	12.89	13.60	12.18	—	12.89	13.83%
DZmm	498	67	13.45	15.26	11.65	13.45	—	All DZss:
DZff	634	81	12.78	15.46	10.09	—	12.78	13.16%
DZmf	454	68	14.98	17.62	12.33	17.62	12.33	All DZos:
DZfm	496	83	16.73	18.15	15.32	15.32	18.15	15.68%
Total	3326	471	14.16	16.00	12.33	14.96	13.50	14.16%

TABLE II

Frequencies of the Co-occurrence of Left (LH) and Right Handedness (RH) in Twin Pairs per Zygosity Category

Zygosity	LH first born		RH first born		Total pairs
	LH second	RH second	LH second	RH second	
MZmm	15	31	20	203	269
MZff	10	38	33	272	353
DZmm	4	34	25	186	249
DZff	5	44	27	241	317
DZmf	3	37	25	162	227
DZfm	10	35	28	175	248

to LH prevalence in second born twins, i.e. the ratio of the odds of LH prevalence in first borns and the odds of LH prevalence in second borns (Landis and Koch, 1977; McCullagh and Nelder, 1989, pp. 219-225). The marginal odds ratio can be interpreted as a measure of marginal heterogeneity. For MZmm twins the odds of LH prevalence in first borns equals $(15 + 31)/(20 + 203) = 0.206$ and the odds of LH prevalence in second borns equals $(15 + 20)/(31 + 203) = 0.150$, yielding a marginal odds ratio of 1.38.

— The usual odds (cross product) ratio, measuring the association between LH in first born and LH in second born.

Table III presents the three coefficients.

Next, each coefficient has been analyzed separately in order to detect possible differences between the twin groups. A model fitting approach has been advocated, using the procedure CATMOD (SAS, 1985), which yields weighted least squares estimates of the model parameters (Grizzle, Starmer and Koch, 1969).

The main results are:

— No differences between twin zygosity groups in the odds of LH in twins (goodness of fit statistic $\chi^2(5) = 5.08$, p = .41),

— No differences between twin zygosity groups of LH prevalence in first born versus second born twins (goodness of fit statistic $\chi^2(5) = 1.64$, p = .90). However, a consistent LH prevalence of first born versus second born was found (common marginal odds ratio LH-first born vs LH-second born = 1.35, $\chi^2(1) = 9.59$, p = .002).

— A significant association between LH in first born and LH in second born in MZmm twins (odds ratio = 4.91, $\chi^2(1) = 16.46$, p<.0001) and an association

TABLE III

Three Coefficients Describing Left-handedness Prevalence in Twin Pairs

Zygosity	Odds LH prevalence	Odds LH 1st vs 2nd	Odds of association LH 1st and LH 2nd
MZmm	0.18	1.38	4.91
MZff	0.15	1.13	2.17
DZmm	0.16	1.37	0.88
DZff	0.15	1.63	1.01
DZmf	0.18	1.52	0.53
DZfm	0.20	1.23	1.79

of borderline significance in MZff twins (odds ratio $= 2.17$, $\chi^2(1) = 3.74$, $p = .053$). In the DZ twin groups no such association between LH in first born and LH in second born was found (goodness of fit $\chi^2(4) = 3.05$, $p = .55$). These results suggest a modest genetic influence on the etiology of LH, particularly in males.

— Using a contrast based upon the odds of LH in first borns and the odds of LH in second borns (not shown in Table III), LH prevalence in boys appeared not different from that in girls ($\chi^2(1) = 1.29$, $p = .26$).

The more conventional method for the estimation of a genetic influence on left-handedness in case of binary twin data, compares the proportion of handedness-discordant pairs in MZ pairs with that in DZ pairs. A lower proportion of discordant pairs in MZ twins relative to DZ twins is considered an indication for the action of some genetic factor. Neither for the MZm versus DZm contrast nor for the MZf versus DZf contrast the proportion of discordant pairs differs significantly: the 95% confidence interval for these two differences ranges between $-.023$ and $.118$ and between $-.039$ and $.085$ for males and females respectively. This is in agreement with data of several other authors (e.g. Zazzo, 1960; Loehlin and Nicols, 1976).

