Genetic and Environmental Influences on the Handedness and Footedness in Japanese Twin Children

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The purpose of this study was to examine the genetic contribution to handedness and footedness in childhood using one of the largest available databases of Japanese twins. The participants were 1131 twin pairs, 1057 males and 1205 females, of 11 or 12 years of age (6th grade of secondary school in the Japanese education system). All data were gathered by questionnaire. The prevalence of left (nonright) handedness was 15% in males and 13% in females. The prevalence of left (nonright) footedness was 13% in males and 11% in females. The similarities between twin pairs, estimated by concordance rates and tetrachoric correlations, suggested a slight genetic effect on male handedness, no genetic effect on female handedness, and no genetic effect on footedness in either sex. Structural equation modeling showed small genetic factors (11%) in male handedness and no genetic factors in female handedness. As to footedness, no genetic factors were observed in either sex. The effects of nonshared environmental factors were large (85%) in males and moderate (44%) in females. Moreover, handedness and footedness tended to be concordant irrespective of sex, with polychoric correlations over r = .70. The results of bivariate genetic analyses were not necessarily satisfactory. For males, no model fit. For females, shared and nonshared environmental factors explained the concordance of handedness and footedness. It was concluded that the genetic effects on handedness and footedness are relatively small, as is their association; moreover, considerably large twin samples are needed to obtain stable and appropriate results.

Although numerous studies have been performed, the determinants of human handedness remain unknown. Theories concerning the causes of right- or left-hand performance in humans vary from purely learned behavior to solely genetics, to a combination of the two (Klar, 2003). The hypothesis that handedness is genetically determined has received mixed support (Medland et al., 2003). Twin studies have been used as one of the most powerful tools to analyze the genetic background of handedness, beginning as early as the 1920s (Sicotte et al., 1999). Classic twin studies, most of which compared concordance rates of left-handedness between monozygotic (MZ) and dizygotic (DZ) twin pairs, have shown that zygosity differences in concordance rates are relatively small. These results may suggest the environmental origin of handedness.

Recently, to reduce random error and sampling bias or increase statistical power, several twin studies using large population-based twin registries (Derom et al., 1996; Medland et al., 2003; Neale, 1988; Orlebeke et al., 1996; Tambs et al., 1987), summaries of a number of studies (McManus, 1985; McManus & Bryden, 1992) or meta-analysis (Sicotte et al., 1999) have been performed. Of them, Neale (1988) analyzed self-reported handedness in 1687 twin pairs aged from 8 to 80 and yielded low estimates for both heritability (~ 20%) and the effects of shared environment (~ 7%). McManus and Bryden's (1992) analysis of 14 studies on twins, including 5489 pairs in total, showed that the proportion of MZ pairs with discordant handedness in the 14 studies was very similar to that in the DZ pairs (21.7% vs. 22.6%). However, considering the proportion of left-handedness between MZ and DZ twins in each study, they concluded that there is a small genetic contribution to handedness. Orlebeke et al. (1996) assessed handedness in 1663 twin pairs and their parents. Their analysis showed a smaller proportion of MZ pairs than DZ pairs with discordant handedness (19.6% vs. 24.5%). Nevertheless, they finally concluded that the environmental explanation is more likely by considering birth order within twins, parental handedness, and sex difference. The meta-analysis of 28 twin studies performed by Sicotte et al. (1999) showed that the proportion of MZ pairs with discordant handedness was significantly lower than in DZ pairs, while the frequency of left-handedness in MZ versus DZ twins yielded no difference. The authors concluded that these results provide strong

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evidence in favor of genetic mechanisms underlying variations in human handedness. Medland et al. (2003) analyzed the largest twin sample to date, consisting of four different studies (7419 pairs in total), and showed that shared environmental factors explained 12% of the variance in the writing hand with nonshared environmental factors explaining the remaining 88% variance, while additive genetic influences explained 27% of the variance in the throwing hand with nonshared environmental factors explaining the remaining 73% variance. This result suggested different genetic contributions to different measures of handedness and the importance of researchers' definition of handedness.

In short, this overview of literature shows that the results of twin studies have been quite controversial. Thus, one might wish to investigate the genetics of laterality with the goal of understanding the biological mechanisms that lead to the preferential use of one hand. Moreover, one may also see links between human handedness and footedness. Contrary to handedness, only a few genetic studies (Coren & Porac, 1980; Reiss et al., 1999) have been performed on footedness. No large-scale twin study exists.

