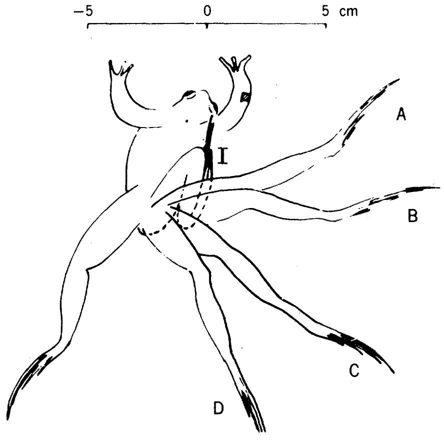

Fig. 3. An intermediate (*I*) and four final postures (A to D) of the hindlimb during the WR in the frog shown in Fig. 2. Not all final postures are displayed. If the forelimb is placed in the forward position, the ultimate position of the hindlimb is at A or B; otherwise postures C or D are taken.

be achieved if flexor and extensor motor neurons are activated not only reciprocally but also simultaneously, as occurs during human elbow movements (*15*). The WR directed to the trunk skin remains effective after deafferentation of the hindlimb (*1*, *4*). The central coactivation of the antagonistic motor neurons is likely to guarantee sufficient stiffness of the movement in this case as well.

Because the frog's hindlimb takes an invariant intermediate posture, at the next decisive stage, the movement no longer depends on the initial position of the leg; motor exactness is thus considerably increased. This mechanism is necessary because there is no time to correct the movement at the final stage: the transition from the intermediate posture to the final one takes 30 to 60 msec in some cases, so that the motor program is likely to be modified only during the preparation for the next wiping. The turtle is another animal that has some mechanism to diminish the dependence of the WR on initial conditions (*16*).

In both theoretical and experimental papers (*15*, *17–19*) the nervous system has been hypothesized to control a movement first by static characteristics of muscles (muscle torque, joint angle). An intersection of the flexor and extensor characteristics defines an equilibrium point of the joint. The central program determines a shift of the equilibrium point, and, as a result, the forced movement to a new equilibrium posture arises. The analysis of the WR shows the equilibrium postures. The choice of the intermediate equilibrium postures depends on the part of the body stimulated (limb or trunk). The choice of the final postures depends on the exact location of the stimulus in space. It is not yet clear whether the velocity of the transition from one equilibrium state of the system to the other may be controlled independently.

In warm-blooded animals such as cats and dogs, during the flexor phase of the scratch reflex (*20*, *21*) the limb occupies a position corresponding to the intermediate one in the frog. During the short extensor phase of scratching, the limb is likely to approximate an equilibrium state corresponding to the final extensor posture in the frog; in warm-blooded animals, however, this state is not achieved, because the central command soon returns the system to the intermediate posture. Thus we hypothesize that the mechanisms of the WR and of the scratch reflex are similar.

OLGA I. FUKSON

Belozersky Interfaculty Laboratory, Moscow State University, Moscow 117234, U.S.S.R.

MICHAEL B. BERKINBLIT

ANATOLY G. FELDMAN

Institute of Problems of Information Transmission, Academy of Sciences, Moscow

References and Notes

1. A. Bickel, *Pflüger's Arch.* **67**, 299 (1897).
2. G. Paton, *Edinburgh Med. Surg. J.* **65**, 251 (1846).
3. E. Pflüger, *Die sensorischen Functionen des Rückenmarkes bei Wirbeltieren* (Berlin, 1853).
4. M. F. Chepelugina, thesis, Moscow Institute of Physiology (1949).
5. A. Huges and M. C. Prestige, *J. Zool.* **152**, 347 (1967).
6. R. E. Baker, M. A. Corner, W. A. M. Veltman, *J. Physiol. (London)* **284**, 181 (1978).
7. M. Holliday and L. Mendell, *J. Comp. Neurol.* **162**, 205 (1975).
8. M. Jacobson and R. E. Baker, *ibid.* **137**, 121 (1969).
9. N. Miner, *ibid.* **105**, 161 (1965).
10. Z. Afelt, *Acta Neurobiol. Exp.* **36**, 593 (1976).
11. L. Franzisket, *Anim. Behav.* **1**, 318 (1963).
12. H. Forssberg, S. Grillner, A. Sjöström, *Acta Physiol. Scand.* **92**, 114 (1974).
13. K. G. Pearson and J. Duysens, *Neural Control of Locomotion*, R. M. Herman, S. Grillner, P. Stein, D. Stuart, Eds. (Plenum, New York, 1976), p. 519.
14. H. Forssberg, S. Grillner, S. Rossignol, *Brain Res.* **85**, 103 (1975).
15. A. G. Feldman, *Central and Reflex Mechanisms in the Control of Movements* (Nauka, Moscow, 1979); *Neuroscience* **5**, 81 (1980); *ibid.*, p. 91.
16. T. Valk-Fai and A. Crowe, *J. Comp. Physiol.* **125**, 351 (1978); *ibid.* **130**, 241 (1979).
17. D. G. Asatryan and A. G. Feldman, *Biophysics* **10**, 925 (1965).
18. A. G. Feldman, *ibid.* **11**, 766 (1966); *ibid.* **19**, 766 (1974).
19. E. Bizzi, A. Polit, P. Morasso, *J. Neurophysiol.* **39**, 435 (1976); A. Polit and E. Bizzi, *Science* **201**, 1235 (1978); *J. Neurophysiol.* **42**, 183 (1979).
20. T. G. Deliagina, A. G. Feldman, I. M. Gelfand, G. N. Orlovsky, *Brain Res.* **100**, 297 (1975).
21. C. S. Sherrington, *J. Physiol. (London)* **34**, 1 (1906).

