duce them, or may be affected by physical properties of the ingested sediment, such as particle size. Finally, the lack of behavioral response with depth may indicate a poor understanding of benthic trophic structure. Depth and food availability in deep-sea sediments may not correspond in a simple inverse proportionality as was recently suggested (*17*).

Spiral and meander traces in the deep sea are not distributed in proportion to assumed food availability. Although the depth stratification of ecologic interactions may in fact represent a gradient in trophic exchange processes, the presence and abundance of foraging traces is species-specific and not depth-correlative. Spiral and meander traces are relatively depth-specific and abundant in Antarctic waters but absent at similar depths in the Arctic. The presence or absence of a trace type may not be taken as a definitive depth indicator. However, because it is unlikely that deep-sea organisms will be studied experimentally, continued use of remote sensing photographic techniques can allow inferences with regard to paleobiologic relations.

JENNIFER A. KITCHELL
Department of Geology and Geophysics, University of Wisconsin–Madison, Madison 53706
JAMES F. KITCHELL
Department of Zoology, Laboratory of Limnology, University of Wisconsin–Madison
DAVID L. CLARK
Department of Geology and Geophysics, University of Wisconsin–Madison
LOUIS DANGEARD
Institut Océanographique, 195 rue Saint-Jacques, Paris, SE, France

References and Notes

1. A. Seilacher, *Neues Jahrb. Geol. Palaeontol. Monatsh.* **1974**, 233 (1974); in *Approaches to Paleoecology*, J. Imbrie and N. Newell, Eds. (Wiley, New York, 1964), p. 296.
2. ——, *Mar. Geol.* **5**, 413 (1967).
3. ——, *Sci. Am.* **217**, 72 (1967).
4. M. Ksiazkiewicz, *Acta Geol. Pol.* **25**, 309 (1975); C. K. Chamberlain and D. L. Clark, *J. Paleontol.* **47**, 663 (1973); T. P. Crimes, in *Trace Fossils*, T. P. Crimes and J. C. Harper, Eds. (Seel House, Liverpool, 1970), p. 101; *Sedimentology* **20**, 105 (1973); C. K. Chamberlain, *Bull. Am. Assoc. Pet. Geol.* **55**, 34 (1971).
5. E. L. Charnov, *Am. Nat.* **110**, 141 (1976); J. M. Emlen, *Ecology: An Evolutionary Approach* (Addison-Wesley, Reading, Mass., 1973), pp. 178–185; T. W. Schoener, *Annu. Rev. Ecol. Syst.* **2**, 369 (1971).
6. A. Seilacher, in *Patterns of Evolution*, A. Hallam, Ed. (Elsevier, Amsterdam, 1977), p. 359.
7. D. M. Raup and A. Seilacher, *Science* **166**, 994 (1969).
8. F. Papentin, *J. Theor. Biol.* **39**, 431 (1973).
9. B. C. Heezen and C. Hollister, *The Face of the Deep* (Oxford Univ. Press, New York, 1971), pp. 175–182.
10. A total of 156 spirals and meanders were measured with a Hewlett-Packard digitizer 9107A.
11. J. A. Kitchell, J. F. Kitchell, G. L. Johnson, K. Hunkins, *Paleobiology*, in press.
12. Linear and exponential regressions were used to assess relationships over the depth range of 2798 to 5051 m for the dependent variables given in the text. None were significantly correlated. All coefficients of determination (r^2) were less than 10 percent.
13. J. F. N. Delgado, *Comm. Serv. Geol. Portugal* (1910).
14. J. Hülsemann, *Nat. Mus.* **96**, 449 (1966).
15. M. Ksiazkiewicz, in *Trace Fossils*, T. P. Crimes and J. C. Harper, Eds. (Seel House, Liverpool, 1970), p. 283.
16. T. P. Crimes, in *Trace Fossils II* (Seel House, Liverpool, in press).
17. R. L. Haedrich and G. T. Rowe, *Nature (London)* **269**, 141 (1977); J. F. Grassle and H. L. Sanders, *Deep-Sea Res.* **20**, 643 (1973); J. W. Valentine, *Lethaia* **4**, 51 (1971); H. L. Sanders and R. R. Hessler, *Science* **163**, 1419 (1969).
18. We thank T. P. Crimes, C. K. Chamberlain, and R. G. Osgood for reviewing the manuscript. Supported by Office of Naval Research contract N00014-76-C-0005. The Smithsonian Oceanographic Sorting Center and the Service d'Etudes et de Conservation des Photographies Sous-Marines, Orleans, France, provided access to the R/V *Eltanin* photographs.

28 November 1977; revised 24 February 1978

Human Lateralization from Head to Foot: Sex-Related Factors

Abstract. *Sex differences in the pattern and maturation of lateral asymmetries of the human brain have been recently found by a number of investigators, suggesting that sex-related factors may differentially affect the two sides of the body. In this study, asymmetries in the size of the two feet were strongly related to sex and handedness, right-handed males having larger right feet and right-handed females having larger left feet, the reverse being seen in non-right-handed individuals. Since these differences were apparent even in children younger than 6 years, the fetal sex steroids may be critical in governing the maturation of both cerebral and pedal asymmetries.*

A number of studies have reported functional differences in the patterns and maturation of cerebral lateralization in males and females (*1*). Witelson (*2*) found that right hemisphere functions mature considerably earlier in boys than in girls, and Reid (*3*) observed that in 5-year-olds the left hemisphere of girls and the right hemisphere of boys was more developed than that of the opposite half of the brain. This sex difference was found not only in right-handed children with language functions specialized to the left hemisphere and visuo-spatial functions to the right, but also in a subset of left-handed children with a reversed pattern of lateralization. Thus, relative hemispheric development as a function of sex was independent of the specializations of the two hemispheres, and the difference in boys and girls cannot, therefore, be attributed to sociocultural factors that might encourage different abilities in male and female children.

Since the differences in the sexes are apparent well before puberty, it seems reasonable to suggest that the fetal sex steroids may play a critical role in determining relative maturational rates of the two half-brains and, possibly, of other bodily regions as well. Specifically, high concentrations of fetal sex hormones, present in the male, may asymmetrically enhance development of the right side of the body, while low concentrations of fetal sex hormones, present in the female, may asymmetrically enhance development of the left side of the body.

Table 1. Distribution of right-handed and non-right-handed male and female subjects with respect to relative foot size.

Relative foot size	Right-handed		Non-right-handed	
	Males	Females	Males	Females
Left > right	2	55	6	0
Equal	10	18	6	2
Right > left	28	14	0	9
Total	40	87	12	11

In this study we compared the sizes of the left and right feet of 150 individuals, 98 female of whom 18 were under age 6, and 52 male of whom 17 were under age 6. All data were collected by J.M.L. from customers in the shoe department of his clothing store located in a small Alabama town (Demopolis) in the western part of the state. Foot asymmetry was rated on a seven-point scale, ± 3 being assigned if one foot was larger than the other by a half shoe size or greater, ± 2 being assigned if one foot was larger than the other by less than half a shoe size, but by a readily obvious degree (approximately a quarter to a half shoe size), ± 1 being assigned when one foot was slightly (less than a quarter shoe size), but definitely, larger than the other, and 0 being assigned when either the feet were equal in size or when, though one foot appeared possibly larger than the other, the observer could not definitely rule out equality (*4*). Negative numbers were given if the left foot was larger than the right and positive numbers if the right foot was larger than the left. Handedness data were also obtained in an interview with the customer or, if a child, the parent. If an individual preferentially used the left hand for any skilled unimanual activity, he was placed into the nondextral group. When parents were uncertain of a young child's hand

0036-8075/78/0616-1291$00.50/0

usage, the child was given a ball to throw and a crayon with which to draw. In none of the 150 individuals was there any difficulty in assignment to the dextral or nondextral group. Data on race, age, and best-fitting shoe size were also recorded, but none of these variables showed any tendency to be associated with foot asymmetry, so subjects were collapsed over these categories.

Table 1 shows the number of dextral and nondextral male and female subjects having no foot-size asymmetry, or having a larger left or larger right foot. Among dextrals there is a significant association between sex and the direction of foot asymmetry [χ^2 (2) = 45.0, $P < .0001$]. Though the number of nondextrals is small, there is again an association between sex and foot asymmetry (*5*), but in the opposite direction. The mean asymmetry scores were 1.2 ± 0.2 for dextral males and -0.9 ± 0.2 for dextral females [t (125) = 8.4, $P < .0001$]. The mean scores for nondextrals were -1.1 ± 0.3 for males and 1.4 ± 0.2 for females [t (21) = 5.8, $P < .0001$]. The pattern of results in childen under age 6 was identical and, if anything, was even more extreme than for the rest of the sample; this result rules out the possibility that pubertal hormones induce asymmetric foot growth. The absolute asymmetry scores, ignoring sign, did not differ as a function of sex or handedness nor, for subjects having asymmetric feet, as a function of which foot was larger. For the group as a whole, the absolute asymmetry score was 1.3 ± 0.1, and for those with asymmetric feet (114 subjects) was 1.7 ± 0.1 (that is, somewhat more than a quarter shoe size).

The observations reported here offer strong evidence for the action of gene products of X- or Y-linked loci in promoting asymmetric development of the feet, the direction of the asymmetry within sexes being governed by the same factors that determine handedness. Thus, our hypothesis, based on the results of Reid (*3*) that the male genome is invariably associated with enhanced right-sided development and the female genome with enhanced left-sided development, was disconfirmed. Even in young children under the age of 6 the left foot was larger in females and the right foot larger in males only in dextral subjects, the reverse pattern being seen in nondextrals. Apparently, though there is a strong effect of sex on the development of both cerebral and pedal asymmetry, the effect is independent of handedness (and the nature of hemispheric specialization) in the former case, but directionally determined by handedness in the latter case. Although for both asymmetric brain maturation and foot growth the critical role of genes on the sex chromosomes seems certain, the mechanisms by which these genes realize their effects evidently differ for the two body regions.

JERRE LEVY
Department of Behavioral Sciences, University of Chicago, Chicago, Illinois 60637

JEROME M. LEVY
301 South Main Avenue, Demopolis, Alabama 36732

References and Notes

1. D. Kimura, *Can. J. Psychol.* **23**, 445 (1969); D. A. Lake and M. P. Bryden, *Brain Lang.* **3**, 266 (1976); H. Lansdell, *Nature (London)* **194**, 852 (1962); J. Levy and M. Reid, *Science* **194**, 337 (1976); J. McGlone and W. Davidson, *Neuropsychologia* **11**, 105 (1973); T. Marcel and P. Rajan, *ibid.* **13**, 489 (1975).
2. S. F. Witelson, *Science* **193**, 425 (1976).
3. M. Reid, in preparation.
4. J.M.L. has had over 50 years experience in fitting shoes, and although, because the magnitude of pedal asymmetry is typically less than half a shoe size, his classification had to be partially subjective, we are confident that no subject classified as asymmetric was symmetric. It is possible, however, that a few subjects classified in the symmetric category may have deserved a rating of ± 1. It should be mentioned, also, that customer cooperation in the project was easily secured, both because J.M.L. has lived in Demopolis all his life and is known by most of the townspeople, and because the town is small and a spirit of cooperation prevails.
5. The exact probability of finding a distribution as unlikely as the one observed is only 3.18×10^{-5}, and we may confidently conclude that in nondextral individuals the distribution of males and females differs with respect to foot-size asymmetry.
6. We express our appreciation to the participants in this study who, though they only sought to be fitted for shoes, graciously gave of their time to make this investigation possible. Perhaps in consequence of our finding that in three-fourths of all people the two feet are of unequal size, it may someday be possible to buy left and right shoes separately, thus securing more comfortable footwear. This work was partially supported by NSF grant BNS 75-23061, a Spencer Foundation grant, and a biomedical grant from the University of Chicago.

19 October 1977; revised 5 April 1978

Substances Moved by Axonal Transport and Released by Nerve Stimulation Have an Innervation-Like Effect on Muscle

Abstract. *Substances which have an innervation-like effect on the cholinesterase activity of organ-cultured rat extensor digitorum longus muscles are moved in nerve by axonal transport, are released from nerve by stimulation, and are present in innervated muscle but apparently absent from denervated muscle. Substances which increase the acetylcholine sensitivity of cultured muscles behave similarly.*

Innervation exerts a profound influence on many of the properties of skeletal muscle (*1–3*). The evidence available suggests that the influence of nerve on muscle is mediated in part by the activity (electrical or mechanical, or both) generated in muscle by nerve (*4*), and in part by mechanisms that are independent of muscle activity (*5–7*). To account for the activity-independent influence of nerve on muscle it has been postulated that muscle properties are influenced by trophic substances (*8*) delivered to muscle by nerve (*1, 3, 5, 9, 10*). Several studies have shown that denervation-like changes occur in muscle when substances that block axonal transport are applied to nerve (*10*). The interpretation of this finding is controversial (*11*), but proponents of the trophic substance hypothesis have interpreted it to mean that substances which normally influence muscle are moved by axonal transport. Musick and Hubbard (*12*) have presented evidence that indicates that protein is released concurrently with acetylcholine (ACh) at the mouse neuromuscular junction and have suggested that this protein might mediate the trophic influence of nerve on muscle.

If the activity-independent influence of nerve on muscle is mediated by trophic substances then one would predict that substances with an innervation-like effect on muscle (i) should be present and moved by axonal transport in nerve, (ii) should be present in innervated muscle (within intramuscular nerve and possibly within muscle itself) but should be absent or present in reduced concentration in denervated muscle, and (iii) should be released from nerve. We have tested each of these predictions examining two muscle properties, cholinesterase (ChE) activity and ACh sensitivity, which are dramatically influenced by innervation. In adult rat muscle, innervation maintains both junctional and extrajunctional ChE activity (*13*) and suppresses extrajunctional ACh sensitivity (*2, 5, 14*). There is evidence that, during development, innervation causes an activity-independent aggregation of ACh receptors from the extrajunctional into the junctional region (*15*). Innervation probably continues to be involved in maintaining high junctional ACh sensitivity in adult muscle, but the extent of this influence is uncertain. Berg and Hall (*16*) have presented data, incidentally and without dis-

 0036-8075/78/0616-1292$00.50/0