One aim of this study was to describe the basic statistics of handedness and footedness in Oriental twins from a cross-cultural perspective, as almost all twin studies have used Caucasian samples. Another aim was to estimate the roles of genetic and environmental influences on the origins of human handedness, footedness, and the association of both traits using one of the largest twin databases available in Japan.

Materials and Methods

Outline of the Present Samples

The participants were a total of 1131 twin pairs, consisting of 1057 males and 1205 females in the sixth grade of primary school, all of whom were applicants to the secondary education school (attached to the faculty of education at the University of Tokyo) from 1981 through 2004 (birth year ranged from 1968 to 1992). At the time the data were collected, most of the twins were 12 years old (Ooki & Asaka, 2005).

Zygosity Classification

The zygosity of the twins was determined primarily by a standard questionnaire (Ooki & Asaka, 2004), which was completed by the mothers. The zygosity of 224 pairs who were actually admitted to the school was determined by DNA/genetic markers as part of entrance procedure to the school, prior to being determined by questionnaire. The zygosity testing included ABO, CcDEe, MNSs, Haptoglobin, Acid phosphatase, Glutamate pyruvate transaminase, Estrase D, HLA-DR, DNA polymorphisms (e.g., beta-globin gene cluster haplotype, Dopamine receptor gene DRD4, Serotonine receptor gene 5-HTT, and mtDNA 9bp deletion), and related tests by blood sample, and DNase2 by urea sample (Ooki, 2005). The pairs were classified as follows: 775 MZ, consisting of 344 male–male and 431 female–female pairs; 321 DZ, consisting of 102 male–male, 92 female–female, 70 male–female and 57 female–male pairs; and 35 of unclassified zygosity (UZ), consisting of 19 male–male and 16 female–female pairs.

Data Collection

Data were collected through hand-delivered questionnaires. Questions were on family structure; obstetric findings on the mothers; the twins' physical growth, motor, language and mental development; the twins' and parents' medical histories; habitual behaviors; and any behavioral problems the twins had had.

Of these questions, items regarding handedness and footedness were analyzed. Handedness was assessed by the question, 'Which hand would your twin children predominantly use to write a letter now?' Footedness was assessed by the question, 'Which foot would your twin children predominantly use to kick a ball now?' Mothers identified the direction of handedness or footedness from three categories: *right*, *either* or *left*. Even if a mother was unable to answer properly, the twin children would be able to answer easily, as they were living together.

As to handedness, the question, 'Have your twin children attempted to change the hands they mainly use?' was also asked. The mothers chose from two categories, *yes* or *no*. This question was associated with permanent changing of hand preference, rather than a temporary change of the hand. Most twin studies published so far have not included the problem of compulsive hand preference changing. Participants who were 'now right-handers who have attempted to change their hand preference compulsively' were treated as left-handers. As these questions were asked to collect data on the total growth and development of twins, not specifically for the study of laterality, strict criteria regarding the definition of handedness and footedness were not used.

Statistical Methods

The prevalence of handedness and footedness was calculated according to sex, including those of unclassified zygosity. Sex difference was tested by the χ^2 test. Next, genetic analysis was performed using MZ and DZ pairs with both twins' complete data on frequency. Twin similarity for ordinal data can be estimated using a concordance rate (McGue, 1992). In the following genetic analyses, the answers were summarized in the form of 2×2 contingency tables ('either' was treated as 'left' according to many other twin studies). The probandwise concordance rate was the proportion of all probands (left-handedness/footedness) that belonged to left-handed/footed concordant pairs. Pairwise concordance rates were the proportion of all left-handed/footed concordant pairs in all pairs with at least one member of each pair being left-handed/left-footed. Probandwise concordance rates were calculated as $2 \times \text{Conc}/(2 \times \text{Conc} + \text{Disconc})$ and pairwise concordance rates were calculated as $\text{Conc}/(\text{Conc} + \text{Disconc})$, assuming complete ascertainment, where Conc

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denotes the numbers of affected concordant pairs and Disconc denotes the numbers of discordant pairs (McGue, 1992).

Moreover, the polygenic multifactorial model, assuming a latent variable called *liability to the trait* is used. The correlation of liability is obtained as polychoric correlation (Neale & Cardon, 1992). The correlation of latent liability was calculated directly from the 2 × 2 table cross-classifying the sidedness of the first and second twin in each twin pair. Phenotypic correlations between handedness and footedness in the same individual according to sex were also calculated as tetrachoric correlations.