This leads to opposite conclusions. The calculation of the odds ratio, rather than the (traditional) proportion of discordant pairs as a measure of association, is independent from possible differences in overall handedness prevalences within each zygosity group. For example, assuming statistical independence and equality of LH in first and second born twins (say, with common proportion P), the proportion of discordant pairs is $2P(1-P)$, which clearly depends on P.

A possible solution is to use a so called chance-corrected association coefficient (Zegers, 1986a). For the proportion of concordant pairs (in the statistical literature known as the simple matching coefficient) this yields Cohen's (1960) kappa (cf Zegers, 1986b). Calculation of this kappa produces the same outcome as is the case with calculation of the odds ratio.

Left-handedness in Parents of Twins

From 1430 fathers and 1598 mothers of twins hand preference data were available. The proportion of left-handers among them is presented in Table IV and is not different from that in the general population (Van den Brekel, 1986; LH frequencies from men and women between 30 and 49 years of age have been taken for comparison with LH of the twin parents). (Fathers: $\chi^2(1, N=2717) = 0.08$, $p = .78$. Mothers: $\chi^2(1, N=2884) = 0.22$, $p = .63$). There is no relationship between LH prevalence of parents and the zygosity of their twin offspring ($\chi^2(4, N=1430) = 0.17$, $p = .99$ and $\chi^2(4, N=1598) = 0.38$, $p = .98$ for fathers and mothers respectively).

Handedness of Parents and Handedness of Their Twin Offspring

In Table V, left-handedness proportions of sons and daughters of all four possible Father $\times$ Mother matings (with regard to handedness: RR, RL, LR and LL) are presented. (NB. Small discrepancies between N ($=$ number of

TABLE IV

Handedness in Parents of Adolescent Twins

Zygosity	Fathers		Mothers	
	Number	% LH	Number	% LH
MZmm	226	10.62	261	10.73
MZff	292	11.30	337	8.90
DZmm	229	10.92	244	9.02
DZff	269	11.52	302	9.60
DZos	414	11.84	454	9.69
Total	1430	11.33	1598	9.57
Population[1]		11.57		10.43

[1] Based on E.J.G. van den Brekel (1986). Left-handedness. *Maandblad Gezondheid (CBS)*, November, 5-10.

parental couples) and total number of children have to be ascribed to missing twin data).

When at least one parent is left-handed, then the probability that one or both of their twin children is left-handed too, is significantly enhanced ($\chi^2(1, N = 2751) = 4.16$, p = .02). This appears to hold for sons only: $\chi^2(1, N = 1266) = 3.49$, p = .03 for sons and $\chi^2(1, N = 1485) = 0.86$, p = 0.17 for daughters. Pairwise comparisons reveal some significant differences that have

TABLE V

Left-handedness in Twin Families

Parental handedness		N	Left-handed twin offspring		
Father	Mother		Sons	Daughters	Total
Right	Right	1103	144/1018 (14.1%)	151/1191 (12.7%)	295/2209 (12.9%)
Right	Left	116	24/110 (22.8%)	23/120 (19.2%)	47/230 (20.4%)
Left	Right	141	23/124 (18.5%)	17/154 (11.0%)	40/278 (14.4%)
Left	Left	18	4/14 (28.6%)	4/20 (20.0%)	8/34 (23.5%)

Pairwise comparisons (not mentioned comparisons are not significant):
Sons. RR versus RL: $\chi^2(1, N = 1128) = 3.84$, p = .025.
Daughters. RR versus RL: $\chi^2(1, N = 1311) = 3.65$, p = .028;
  RL versus LR: $\chi^2(1, N = 274) = 2.77$, p = .048;
Total. RR versus RL: $\chi^2(1, N = 2439) = 8.09$, p = .002;
  RR versus LL: $\chi^2(1, N = 2243) = 2.64$, p = .05;
  RL versus LR: $\chi^2(1, N = 508) = 3.08$, p = .039.