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Biological and Sociocultural Effects on Handedness: Comparison Between Biological and Adoptive Families

Abstract. *Data from adoption studies on handedness indicate that the effects of shared biological heritage are more powerful determinants of hand preference than sociocultural factors. Biological offspring were found to show nonrandom distributions of right- and non-right-handedness as a function of parental handedness; these distributions were consistent with the results of previous family studies. In contrast, the handedness distribution of adopted children as a function of parental handedness was essentially random.*

Despite more than 50 years of systematic scientific inquiry, the question of whether genetic factors are involved in the intergenerational transmission of handedness is still unresolved. Recently, Annett (*1*) reviewed genetic and nongenetic models for the inheritance of handedness and pointed out that few conclusions about genetic influences on handedness can be firmly drawn until the results of studies of hand preference in adoptees and their families are known. Collins (*2*) also has asserted that only a cross-fostering design will enable us to assess the importance of the early environment in the development of hand preference. If growing up in a right-handed world exerts an overwhelming bias toward right-handedness, one would expect to find few if any left-handers in families in which the parents are right-handed.

Studies of handedness in biological families have generally found that the proportion of non-right-handed offspring was greatest when neither parent was right-handed and was lowest when both parents were right-handed (*1*, *3–6*). Although some studies have found support for a maternal effect in matings in which one parent was right-handed and the other had a mixed or left-handed preference (*1*, *3*, *5*), others have failed to confirm such an effect (*6*).

In this study, I assessed hand preference in three samples of adopted children and their adoptive parents and in two control groups of biological relatives. The results are considered in the context of the existing literature on fam-

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Table 1. Incidence of left- or non-right-handedness in parental and offspring generations.

Handedness	Parents			Children		
	Total	Left or non-right (*N*)	Left or non-right (%)	Total	Left or non-right (*N*)	Left or non-right (%)
Left						
Biological	410	31	7.6	403	53	13.2
Adoptive	572	42	7.3	415	56	13.5
Non-right						
Biological	410	127	31.0	403	209	51.9
Adoptive	572	172	30.1	415	200	48.2

ily resemblance in handedness. Twin studies are not considered here because of multiple nongenetic factors that may be related to the increased incidence of non-right-handedness in both monozygotic and dizygotic pairs (*7*).

The samples of adoptive families were assessed in a series of family studies in Minnesota. With the cooperation of the Minnesota Department of Public Welfare, families who had adopted their children in infancy (before their first birthday) and whose children were between 16 and 22 years of age were contacted by mail. Participation in a study of cognitive performance and personality was solicited from these families. They could participate either in person (at the University of Minnesota) or through the mail. Handedness data were collected from the parents and children of 195 of the participating adoptive families. Some ($N = 106$) of the families came to the university for about 3 hours of assessment (adoptive sample 1). The remaining 89 families participated through the mail (adoptive sample 2). A control group of 130 biologically related families, solicited by newspaper advertisements and referred by friends who had already participated in the study, came to the university for in-person assessments (biological sample 1). The final adoptive sample was a racially mixed (*8*) group of children adopted by white parents, many of whom also had biological children. In the 91 families in this sample for whom handedness data were available, there were 155 adopted children (adoptive sample 3) and 131 biological children (biological sample 2). Of the transracially adopted children, 99 were placed in their adoptive homes during the first year of life. In an attempt to control for age of adoption across the three adoptive samples, only these 99 infant adoptees were included in the analyses.