Structural equation modeling techniques were used to estimate the variance components and to compare different genetic models by carrying out standard univariate twin analysis. These models postulated four sources of variance in liability to the traits: additive genetic factor (A), nonadditive genetic factor (D), shared or common environmental factor (C) or nonshared or individual-specific environmental factor (E). The proportion of the total variance in liability due to additive and nonadditive genetic factors and shared and nonshared environmental factors were termed a^2, d^2, c^2 and e^2, respectively, where a, d, c, and e denote each path coefficient from latent variables (A, D, C, E) to observed variables. It is possible to fit models based on the different combinations of these four parameters. The best fitting model was chosen using the information criteria of Akaike (AIC; Akaike, 1987), the chi-square value minus twice the degree of freedom. The model with the lowest value of AIC reflects the best balance of goodness-of-fit and parsimony. Bivariate genetic analyses using Cholesky decomposition method were also performed.

Basic statistics were computed using PC SAS version 8.02 (1999). Structural equation modeling was performed by the LISREL8 (Jöreskog & Sorbom, 1993) and Mx (Neale, 2000) software package.

Ethical Issues

Informed consent concerning the statistical analysis of the data was obtained from each twin and his or her parents in writing as part of the application process.

Results

Prevalence of Handedness and Footedness

The prevalence and number of participants in each frequency category for the occurrence of handedness and footedness are given in Table 1.

No sex difference was observed as to left-handedness, whereas left-footedness was more common in males than in females.

Handedness and footedness were not significantly related to zygosity irrespective of sex (handedness, $\chi^2 = 1.52$, $p = .47$; footedness, $\chi^2 = 1.02$, $p = .60$).

Concordance in Twin Pairs

Table 2 shows pairwise and probandwise concordance rates.

Table 1

Prevalence Rates of Handedness and Footedness According to Sex

			Males	Females	*p*
	N		1057	1205	
Handedness	Right	unchanged	854 (85.3%)	1007 (86.9%)	
		changed[a]	34 (3.4%)	31 (2.7%)	
	Either		29 (2.9%)	37 (3.2%)	
	Left		84 (8.4%)	84 (7.2%)	*ns*
	Missing value		56	46	
Footedness	Right		821 (86.8%)	966 (89.2%)	
	Either		29 (3.1%)	48 (4.4%)	
	Left		96 (10.1%)	69 (6.4%)	.0029
	Missing value		111	122	

Note: a = Participants who were 'right-handers at data collection who have attempted to change their hand preference compulsively'. They were treated as left-handers in the following genetic analyses.
Sex difference was tested by χ^2 test.

The concordance rates of left-handedness were higher in MZ pairs compared to DZ pairs. The concordance rates of left-footedness were higher in DZ pairs compared to MZ pairs, suggesting large environmental effect on this trait.

Tetrachoric correlations are also shown in Table 2. The handedness correlations were slightly higher in MZ pairs than in DZ pairs, suggesting that the genetic factors, if they exist, are small. The correlation of DZ male pairs was negative. This is because of the relatively low of right-handed concordant pairs and higher percentage of discordant pairs compared to other groups according to sex and zygosity combination.

Association between handedness and footedness in the same individual is also shown in Table 2. Tetrachoric correlations showed relatively high value, suggesting strong association between handedness and footedness. If correlations were calculated according to sex irrespective of zygosity, the value was .71 ($n = 946$) for males, and .76 ($n = 1083$) for females.

Models of Genetic and Environmental Factors

The results of the genetic analyses are summarized in Table 3.

The fit of the models were relatively good. With handedness, a small genetic factor (11%) and large nonshared environmental factor (89%) was observed in males, whereas no genetic factor was observed in females. With footedness, no genetic contribution was detected in both males and females. The effect of a nonshared environmental factor was large in males (85%) and moderate (44%) in females.

Then, bivariate genetic analysis was performed according to sex. As only one left-handed and left-footed cross-concordant pair (Twin 1 is left-handed and Twin 2 is left-footed, or the opposite) existed among DZ males, one of the cross-correlations was not calculated. Therefore, model fitting was not performed for males, and performed only for females (MZ = 387 pairs and DZ = 84 pairs). Phenotypic correlations of handedness

Table 2

Concordance Rates and Polychoric Correlations of Handedness and Footedness According to Zygosity and Sex Combinations

		MZ			DZ			
		MM	FF	Total	MM	FF	Total (same-sex)	FM
	N (total pairs)	344	431	775	102	92	194	127
Handedness	Discordant	.22 (72/322)	.20 (84/412)	.21 (156/734)	.29 (28/97)	.20 (18/89)	.25 (46/186)	.22 (27/125)
	Pairwise concordance rate	.10 (8/80)	.16 (16/100)	.13 (24/180)	.07 (2/30)	.14 (3/21)	.10 (5/51)	.07 (2/29)
	Probandwise concordance rate	.18 (16/88)	.28 (32/116)	.24 (48/204)	.13 (4/32)	.25 (6/24)	.18 (10/56)	.13 (4/31)
	Polychoric *r*	.13	.32	.24	–.09	.29	.10	.02
	N (pairs with missing data for both twins)	22	19	41	5	3	8	2
	N (pairs with missing data for one twin)	0	0	0	0	0	0	0
Footedness	Discordant	.21 (63/306)	.14 (54/387)	.17 (117/693)	.22 (20/92)	.14 (12/84)	.18 (32/176)	.15 (17/113)
	Pairwise concordance rate	.09 (6/69)	.22 (15/69)	.15 (21/138)	.17 (4/24)	.29 (5/17)	.22 (9/41)	.11 (2/19)
	Probandwise concordance rate	.16 (12/75)	.36 (30/84)	.26 (42/159)	.29 (8/28)	.45 (10/22)	.36 (18/50)	.19 (4/21)
	Polychoric *r*	.11	.54	.36	.32	.66	.49	.27
	N (pairs with missing data for both twins)	36	43	79	10	7	17	13
	N (pairs with missing data for one twin)	2	1	3	0	1	1	1
Phenotypic correlations between handedness and footedness in the same individual[a]	*N* (pairs with complete data)	306	387	693	92	84	176	113
	Twin 1	.83	.73	.78	.35	.85	.62	.70
	Twin 2	.81	.75	.77	.29	.85	.60	.58

Note: MZ = monozygotic; DZ = dizygotic; MM = male–male; FF = female–female; FM = female–male.
a = phenotypic correlations between handedness and footedness were calculated as tetrachoric correlations.

Table 3
Results of Model Fitting

	AIC	*p*	Path coefficients						Variance component (%) with 95% confidence intervals					
			a_m	c_m	e_m	a_f	c_f	e_f	A_m	C_m	E_m	A_f	C_f	E_f
Handedness	–3.70	*ns*	.33		.94		.56	.83	11 (0–21)		89 (79–100)		31 (24–39)	69 (61–76)
Footedness	.70	*ns*		.39	.92		.75	.66		15 (4–23)	85 (77–93)		56 (41–61)	44 (39–50)

Note: MZ = monozygotic; DZ = dizygotic; *ns* = nonsignificant; m = male, f = female.

and footedness in the same individual were very high, irrespective of zygosity and birth order. MZ pairs showed nearly the same correlations as DZ pairs regarding handedness, whereas MZ pairs showed lower correlations than DZ pairs regarding footedness. Cross-correlations between handedness and footedness of MZ pairs were nearly the same as those of DZ pairs. The fitting of the model was not satisfactory. The path coefficients of the best fitting model (CE model, AIC = 54) are shown in Figure 1 as reference. The phenotypic correlation between handedness and footedness was explained by shared and nonshared environmental factors, especially the former.

Discussion

It is very difficult to obtain accurate population prevalence of handedness or footedness in children. Prevalence of these traits depends on the sample size, the age of participants at data collection, methods of measurement, and so on. No sex difference in handedness was observed among the present participants, contrary to many reports. On the other hand, a significant sex difference was observed in footedness. The prevalence of left-handedness in the present sample was at least 8.0% in males and 7.0% in females, as shown in Table 1. In the present study, left-handed children were those who use either hand, or who now use the right hand but have experienced compulsive changes in hand preference. The prevalence of left-handers therefore rose to 15% in males and 13% in females. This percentage is surely higher than expected in singletons or other Asian countries, such as in a recent study of Korean college students (Kang & Harris, 2000). According to Hatta and Kawakami (1994), the prevalence of nonright-handers among male and female Japanese students (mainly college students) was 13% and 8% in 1993, respectively, and the prevalence of left-handers has been gradually increasing. Cultural pressure to use the right hand has not been so strict in Japan recently, especially in urban areas. Part of the high prevalence of left-handedness in the present participants may be related to the fact that they all live in the center of Tokyo, where cultural pressure to use the right hand may be relatively low.

The results of the three large-scale twin studies published to date are summarized in Table 4. Compared to other studies, the prevalence of left-handedness ('left' and 'either') in the present sample was by no means higher, though the percentage of discordant male pairs of DZ was considerably higher.

