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A translation of this paper into French is to appear in Le Bulletin de Pschologie de La Sorbonne, in an issue in honour of Professor Réne Zazzo.

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HANDEDNESS IN TWINS: The Right Shift Theory

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#### Summary

The right shift (RS) theory suggests that the main determinant of handedness in man, as in other mammals, is chance. The chances are biased toward right handedness in humans as a by-product of a single gene (rst) which gives some advantage to the left hemisphere for speech development; in the absence of the gene, brainedness and handedness depend on chance alone, and chances which are independent.

The origin of the theory and its implications for the relationship between laterality for speech and handedness are outlined. The parameters assumed for the genetic model are derived from the neuropsychological analysis, and shown to predict distributions of handedness in families. The interpretation of twin data leads to the hypothesis that the expression of the <u>rst</u> gene is reduced in twins compared with the singleborn, as it is also reduced in males compared with females. New findings are reported which support this hypothesis. An example of the application of the RS theory in predicting the distribution of handedness in MZ and DZ twin pairs, for incidences of left handedness close to those observed in the personal data of Zazzo (1960) are given in an appendix.

The right shift (RS) theory of handedness was born in a "Aha" experience in 1971, as a solution to a group of questions posed by my researches of the 1960s. The implications of that solution for several other questions about human laterality were not immediately obvious but have been explored in turn, including questions about the relationships between handedness and brainedness for speech, and questions about a genetic influence on human handedness. I am honoured by the invitation to contribute to this volume, and pleased to have the opportunity to outline the implications of the theory for handedness in twins. First, the RS theory must be briefly explained and its relevance to cerebral dominance and to genetic theories considered, before turning to twin laterality. To avoid excess citations, particular papers will be referred to only when necessary; except for some new data to be reported at the end, all the work mentioned is reviewed in Annett (1985).

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#### The Right Shift Theory

There were four main facts for which I was seeking an explanation  $\frac{1}{2}$  in the late 1960s.

1. The distribution of human hand preference.

When subjects were observed performing several actions or were asked about them by questionnaire and classified as consistent left-handers, mixed-handers and consistent right-handers, the proportions were about 4, 30, 66 percent, respectively, in several personal samples, and in others in the literature which could be classified according to my criteria. Consistent handers

performed no action with the other hand, and mixed-handers always had a definite preference for the other hand for at least one action ("either" responses alone were never counted as criteria of mixed handedness).

#### 2. Non-human Hand Freferences

The evidence available for handedness in other mammals, including primates, when individual animals could be classified as consistent left, mixed or consistent right suggested that the proportions are about 25, 50, 25 respectively. This was true, for example, of chimpanzees (Finch, 1941), monkeys (Warren, 1953) and mice (Collins, 1969).

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#### 3. The Distribution of Human Hand Skill

When schoolchildren and undergraduates were asked to try the skill of each hand in moving pegs as quickly as possible, and the differences between the means of 3-5 trials for each hand were plotted, the distribution was always found to be continuous, unimodal and approximating a normal curve.

# 4. The Association of Hand Preference and Hand Skill

When data for hand preference and for peg moving times were correlated in both undergraduate and school samples, it was evident: that there is a strong correlation between degrees of right and left hand preference and degrees of right and left hand skill. Apparent findings to the contrary in the literature seem to be due to taking subjects who are predominantly mixed handed and classifying them into discrete groups as "left" or "right" and then being surprised to find overlap between the groups, instead of recognising that both preference and skill are distributed continuously over a wide spectrum.

The puzzle of the relationship between hand preference and hand skill, and between the 4, 30, 66 percent in humans and 25, 50, 25 percent in other primates was resolved when these facts were represented as in Figure 1 (Annett, 1987 in press). The base line, or abscissa represents differences between the hands in skill. To the left are those with left hand superiority, to the right those with right hand superiority and in the centre, at : about 0, those who are equally skilled with each hand. The RS solution came when I used tables of the normal distribution function to discover what distance along the baseline would be needed to give the percentages of left and mixed handers found for non-human and human preference. Each L, M, and R, in Figure 1 🔅 represents 1 percent under the normal curve.

For non-humans, the threshold dividing consistent left from mixed handers must be at -0.67z, and that dividing mixed handers from consistent right handers at +0.67z, a difference of 1.34z. For humans, the locations of the corresponding thresholds is -1.75 and -0.41. The difference is also 1.34. That is, the distance along the X-axis of the normal distribution function required to represent mixed handers in humans and in other mammals is the same. The only feature which differs between the distributions required to represent hand preference in humans and ? in other primates and mammals studied for forelimb preferences, is that the human distribution has a mean to the right of O, whereas in other species the mean is at O.

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(It is important to note two points about laterality in nonhumans. First, strong hand preferences may be found in individual animals, even though there is no evident <u>species</u> bias to one side. Second, some birds or fish do show species biases which probably evolved independently of the human species bias. The important point for the RS theory is that the human asymmetry distribution could resemble that of other primates in all respects except that it is shifted to the right.)

The first main advantage which follows from looking at hand preference as dependent on a continuum of differences in hand skill is that the vexed question of the true incidence of left handedness becomes meaningless. The incidence depends on where the threshold is located along the X-axis; it may be drawn anywhere between the criterion of pure left handedness (giving an incidence of about 3 percent), to a criterion of any left hand preference in someone who is predominantly right handed (about 33 percent). This is the range of incidences found in a survey of the literature by Hecaen and Ajuriaguerra (1964).

A second related advantage is that the threshold can be thought of as movable to the left or the right depending not only on changes of criteria, but also on changes in socio-cultural pressures against sinistrality. When prejudices against use of the left hand are strong, those resisting the pressure to use the right hand are likely to be those whose L-R skill differences strongly favour the left hand, so the threshold would be further to the left (along the X axis of Figure 1). As pressures relax, the threshold would return toward the right, while the underlying distributions can be thought of as unchanged.

A third advantage is that one can dissociate two main

features of human handedness, first, the distribution of L-R differences (the normal curve) and second the location of the distribution along the X axis (the shift to the right). The first is probably shared with other species, in which there is no evidence of a genetic influence on paw preferences, while the second, which is unique to man, could be the source of the genetic influence detected in human samples. The first could be due to chance alone, like the toss of a coin, while the second could be a genetic constant, like a small bias to the coin.

#### Cerebral Dominance for Speech

In working out the implications of the above analysis for questions about human laterality, the greatest puzzle needing attention was that of the relationship between handedness and cerebral dominance. What would follow from the assumption that the right shift of the human handedness distribution is due to something which facilitates the development of speech in the left hemisphere? No matter how intelligent our primate cousins, they do not have Broca's areas, nor the vocal apparatus necessary for speech. Perhaps humans are biased toward right handedness as a by-product of a factor which gives some advantage to the left hemisphere for speech development.

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If this is so, the next question to arise is the origin of <u>right</u> hemisphere speech. Of course some might argue that all cases of right hemisphere speech are pathological in origin, but this seems unlikely since many cases were found in young men with war head injuries. The simplest suggestion, which must be adopted as a <u>null</u> hypothesis until disproved, is that some people lack the RS factor, and in such cases, handedness and arphi brainedness are due to chance alone. If some humans lack the RS factor, they would be distributed for handedness like the nonhumans in Figure 1.

The proportion of those with right hemisphere speech who are classified as left handed would depend, of course, where the threshold is drawn. For most human samples, using a fairly strict : criterion such as writing with the left hand, giving an incidence of about 10 percent, the threshold must be drawn to the 3 <u>left</u> of O. From this, it follows that among right brained speakers, on such a criterion, there would be more right handers than left handers. Examining the data for hand preference in dysphasics with unilateral cerebral lesions shows that among the German (Conrad, 1949) and British (Newcombe and Ratcliff, 1973) war wound series, this prediction was fulfilled. Among clinic samples, where there was presumably greater opportunity to question patients and their relatives about hand preferences, this was not true, but the incidences of left handedness reported 🖟 among dysphasics were very high. Hécaen and Ajuriaguerra's (1964) dyspashics included about 28 percent classified as left handed. In terms of Figure 1 this suggests that the threshold would need to be drawn very much further to the right. This is what would be expected if the interviewer were accepting any evidence of sinistral tendencies as sufficient for classification as a left hander, and hence it is not surprising that among clinical series, cases of dysphasia following right cerebral lesions are rarely classified as right handed (Gloning and Quatember, 1966; Hécaen and Ajuriaguerra, 1964). The question of

the relationship between cerebral dominance and handedness has been difficult to answer because differing criteria have cut off ...
differing regions of the asymmetry distribution.

