ments at the onset of sustained drum rotation, but others were unable to detect any optokinetic response.

12. L. E. Rhodes, R. E. Dustman, E. C. Beck, *Electroencephalogr. Clin. Neurophysiol.* **27**, 364 (1969).
13. Evoked potential testing with checkerboard patterns [see S. Sokol, *Arch. Ophthalmol.* **88**, 619 (1972); D. Regan, in *Evoked Potentials in Psychology, Sensory Physiology and Clinical Medicine* (Chapman and Hall, London, 1972), pp. 55-61, 211-213] was also performed, and normal responses were obtained over a wide range of pattern alternation frequencies. Response amplitude was about one-half normal over the range from 5 to 8 hertz. Responses were symmetrical over both hemispheres. This testing was performed by Dr. S. P. