Proc. Natl. Acad. Sci. USA
Vol. 91, pp. 5030–5032, May 1994
Neurobiology

Manual asymmetry and handedness

(trophic interactions/somatic symmetry)

DALE PURVES*, LEONARD E. WHITE, AND TIMOTHY J. ANDREWS

Duke University Medical Center, Department of Neurobiology, Durham, NC 27710

Contributed by Dale Purves, February 2, 1994

ABSTRACT **Volumetric measurements show that right-handed individuals have larger right hands than left hands. In contrast, the hands of left-handers are much more nearly symmetrical. Based on what is known about trophic interactions between neurons and targets, these findings predict a corresponding asymmetry of the relevant parts of the sensorimotor system in right-handers. The lack of an opposite-hand asymmetry among left-handers further implies that right- and left-handed phenotypes do not arise according to the same developmental rules.**

Nerve cells and their targets are linked by long-term trophic interactions that coordinate somatic and neural growth (see ref. 1 and below). If one hand is generally larger than the other—as some earlier studies of the human metacarpals suggest (2, 3)—then this asymmetry should be reflected in the size of the related neural structures. As a first step in exploring this neurosomatic relationship, we have measured the volume of the two hands among right- and left-handers.

We solicited 52 adult volunteers (students, faculty, and staff from Duke University) who described themselves as right-handers and 50 who considered themselves left-handers (Table 1). The volumes of the two hands were measured for each subject by a simple water displacement technique (Fig. 1). Among self-described right-handers, the right hand was larger than the left in 48 of 52 individuals [difference = 3.5 ± 0.4% (mean ± SEM); $P < 0.000001$, paired t test] (Fig. 2*A*). In contrast, the 50 self-described left handers showed no significant asymmetry in the size of the two hands (mean difference = −0.3 ± 0.5%; $P > 0.5$) (Fig. 2*B*).

To circumvent the ambiguities of self-description with respect to handedness, hand use was scored quantitatively by a questionnaire that covered a wide variety of manual preference tasks (4). We then plotted differences in hand size as a function of each person's score (Fig. 3). Although nearly all the self-described right-handers had scores indicating strong right-hand preference for the full range of tasks, the self-described left-handers varied greatly in this respect (see also ref. 5). Considering only individuals who showed a marked leftward preference on the handedness questionnaire (those who scored from 0 to 10), strong left-handers do have a significantly larger left hand (mean difference = −1.4 ± 0.6%; $P < 0.05$). However, this asymmetry among the strongest left-handers is less than half of that observed among right-handers. Whether from the perspective of hand size or preferred hand use, therefore, left handers are substantially less biased toward the left than right handers are biased toward the right.

The larger size of the right hand among right-handers (and the less marked difference among left-handers) presumably arises, at least in part, by differential use. Chronically exercised muscles hypertrophy, whereas unused or denervated muscles atrophy (6, 7). The difference in the size of the two forearms of highly accomplished tennis players, for example, is greater than that of controls, apparently because of the extensive unilateral limb exercise required by this sport (8). Nevertheless, not all measurements of somatic asymmetry accord with the view that lateral differences arise solely by differential use. The second metacarpal, for example, is consistently larger on the right among both right-handers and nominal left-handers (2, 3). Similarly, the central pattern of fingerprints tends to be more complex on the digits of the right hand than the left (9), a finding that again implies some degree of intrinsic somatic asymmetry. In the light of these observations, a prudent view is that both differential use and use-independent factors contribute to hand asymmetry that we describe.

Whether from chronic use during development or other reasons, the larger right hand of most right-handers is of particular interest in the context of trophic interactions between neurons and their targets. As noted, many studies have shown that the size of neural centers and their constituent nerve cells reflects the size of the relevant peripheral structures (1). In the autonomic innervation of smooth muscle and glands, for instance, altering target size directly

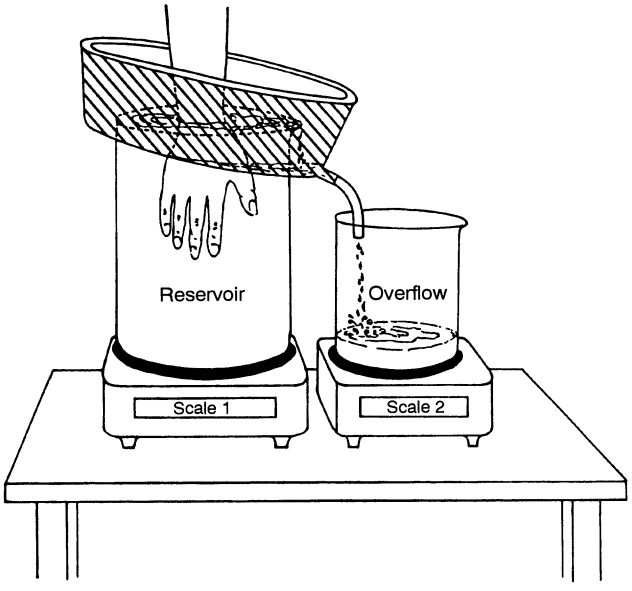

FIG. 1. Diagram of apparatus used to measure hand size by water displacement. A reservoir was filled and the initial weight of the water in the reservoir determined. Subjects were then asked to submerge their right hand in the reservoir to exactly the level of the first major wrist crease, which was marked with indelible ink on the palmar side. The amount of water displaced was measured by weighing the overflow on a scale accurate to 0.1 g; the weight of the displaced water was rounded off to the nearest gram, and the determination was repeated three times. The procedure was then repeated exactly for the left hand. The value for each hand was taken as the average of the three determinations.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

*To whom reprint requests should be addressed.

Table 1. Characteristics of the subjects studied, grouped according to self-described handedness

	Right-handers		Left-handers	
	Male	Female	Male	Female
Number of subjects	26	26	20	30
Age, years	31 ± 2	33 ± 3	27 ± 2	26 ± 2
% difference in hand size	3.4 ± 0.5	3.5 ± 0.6	−0.4 ± 0.7	−0.2 ± 0.7
Hand preference score	90 ± 2	92 ± 2	36 ± 5	24 ± 4

Percentage difference in hand size was determined as $R - L/[(R + L)/2] \times 100$, where R is right-hand size and L is left-hand size. See Fig. 3 for an explanation of the hand preference scores. Data are the mean ± SEM.

affects the size of innervating neurons and the complexity of their axonal and dendritic arborizations (10, 11). Numerous less direct examples support the proportionality of central neural representations and the amount of peripheral machinery (e.g., sensory receptors, muscle fibers, and glands) that such centers must monitor and motivate (1). Thus, the larger size of the right hand (and presumably the rest of the upper limb) implies a proportionally greater amount of related sensorimotor apparatus at all levels of the nervous system; conversely, the lack of significant hand asymmetry among left-handers argues that an opposite nervous system asymmetry will not be characteristic of this group. This implication accords with a preliminary study of the human sensorimotor cortex (12) that shows a leftward hemispheric asymmetry of the dorsal part of central sulcus, where hand and upper limb are represented.

This work was supported by National Institutes of Health Research Grant NS29187.

1. Purves, D. (1988) *Body and Brain: A Trophic Theory of Neural Connections* (Harvard Univ. Press, Cambridge, MA).
2. Garn, S. M., Mayor, G. H. & Shaw, H. A. (1976) *Am. J. Phys. Anthropol.* **45**, 209–210.
3. Plato, C. C., Wood, J. L. & Norris, A. H. (1980) *Am. J. Phys. Anthropol.* **52**, 27–31.

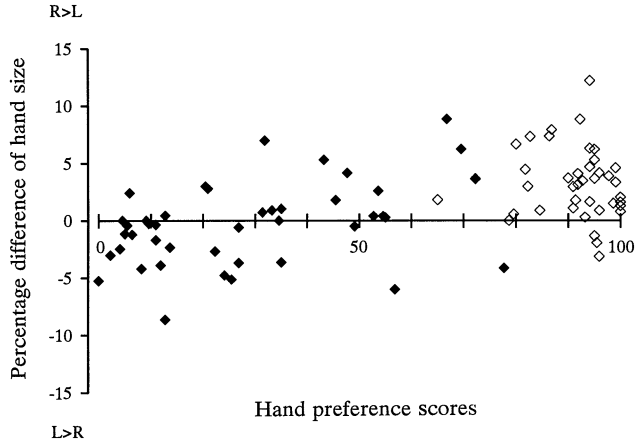

FIG. 3. Hand asymmetry [expressed as percentage difference; positive values = right (R) > left (L)] plotted against hand preference scores for self-described right-handers (open symbols) and left-handers (solid symbols). Handedness scores were determined by a questionnaire that included 55 manual and limb preference tasks (ref. 4; see also ref. 5). A score of zero indicates that for each of the tasks the subject always preferred to use the left hand, whereas a score of 100 indicates a uniform right-hand preference.