been indicated at the bottom of the table. Comparisons with the LL mating category might lack significance because of the very low cell frequencies in this category, as a consequence of which the 95% confidence interval varies between 9 and 61% for LL sons and between 6 and 46% for LL daughters. The table is nevertheless compatible with the idea that there is no association between LH of fathers and LH of their daughters, contrary to the association between LH of mothers and LH of their daughters and sons as well as LH of
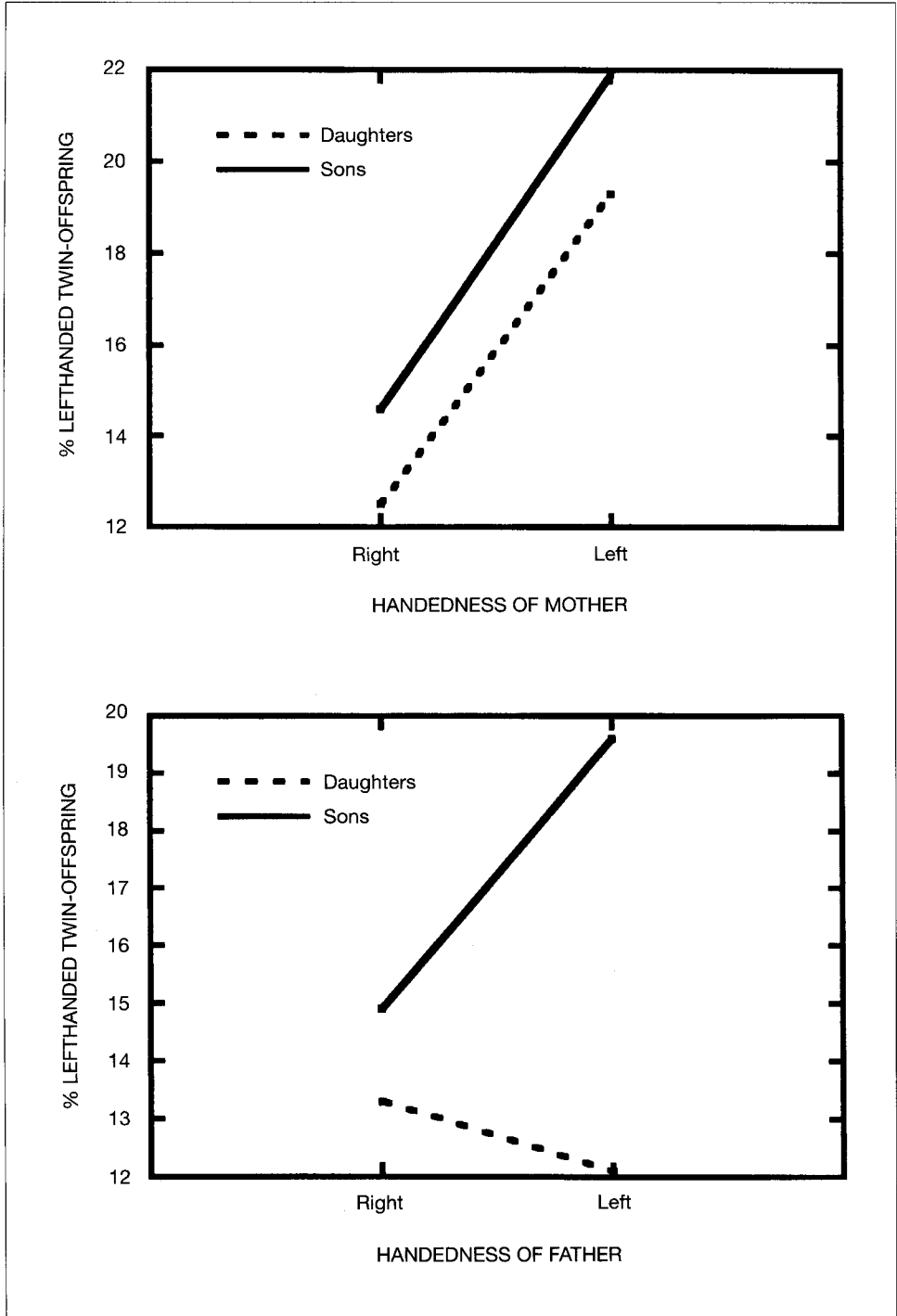
Fig. 1 – *Proportions of left-handed twin sons and twin daughters as a function of handedness of mother (upper panel) and handedness of father (lower panel).*

fathers and LH of sons. Figure 1 presents the proportion of left-handed sons and daughters as a function of handedness of mother (upper panel) and as a function of handedness of father (lower panel).