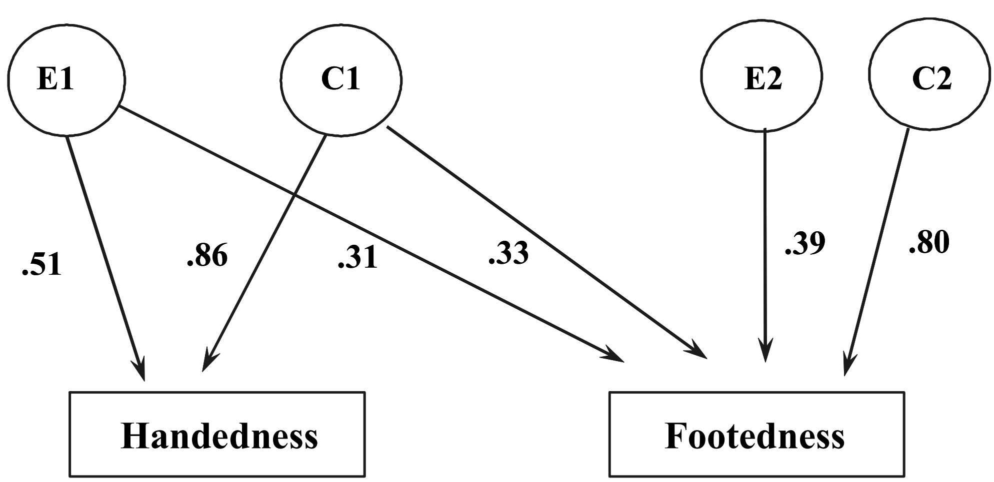

Figure 1
Path coefficient of best fitting Bivariate Cholesky Decomposition Model for females. C = shared environmental factor; E = nonshared environmental factor. The proportions of the total variance in liability due to sharedenvironmentaland nonshared environmental factors were calculated by squaring each path coefficient from latent variables (C and E) to observed variables.

Table 4

Summaries of Twin Studies on Handedness using Large Sample Size Containing over 1000 Pairs

	Age	Method used to determine		Left-handedness[a]	Observed frequencies					Genetic analysis			
					MZMM	MZFF	DZMM	DZFF	DZOS		A	C	E
Neale (1988) $N = 1687$	8–80 years	Self-report	Are you right- or left-handed?	Prevalence (%)	13.2	11.7	16.7	12.7	14.8	(Male)	20	7	73
				Discordant pairs (%)	20.8	17.9	20.6	21.0	24.1	(Female)	20	6	74
				L–L pairs (%)	2.8	2.7	3.7	2.3	2.8				
Orlebeke et al. (1996) $N = 1663$	12–22 years	Self-report	Do you consider yourself predominantly right-handed or predominantly left-handed?	Prevalence (%)	15.1	12.9	13.5	12.8	15.9	No detailed genetic analysis was performed.			
				Discordant pairs (%)	19.0	20.1	23.7	22.4	26.3				
				L–L pairs (%)	5.6	2.8	1.6	1.6	2.7				
Medland et al. (2003) $N = 7419$	Wide range[b]	Self-report	Which hand would you use to write a letter/throw a ball?	Prevalence (%)	12.4	13.8	12.2	13.7	12.6	Writing		12	88
				Discordant pairs (%)	20.1	22.4	19.6	23.0	20.1	Throwing	27		73
				L–L pairs (%)	2.0	2.9	2.6	2.2	2.2				
Present study $N = 1131$	11–12 years	Maternal report	Which hand would your twin children predominantly use?	Prevalence (%)	13.7	14.1	16.5	13.5	12.4	(Male)	11		89
				Discordant pairs (%)	22.4	20.4	28.9	20.2	21.6	(Female)		31	69
				L–L pairs (%)	2.5	3.9	2.1	3.4	1.6				

Note: a = ambidextrous participants are assigned as left-handers.
b = age was defined as years of birth rather than age at data collection.
MZ = monozygotic; DZ = dizygotic; MM = male–male; FF = female–female; OS = opposite-sex; L–L pairs (%) = % of left-handed concordant twin pairs.