Families in all samples were unselected with respect to handedness. Complete handedness information was available from 286 adoptive families and 205 biological families. Hand preference in subjects who were 16 years of age or older was assessed by Oldfield's (*9*) Edinburgh Handedness Inventory, a questionnaire on the direction and strength of manual preference for ten tasks (such as writing, throwing, opening a lid, using scissors). Children between 4 and 16 years old (all from the transracial adoption study) were assessed individually with a handedness kit that required them to act out each item on the Edinburgh Inventory. For all subjects, a handedness index score was computed by dividing the difference between right and left responses by the total number of responses and multiplying the ratio by 100. The scores therefore ranged from -100 (left-handed for all items) to $+100$ (completely right-handed).

Many of the early family studies considered handedness as a dichotomous (right versus left) variable, whereas more recent studies have included ambidexterity in the definition of non-right-handedness. In order to facilitate comparisons with the existing literature, I analyzed the family data in two ways: (i) All subjects whose handedness index scores were at or below 0 were classified as left-handed and all those who scored above 0 as right-handed. (ii) Subjects who indicated almost exclusive preference for the right hand (scores of 80 or above) were designated strong right-handers; all other subjects, who might colloquially be called ambidextrous or left-handed, were classified as non-right-handers. As in all previous family studies of handedness (*1, 3, 5*), right-handedness was much more common in the parental than in the offspring generation, regardless of criteria used. There were clearly no differences between the adoptive and biological samples in the overall distributions of parental and offspring handedness (Table 1).

Table 2. Distribution of mating types by parental handedness in biological and adoptive families.

Parental handedness (father × mother)	All biological families	All adoptive families
Right × right	175	244
Right × left	17	13
Left × right	12	25
Left × left	1	4
Total	205	286
Right × right	98	146
Right × non-right	37	40
Non-right × right	50	68
Non-right × non-right	20	32
Total	205	286

The inclusion of a broader classification of non-right-handedness had several advantages: (i) The definition of non-right-handedness was not constrained by an arbitrary zero boundary and therefore included ambidextrous individuals who happened to have a slight preference for the right hand. (ii) The number of subjects in the non-right-handed category for both parental and offspring generations was greatly increased by relaxing the criterion for deviation from a right-handed norm. Only 7.4 percent of the parents and 13.3 percent of the offspring qualified as left-handers, while 30.4 percent of the parents and 50.0 percent of the children were classified as non-right-handers according to the criterion described above. (iii) The size of the rarest mating combination (non-right × non-right) was substantially increased (Table 2).

Distributions of offspring handedness were tabulated as a function of parental handedness mating types separately by each handedness criterion (Table 3). The five samples of offspring were collapsed into two groups after it was determined that there were no significant differences in the distributions of offspring handedness as a function of parental handedness mating types either across the two biological samples or across the three early adoptive samples. It should be noted that left-father × left-mother matings were excluded from Table 3 since there were only five such matings in the combined biological and adoptive samples. Distributions of left-handed offspring across the three remaining types were compared separately within the biological and adoptive samples. While left-handedness in children was significantly related to parental left-handedness in the biological sample [$\chi^2(2) = 9.15, P < .025$], no significant relationship was found in the adoptive sample (*10*). The proportions of left-handed children from right-father × left-mother matings were virtually identical

Table 3. Offspring handedness distributions as a function of parental handedness in biological and adoptive families.

Parental handedness (father × mother)	Biological offspring					Adopted offspring				
	Total (No.)	Right-handed		Left-handed		Total (No.)	Right-handed		Left-handed	
		Number	Percent	Number	Percent		Number	Percent	Number	Percent
Right versus left (total)*	400	348	87	52	13	408	354	87	54	13
Right × right	340	303	89	37	11	355	307	86	48	14
Right × left	38	29	76	9	24	16	12	75	4	25
Left × right	22	16	73	6	27	37	35	95	2	5
Left × left†										
		Strong right-handed		Non-right-handed			Strong right-handed		Non-right-handed	
Strong right versus non-right (total)‡	403	194	48	209	52	415	215	52	200	48
Strong right × strong right	194	103	53	91	47	228	124	54	104	46
Strong right × non-right	69	34	49	35	51	54	20	37	34	63
Non-right × strong right	101	46	46	55	54	91	48	53	43	47
Non-right × non-right	39	11	28	28	72	42	23	55	19	45

*Left-handedness is defined as all Edinburgh Inventory scores ≤ 0 (-100 through 0) and right-handedness as all scores > 0 (.01 through +100). †Left × left matings were excluded because there was only one such mating in the biological sample and only four in the adoptive sample. ‡Strong right-handers are all subjects with Edinburgh scores $\geq +80.00$; non-right-handers have scores $< +80.00$ (-100.00 through 79.99).

in the biological and adoptive samples, however, although the right-mother × left-father matings were related to a much higher incidence of left-handedness in biological than in adoptive children.