Birth Weight

Birth weight appears to be associated with LH prevalence in first born twins: low (9.1%) when birth weight is substantially larger (>750 grams)[1] compared to the co-twin, increasing gradually to 23.1% when birth weight is more than 750 lower than that of the co-twin. This contrast (8/87 = 9.19% versus 9/39 = 23.08%, tested two-sided) is significant: $\chi^2(1, N = 126) = 3.33$, p = .03. When *all* first born twins that weigh more than their second born co-twin are compared with all first born twins that weigh less than their co-twin, the difference in LH prevalence (110/730 = 15.09% verus 111/598 = 18.56%) is still in the same direction but not significant: $\chi^2(1, N = 1328) = 2.69$, two-sided p = .10. The analogue statistical tests for the second born twin are far from significant: $\chi^2(1, N = 123) = 0.001$, p = .48 (13/85 = 15.29% versus 5/38 = 13.16%) and $\chi^2(1, N = 1328) = 0.006$, p = .47 (91/729 = 12.48% versus 73/599 = 12.19%) for the most extreme contrast (750 grams heavier versus 750 lighter than the co-twin) and the less extreme contrast (heavier versus lighter than the co-twin) respectively.

DISCUSSION

Though a LH prevalence of 471/3326 has to be considered as rather high, it is doubtfull whether this figure is elevated relative to that in the population in general. It should be admitted that in the population survey the sample size per age category is not very large. This may have influenced the comparison. The method and the sample size in the Davis and Annett study are far superior. Moreover, other investigators found an access of LH among twins too (e.g. Williams, Buss and Eskenazi, 1992).

More important for the nurture-nature debate on left-handedness are other observations we did in our twin sample. In accordance with — but not necessarily compelling to — a genetic model is the significant enhanced proportion of concordant pairs among MZmm twins compared DZmm twins. The analogue difference in concordance in female twins was considerably less and of borderline significance. This observation is compatible with the one showing that LH of fathers is associated with LH of their sons but not with LH of their daughters, whereas LH of mothers seems to be associated with equally enhanced LH in both sons and daughters.

Difficult to handle in the context of a genetic transmission model are the significantly higher LH prevalence figures in first born twins than in second

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[1] Treating birth weight in terms of intra-pair birth weight difference has the advantage that the effect of gestational age on birth weight is eliminated automatically.

born co-twins. This birth order effect can not be ascribed to reduced gene expression because of differential maturation since first born twins weigh an average of 60 grams more than second born twins (Orlebeke et al., 1993). It is possible that the birth order effect can be considered as a special case of parity, primiparae being more at risk for birth stress. Birth stress seems to increase the probability of LH (Williams et al., 1992). Several investigators have reported an increased LH prevalence among oldest children compared to younger sibs (e.g. Bakan, 1977; Annett and Ockwell, 1980; Badian, 1983; London, Kibbee and Holt, 1985). Others (Hicks et al., 1978; Searleman et al., 1980; Dellatolas et al., 1991) could not confirm these findings.

Low birth weight is associated with an increased probability of LH. This is significant for first born twins only (Figure 2). It suggests that LH is associated with intra-uterine growth disturbances – for which a large intra-pair birth weight diparity is an indication – and that the first born twin could be more vulnerable when birth weight is low than the second born, perhaps because of the enhanced parity-related birth stress, as suggested above.