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An interesting question for the RS theory is, what proportion of the total population has right hemisphere speech, irrespective of handedness? Zangwill (1967) identified 5 series in the literature which can be used to estimate incidences for the general population. The epileptic brains studied in Montreal (Rasmussen and Milner, 1975) cannot be used for this purpose since those studied by the Wada test were highly selected as well as abnormal. In these 5 series, the average proportion of dysphasics with unilateral lesion, in whom the lesion was right sided was 9.27 percent. The evidence is consistent between several series. For example, in the sample of Hecaen and Ajuriaquerra, the incidence of right sided lesions among dysphasics was 9.6 percent. Among cases suffering aphasia as an epileptic aura in the British war wound series, the proportion of right sided cases was 9.4 percent (Russell and Espir, 1961). Looking for a further check on the incidence of right hemisphere speech. I recently re-worked the data in the archives of the British War Wound series, including all cases, whether handedness were known or not, and found an incidence of 9.2 percent. The importance of these estimates will be evident in the next section.

#### The Genetic Hypothesis

Research on the genetics of handedness has led to two main findings. First, there seems to be no evidence of a genetic influence on the handedness of the mammals so far

studied, and second, in humans there does seem to be evidence for a consistent but small genetic influence. What would follow from the assumption that the genetic influence in man concerns the shift to the right only, while there is no genetic determination of the distribution itself? This would imply that handedness arises by chance, afresh in the growth of each individual (possibly through random accidents in the building of the two sides of the body) in all mammals, but that the chances in man are weighted by a factor which increases the probability of right handedness, like a bias to the toss of a coin as mentioned above.

It is important to be clear that the model is probabilistic and not deterministic for handedness. Left brainedness for speech could be determined by a gene which influences brain growth at some critical stage of development, and give an associated boost toward right handedness, which may not outweigh a strong chance bias to left handedness. Hence deterministic statements cannot be made about handedness, or about the relations between handedness and brainedness, only probabilistic ones.

From the incidence of right hemisphere speech estimated for the general population above (9.27 percent) it may be inferred that if speech determination arises by chance in those who lack the RS factor, some 18.54 percent of the population lack the factor. Since genes are carried in pairs, such an individual must be rs= (lacking the gene on both chromosomes); the square root of this proportion gives us the frequency of the rs= gene (0.43) and by subtraction, the frequency of the rs+ gene (0.57).

The other main feature of the model required to test the genetic hypothesis is the extent of shift of the human RS distribution, with respect to the unshifted proportion of the population. (The rs-- by definition have a mean at 0; the locations of the means of the <u>rst-</u> and the <u>rst+</u> distributions to the right of 0 must be known if the proportions of left and right [ handers within each genotype are to be inferred, for any threshold that might be drawn along the X-axis.) The extent of shift was estimated first from data for dysphasics with unilateral cerebral lesions and later from computer searches for the best fit to data for L-R peg moving time in my collected samples of undergraduates and schoolchildren.

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Predictions of the proportions of left handers in the families of 0, 1 or 2 left handed parents were first published (Annett, 1978) for the assumption of complete dominance and without attention to sex differences (rst- and rstt in both sexes & assumed to have a mean about 1.97z to the right of the mean of O for the <u>rs--</u>). The numbers of left handers in each family type could be predicted within reasonable limits for the data of Chamberlain (1928), Rife (1940) and for several personal samples. 📱 The samples differ, of course, for incidences of left handedness, \* and within all samples there are differences between generations. : The successful predictions depend on estimating the threshold for s each generation and sample from the actual incidences observed; the genotype distributions can then be worked out and the straightforward Mendelian predictions for combinations of rstt. rs+-, rs-- genotypes calculated. In samples where the calculations could be repeated at two levels of incidence (strict

and generous), good fits were found at both levels, giving .grounds for confidence that the underlying distributions must be similar to those postulated.

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Further calculations were made to allow for sex differences (Annett, 1979) and for absence of dominance (Annett, 1985). Tests 3 of peg moving performance, found females more biased to the right hand than males in all of my samples. Through a process of computer modelling of the assumptions of the model and testing for fit against empirical data for L-R peg moving, the best estimates of shift were put at 1.0z for <u>rs+-</u> and 2.0z for <u>rs++</u> in males (assuming absence of dominance) and 1.2z and 2.4z respectively in females. Using these estimates of shift for family handedness calculations then found excellent fits for all samples for which there was self-report in both generations (including that of Ashton, 1982, from the Hawaii population study which could be examined at two levels of criterion, McGee and Cozad,1980). Fits were less good in samples depending on student report of parental and sibling handedness, but the fits were greatly improved by the assumption that parental left handedness, especially in mothers, had been slightly underestimated.