For the analyses of offspring handedness as a function of parental handedness according to the second classification scheme (non-right-handedness versus strong right-handedness), there were enough couples in both the biological ($N = 20$) and adoptive ($N = 32$) families to include offspring from non-right × non-right matings. Again, parental handedness was significantly related to offspring handedness distributions within the biological [$\chi^2(3) = 8.42, P < .05$], but not the adoptive [χ^2 (3) = 5.52] sample. The proportion of adopted non-right-handed children was about the same whether both parents were strongly right-handed, both were non-right-handed, or the father was non-right-handed and the mother right-handed (Table 3). An elevated incidence of non-right-handedness was found only when the adoptive mother was non-right-handed and the father strongly right-handed. In the biological sample, the most striking deviation from a random distribution across mating types was found when both parents were non-right-handed. Fewer than 30 percent of the biological children from such matings were strong right-handers.

The results from the biological sample are consistent with reports from other family studies of handedness. Strong support for specific effects of either maternal or paternal left-handedness is not evident in the existing literature. However, in every major family study of handedness (*1, 3, 5*), the incidence of left- or non-right-handedness in offspring was higher if either or both of the parents was left- or non-right-handed than if both parents were right-handed. Data from seven family studies of handedness (*1, 3–6*) were examined, and in every case the lowest incidence of non-right-handedness in biological families was among the offspring of two right-handed parents. For the adoptive children, in my study, however, the incidence of non-right-handedness did not vary systematically with parental handedness.

Although handedness data from much larger adoptive samples must be gathered before models of the relative contributions of biological and sociocultural factors can legitimately be formulated, some tentative conclusions can be drawn. (i) Because of the high rates of non-right-handedness in both biological and adoptive children reared in families with two strongly right-handed parents, social learning factors cannot be invoked as the sole explanation for the occurrence of left-handedness. (ii) Since non-right-handedness among parents was significantly and systematically related to non-right-handedness in biological but not in adoptive children, genetic factors do influence individual differences in handedness. The additional effects of prenatal and perinatal events on handedness have not been assessed here and could, of course, have contributed to the variation in hand preference and skill. (iii) The possibility that maternal sociocultural factors may affect offspring handedness in adoptive families cannot be completely ruled out. However, such a conclusion would be difficult to reconcile with the absence of a specific maternal effect in biological families and with the low incidence of sinistrality among adoptive children with two non-right-handed parents. The study provides an unambiguous demonstration that the frequently reported elevation in left-handedness among the children of two left-handed parents cannot be attributed to social factors and is more likely due to common biological heritage.

LOUISE CARTER-SALTZMAN
Department of Psychology,
University of Washington,
Seattle 98195

References and Notes

1. M. Annett, *Behav. Genet.* **8**, 227 (1978).
2. R. L. Collins, *Ann. N.Y. Acad. Sci.* **299**, 283 (1977).
3. M. Annett, *Ann. Hum. Genet.* **37**, 93 (1973).
4. H. D. Chamberlain, *J. Hered.* **19**, 557 (1928); F. Ramaley, *Am. Nat.* **47**, 730 (1913).
5. A. Falek, *Am. J. Hum. Genet.* **11**, 52 (1959).
6. D. J. Merrell, *Hum. Biol.* **29**, 314 (1957); D. C. Rife, *Genetics* **25**, 178 (1940).
7. J. Levy and T. Nagylaki, *Genetics* **72**, 117 (1972); L. Carter-Saltzman, S. Scarr-Salapatek, W. Barker, S. Katz, *Behav. Genet.* **6**, 189 (1976); J. Levy, *ibid.*, p. 429.
8. Of the 176 adopted children, 130 were socially classified as black, 25 were white, and 21 were Asian or Indian.
9. R. C. Oldfield, *Neuropsychologica* **9**, 97 (1971).
10. Calculation of χ^2 for the adoptive sample was precluded because the expected frequency in two of the cells was less than 5. Therefore, z scores were calculated to compare the proportions of left-handed offspring in right-father × left-mother ($z = 1.292$, not significant), and right-mother × left-father ($z = 1.401$, not significant) matings to right-father × right-mother matings. A similar analysis in the biological sample confirmed the results of the chi-square analysis [for right-father × left-mother versus right-father × right-mother ($z = 2.288, P < .05$) and for left-father × right-mother versus right-father × right-mother ($z = 2.301, P < .05$)].
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