The relevant environmental factor one could speculate about is something that is "produced" by the mother and which in itself can have a genetic origin. In Figure 1 it can be seen that both boys and girls are more likely to be LH
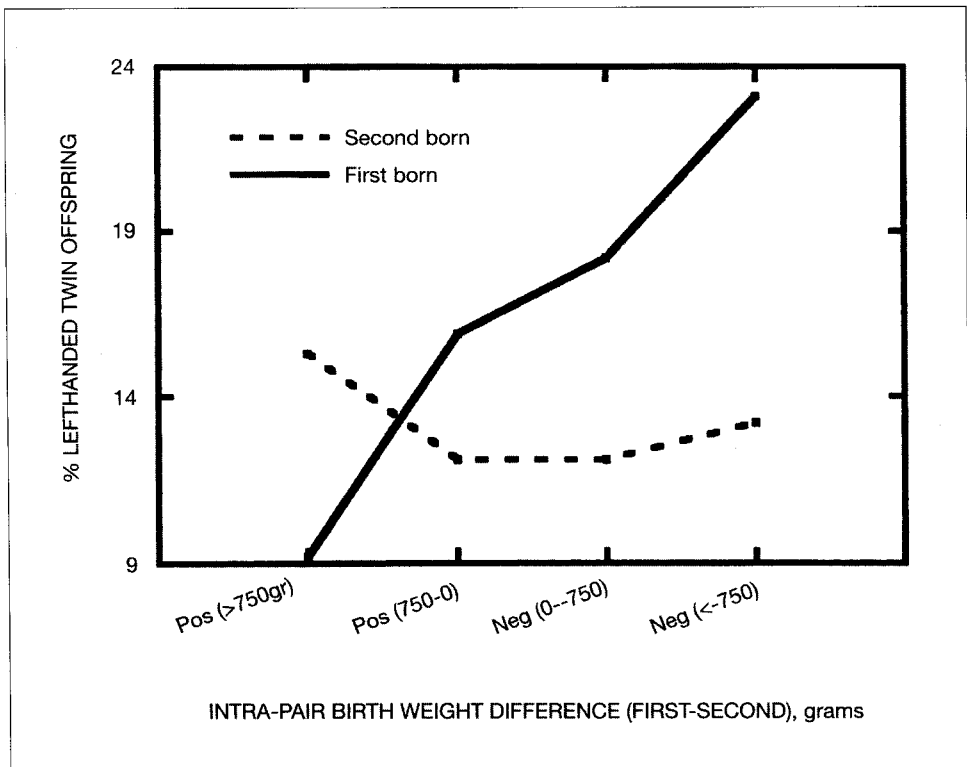

Fig. 2 – *Proportions of left-handed first born and second born twin offspring as a function of birth weight disparity within pairs.*

when their mother is LH relative to children from RR parents than when (only) father is LH. LH of fathers does not affect the probability of LH in their daughters at all but does so very likely in their sons. This is compatible with the significant MZmm intra-pair association relative to DZmm pairs and no such an association in MZff pairs relative to DZff pairs. In a meta analysis carried out by McManus and Bryden (1992) on 72.600 offspring from 25 set parent-child data, the LH-proportion of both sons and daughters increases from about 10% in children from RR parents to about 20% in children from R(father)L(mother) parents. LH prevalence among daughters however does not increase when father is LH too (thus in LL parents). Sons on the other hand seem to be (more) susceptible to become LH if their father is LH. This is in agreement with our own twin data set as presented in Table IV and Figure 1.

This makes it possible that LH is caused by exposure to some prenatal environmental condition (which itself can be genetically based) in the mother. The genes concerned are sometimes transferred to the offspring (sons and daughters) and sometimes not and could form the underlying basis for LH "running in families". In addition, the data suggest also a Y-chromosomal contribution because of the apparently stronger association between LH of fathers and LH of their sons compared to LH of their daughters. One option could be that the maternal gene codes for the production of some hormone (e.g. testosteron) and that the Y-chromosomal gene (may be SRY) – always transmitted but to sons only – codes (very likely via switching on an autosomal gene) for own (fetal) testosteron production. Under suboptimal intra-uterine conditions, leading to growth retardation and consequent low birth weight, and conditions of enhanced birth stress, the fetus is supposedly more vulnerable for such hormonal influences. And such conditions are of course more prevalent among twin pregnancies than among singleton pregnancies (Bleker, Breur and Huidekoper, 1979).

Such a speculative environmental solution is compatible with several aspects of our and others data.

For these reasons we think that the conclusion by Davis and Annett (1994) that the enhanced prevalence of left-handedness among twins, relative to singletons, can be considered as a *"robust and substantial empirical support for the RS theory of handedness"* (page 110), is disputable.

CONCLUSIONS

The enhanced left-handedness (LH) prevalence among first born twins relative to second born twins, is an indication for an environmental influence on the etiology of LH. Furthermore, the way parental handedness is associated with handedness of their (twin) offspring suggests a separate role for the mother, creating a (X)-chromosomal based (hormonal?) environmental for the fetus, and for the father, contributing to the (hormonal) genotype of his sons. This standpoint is in agreement with the significant enhanced handedness association in MZmm pairs compared to DZmm pairs and the absence of such a difference in handedness association between MZff and DZff pairs. These effects may be

amplified by reduced birth weight and by birth stress (as suggested by the birth order effect on LH).

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