The author selected a broad definition of left-handedness for three reasons. First, the prevalence of left-handedness itself, the percentage of discordant pairs, and the percentage of left-handed concordant pairs did not differ significantly from those obtained from the three large reliable twin studies mentioned above. Second, the effect of the difference in the definition of handedness was random within certain twin pairs, irrespective of sex and zygosity. In other words, the difference in the definition was assumed to have no systematic influence on the discordance rates in favor of a particular sex or zygosity. It is not likely that DZ male pairs, for example, became more discordant by the definition of left-handedness. Third, it is desirable to calculate all five correlations among the zygosity and sex combinations in order to perform structural equation modeling properly; this was one of the main aims of the present study.

This technique may have unexpected problems, therefore all analyses were performed using another definition of handedness: participants who switched to right-handedness were treated as right-handers or omitted from the analyses. The results showed nearly the same tendencies in the concordance rates and tetrachoric correlations, irrespective of which handedness definition was used. The largest and most definitive difference in the results according to the definitions was that if left-handedness was defined strictly, no left-handed concordant pairs existed among the DZ male pairs, and therefore a tetrachoric correlation was not calculated. As a result, structural equation modeling was not properly performed.

The sample size of the present study was not small compared to the many previous twin studies. Nevertheless, the concordance rates and polychoric correlations appeared complicated. No genetic contribution was detected for footedness. A small genetic effect was detected for handedness in males. Overall, the contribution of genetic factors to handedness and footedness was small, whereas environmental effects, especially that of nonshared environmental effects, were large.

Little genetic contribution and large nonshared environmental contribution to handedness has been the consistent result of reliable twin studies. The ability to show that a genetic effect is important depends on many factors. These include (a) the actual size of the genetic effect in the population, (b) the actual size of the sample chosen for study and (c) the level of measurement used — categorical, ordinal, or continuous, and so on. All of these considerations are essential as to the question of power (Neale & Cardon, 1992). Since most twin studies, including the present one, use binary data, many more pairs are required to get the same information compared to when using a continuous variable. Clear genetic effects are unlikely to be detected as long as binary data is used for twin study design. A quantitative continuous measure of the degree of handedness through a detailed questionnaire would be one method of avoiding the loss of statistic power in detecting genetic effect.

To date, many twin studies have ignored the sex difference of similarity because of very small sample size, or because opposite-sex DZ pairs are not included. By including information from opposite-sex DZ pairs, the present results suggest the importance of the sex difference of similarity as to both handedness and footedness. Even if concordance rates were calculated by pooling over sex, opposite-sex DZ pairs should not be included if sex limitation is found. Moreover, as the difference in concordance rates of handedness between MZ and DZ pairs was in itself not so large, classic twin studies using concordance rates yielded inconsistent results as to the contribution of genetic factors (McManus & Bryden, 1992; Orlebeke et al., 1996). In addition, this is one of the reasons for the general underpowering of twin studies of handedness.

The direction of handedness and footedness is often concordant. High polychoric correlations over .70 were observed irrespective of sex. Twin studies focusing on footedness have been very limited, and the sample sizes have been small. Reiss et al. (1999) examined the laterality of hands, feet, eyes and ears in twins. They observed statistically significant correlations between foot preference and hand preference/dominance, irrespective of zygosity. They found no differences in prevalence and concordance between MZ and DZ twins for any of the lateralities. A bivariate genetic study of handedness and footedness has never been performed.

Present bivariate genetic models could not necessarily explain the high correlations between handedness and footedness. A bivariate CE model was selected as the best fitting model for females, though the fit was far from satisfactory. Only shared and nonshared environmental effects contributed to the association of handedness and footedness.

The limitations of this study are as follows. First, the prevalence was calculated only by simple questions, not by a systematic questionnaire or observation. Second, unexpected biases may exist based on the definition of left-handedness itself. Third, the participants may have been too young to achieve the highest possible accuracy. Since handedness in children varies greatly with age, it is desirable to increase the accuracy of information on the age at which changes in handedness or footedness occur, as well as on the duration of those changes. On the other hand, there is an evidence that right–left hand skill asymmetry is constant with age, although actual times for hand skill (e.g., peg moving time) differ with age (Annett, 2002). The present results should be interpreted as average genetic or environmental influences in 11- or 12-year-old children.

In spite of these limitations, it was suggested that the etiology of handedness and footedness or their association was in the most part attributable to nongenetic factors. However, to obtain stable results from a standard twin study method of structural equation modeling, considerably large sample size is needed. This makes twin studies of handedness difficult. Although the twin study may be seen in isolation as rejecting the influence of genetic factors on lateralization, it must be recognized that genetic models incorporating a chance factor (Annett, 1985; McManus, 1985) or cultural processes (Laland et al., 1995) also predict low concordance rates and little zygosity difference in twin data.

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