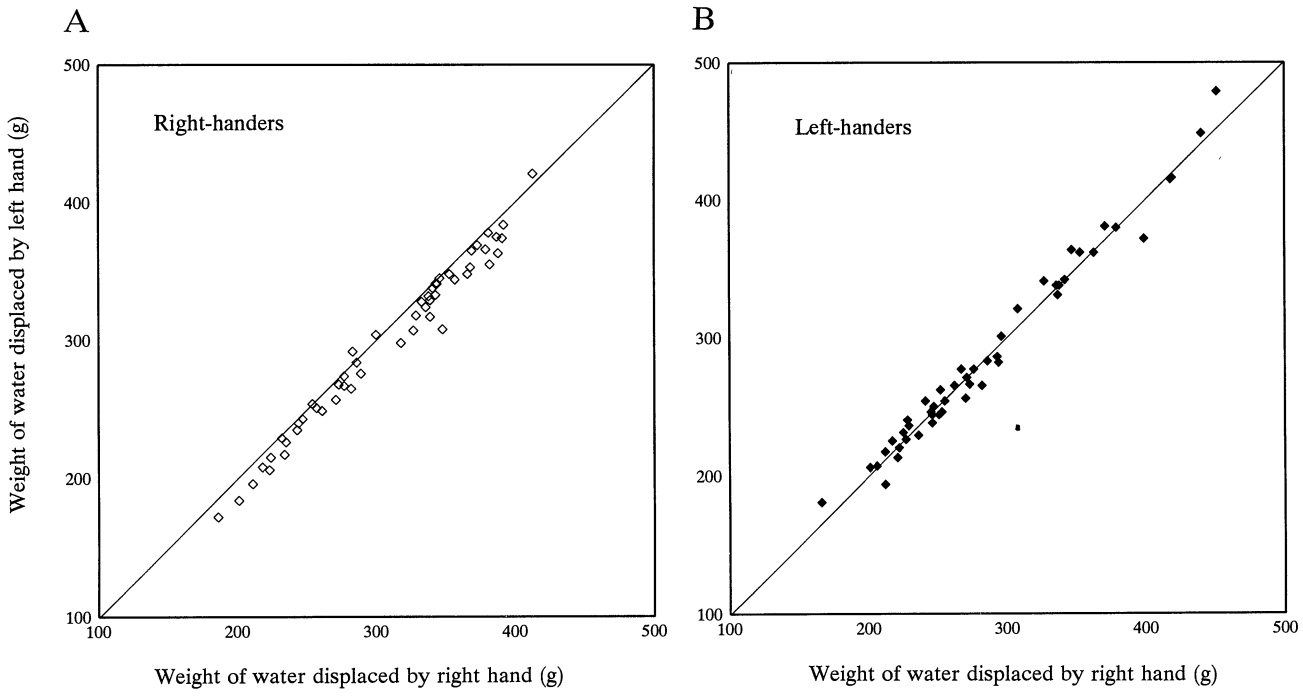

FIG. 2. Hand size asymmetry among right- and left-handers. (*A*) Left-hand water displacement plotted against right-hand displacement for 52 nominally right-handed subjects. For most individuals, the right hand was larger than the left. (*B*) Similar plot of 50 nominally left-handed subjects; there was no significant difference between the size of the two hands in this group (see text).

4. Healey, J. M., Liederman, J. & Geschwind, N. (1986) *Cortex* **22,** 33–53.
5. Oldfield, R. C. (1971) *Neuropsychologia* **9,** 97–114.
6. Jones, D. A., Rutherford, O. M. & Parker, D. F. (1989) *Quart. J. Exp. Physiol.* **74,** 233–256.
7. Tower, S. S. (1939) *Physiol. Rev.* **19,** 1–48.
8. Buskirk, E. R., Andersen, K. L. & Brozek, J. (1956) *Res. Quart.* **27,** 127–131.
9. Holt, S. B. (1968) *The Genetics of Dermal Ridges* (Thomas, Springfield, IL).
10. Purves, D., Snider, W. D. & Voyvodic, J. T. (1988) *Nature (London)* **336,** 123–128.
11. Voyvodic, J. T. (1989) *J. Neurosci.* **9,** 1997–2010.
12. White, L. E., Lucas, G., Richards, A. & Purves, D. (1994) *Nature (London)* **368,** 197–198.