#### Left handedness in twins

It is evident from the above that the genetic interpretation of the RS model is very powerful in accounting for handedness in families. How well can the model predict handedness in twin pairs? There is no difficulty, of course in accounting for differences between twins, even MZ ones, since the main determinants of handedness are expected to be chance. The

proportions of RR, RL and LL pairs should be predictable for any given incidence of left handedness, on the assumption that MZ twins are identical for the three genotypes, while DZ twins resemble each other like ordinary siblings. When these calculations were done, using the same assumptions for the parameters of the model as for family handedness, the observed distribution of handedness in twin pairs was significantly different from that predicted.

It was discovered that to account for handedness in twin pairs it must be assumed that twins are less shifted to the right than singletons. For the 1978 analyses, where the general shift had been taken to be about 1.9z, a shift of 1.0z was appropriate for twins. When all other assumptions of the model were retained, : but the shift reduced by nearly 50 percent, the predicted distribution of RR, RL and LL twin pairs agreed with that observed in all the data assembled by Zazzo (1960) for 1210 MZ pairs (chi square 0.0045) and for 1145 DZ pairs (chi square 0.1049). In later calculations based on absence of dominance and taking sex differences into account, twin data could be predicted at several levels of incidence, assuming a reduction of shift by 33 percent in twins compared with singletons (Annett, 1985). An example of the calculations required to predict assortment in twin pairs is given in Appendix 1, using slightly different assumptions about the difference between twins and singletons, and matching the incidences of left handedness to those found by Zazzo (1960) in personal data.

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Evidence for a smaller RS in twins

When it was found that a reduction in RS was necessary to account for handedness in twin pairs, it seemed , at first, an unwelcome complication of the model. Indeed, some have arqued that the RS model itself must be doubted if it cannot account for twin handedness without introducing an extra assumption (Boklage, 1981; McManus, 1980). However, I now regard this finding as one of the important discoveries of the RS model. The possibility that the <u>rs+</u> gene is less expressed in twins than singletons fits very well with the idea that the gene facilitates language development; one of the most consistent findings for twins is a delay in language growth. The difference between twins and singletons has a parallel in the difference between males and females since the latter are further shifted to the right than the former. Females also tend to be more mature at birth than males. These observations suggest the possibility that the expression of the <u>rs+</u> gene depends on factors related to rates of cerebral maturation in late fetal life when the growth of twins is normally slowed in comparison with that of singletons. Since MZ and DZ twins seem to require a similar reduction of shift to account for their handedness distributions, the lesser RS is likely to be related to factors associated with twin birth itself, and not associated with zygosity. Contrary to the view of McManus that the hypothesis of a lesser RS in twins than singletons is ad hoc, I would argue that this is just what should be predicted. How can this interpretation be independently tested?

If the expression of the  $\underline{rs+}$  gene is reduced in twins

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compared with singletons, the incidence of left handedness should be higher in twins than in singletons. This difference was not found by Zazzo (1960) nor is it evident in the literature (McManus, 1980). My handedness questionnaire included a question on twin birth, in case it should prove to be a relevant variable. For many years I believed that the evidence in favour of a higher incidence of left handedness in twins was inconclusive. Good evidence would require very large samples, in which handedness was assessed in the same way for twins and singleborn. Such evidence is now available in population surveys. A recent survey of the UK adult population for hearing difficulties included questions on twin birth and on handedness; about 3,000 people were sampled in 4 regions, Scotland, Wales, the south and midlands of England. Analyses by region, and by sex and age found higher incidences of left handedness in twins than singleborn in every comparison (Davis, personal communication).

New findings can now be reported for a survey of children in the UK. A National Child Development Study (NCDS) has been based on a cohort of all children born in the UK in one week in 1958, and followed up at 7, 11, and later years of age. Assessments of hand preference were made by questions to the mother at 7 and 11 years, and by observations of the hand used for throwing a ball of paper, recorded by the Doctor (medical practitioner) at 7 and 11 years. There are 5 items in the data archive relating to hand preference, and 10 possible comparisons when each sex is considered separately. For all of the 10 comparisons, the incidence of left handedness is higher in those of twin than

single birth. For example, in the observations of throwing at 11 years, the percentages were 11.0 in 6410 male and 8.0 in 6099 ... female singletons but 15.5 in 148 male and 9.6 in 135 female twins. It is evident that the differences are not large, and hence would be difficult to detect in smaller samples, but the consistency of the finding in so many sets of data puts its existence beyond reasonable doubt. (Subjects for this analysis were selected so as to minimize the possibility of pathological left—handedness, by excluding those whose times for manual dexterity tests differed by more than 2 s.d. from the mean for each hand, and also excluding all for whom the Doctor could not give a clear right or left handed classification at 11 years.)

A more direct test can be made of the hypothesis that twins are less shifted to the right than singletons by comparing the distributions of differences between the hands, for the dexterity tests used in the NCDS survey. At 11 years, the children were given two timed tests of hand movement by the Doctor, one of placing a pencil mark in as many squares as possible of squared paper, and the other of transferring match sticks from one match box to another. Each task was performed by each hand. When cases are selected as described above, and differences between hands calculated for twins and for singletons, the means for twins were found to be significantly smaller ( that is, less biased to the right hand) than those of singletons (F ratio= 6.72 with df 1:12466 for the square marking test and F ratio= 8.72 with df 1:12078 for the match sorting test, both with p < .01).

Table 1 shows the means and standard deviations of differences between hands for square marking for each sex

separately. This shows that females were more strongly biased to the right hand than males, and singletons more biased to the right than twins; as expected the largest difference between hands was for single born females and the smallest difference was for twin born males. Twin females and singleborn males resemble each other in extent of RS. This pattern of scores is as expected on the hypothesis of differences of expression of the <u>rs+</u> gene between the sexes and between twins and the singleborn, but a test of the hypothesis could not be made without findings for a very large sample such as NCDS.

These findings for twins represent the most recent of a series of stages in which the implications of the RS insight of 1971 continue to be worked out. They encourage further research to discover the gene responsible for the RS, and to analyse the processes of cerebral hemsiphere development through which the gene is expressed. The search must look for normal variations in the processes of brain growth, not abnormal ones, though of course it is not always possible to draw a clear line between the the normal and the pathological. Recent attempts to explain handedness and associated asymmetries in terms of abnormalities of fetal hormones (Geschwind and Galaburda 1985) would not predict, as far as I am aware, that female twins resemble male singletons for differences in hand skill. The RS theory suggests that an explanation will be found in terms of normal variation in patterns of brain growth, although the details of these patterns are not known at present.

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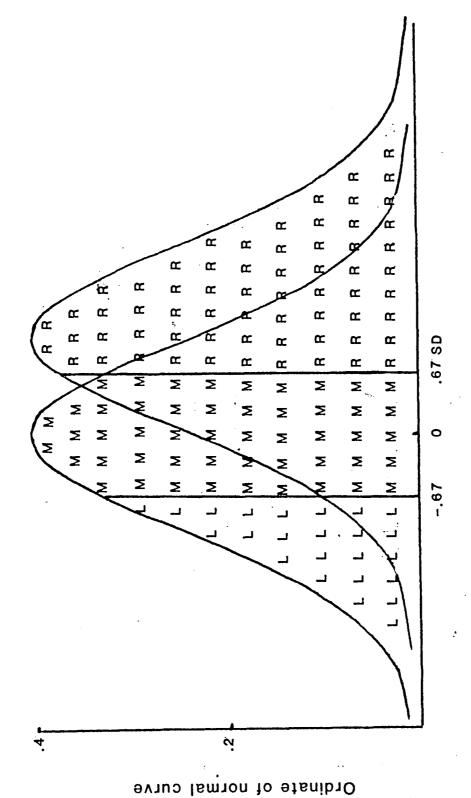
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Table 1 Difference between the hands in number of squares marked with a pencil in 1 minute: NCDS UK survey.

		Singletons	Twins
Male	<u>:</u> \$		
	N	6243	146
	Mean	18.4	14.7
	s.d.	20.7	21.9
Fems	ales		
	N	5948	131
	Mean	21.6	18 9
	s.d.	20.5	19.4



Left minus right hand time

 $\frac{\text{Appendix 1.}}{\text{in twin pairs}} \quad \text{An example of the application of the RS model to the calculation of handedness} \quad \text{$:} \quad$ 

# 1. Assumptions for singleborn (Threshold of sinistrality at -0.4z of the $\underline{rs--}$ distribution)

Extent of shift for  $\underline{rs+-}$  and  $\underline{rs++}$  genotypes are 1.0z nd 2.0z for males nd 1.2z and 2.4z for females respectively.

		Males			Females				
Genotype	Frequency in population	Threshold		on left-handed population	Threshold		on left-handed population		
5++	.3242	~2.4	.0082	.0027	-2.8	.0026	.0008		
5+-	.4904	-1.4	.0808	.0396	-1.6	.0548	.0269		
5	.1854	-0,4	÷3446	.0639	-0.4	.3446	.0639		
				.1062			.0916		

2. Assumptions for twins (Threshold of sinistrality at -0.4z of the <u>rs--</u> distribution) Extent of shift smaller for twins than singleborn by 0.25z and 0.5z for <u>rs+-</u> and <u>rs++</u> genotypes respectively - for both sexes and both MZ and DZ twins.

		Males			Females		
Genotype	Frequency in population	Threshold		on left-handed population			on left-handed population
rs++	.3242	-1.9	.0287	.0093	-2.3	.0107	.0035
rs+-	.4904	-1.15	.1251	.0613	-1.35	.0885	.0434
rs	.1854	-0.4	.3446	.0639	-0.4	.3446	.0639
				.1345			.1108

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# Appendix 1. (continued)

## 3. Predictions of MZ twins

<i>.</i>		Males			Females				
Genotypes	Frequency in population				•		•		•
rs++,rs++	.3242	.0287	.3059	.0181	.0003	.0107	.3713	.0069	.00004
rst-,rst-	.4904	.1251	.3754	.1094	.0077	.0885	.4074	.0791	.00384
rs,rs	. 1854	.3446	.0796	.0837	.0220	.3446	.0796	.0837	.02202
			.7609	.2112	.0300		.8043	.1697	.02590
Zazzo (196	50)	130 pairs				129 pairs			
		expected no	98.9	27.5	3.9	expected no	103.7	21.9	3,3
		observed no	95	31	4	observed no	104	20	5
		chi square	.155	.457	.003=0.6	15	.001	.163	.824=0.9

# 4. Predictions of DZ twins: (as above but for each of the 9 possible genotype pairings)

	Males			Females				
		RR	RL	LL		RR	RL	LL
Predicted proportions		.7550	.2213	.0237		.7972	.1839	.0185
Zazzo (1960)	91 pairs: expected no observed no				82 pairs: expected no observed no			
	chi square	.158	.064	2.161=2.	383	.002	.000	.151=.15

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### NATIONAL CHILD DEVELOPMENT STUDY

The National Child Development Study (NCDS) is a continuing longitudinal study which is seeking to follow the lives of all those living in Great Britain who were born between 3 and 9 March, 1958.

It has its origins in the Perinatal Mortality Survey (PMS). This was sponsored by the National Birthday Trust Fund and designed to examine the social and obstetric factors associated with the early death or abnormality among the 17,000 children born in England, Scotland and Wales in that one week.

To date there have been four attempts to trace all members of the birth cohort in order to monitor their physical, educational and social development. These were carried out by the National Children's Bureau in 1965 (when they were aged 7), in 1969 (when they were aged 11), in 1974 (when they were aged 16) and in 1981 (when they were aged 23). In addition, in 1978, details of public examination entry and performance were obtained from the schools, sixth-form colleges and FE colleges.

For the birth survey information was obtained from the mother and from medical records by the midwife. For the purposes of the first three NCDS surveys, information was obtained from parents (who were interviewed by health visitors), head teachers and class teachers (who completed questionnaires), the schools health service (who carried out medical examinations) and the subjects themselves (who completed tests of ability and, latterly, questionnaires). In addition the birth cohort was augmented by including immigrants born in the relevant week in the target sample for NCDS1-3.

The 1981 survey differs in that information was obtained from the subject (who was interviewed by a professional survey research interviewer) and from the 1971 and 1981 Censuses (from which variables describing area of residence were taken). Similarly, during the collection of exam data in 1978 information was obtained (by post) only from the schools attended at the time of the third follow-up in 1974 (and from sixth-form and FE colleges, when these were identified by schools). On these last two occasions case no attempt was made to include new immigrants in the survey.

All NCDS data from the surveys identified above are held by the ESRC Data Archive at the University of Essex and are available for secondary analysis by researchers in universities and elsewhere. The Archive also holds a number of NCDS-related files (for example, of data collected in the course of a special study of handicapped school-leavers, at age 18; and the data from the 5% feasibility study, conducted at age 20, which preceded the 1981 follow-up), which are similarly available for secondary analysis.

Further details about the National Child Development Study can be obtained from the NCDS User Support Group.

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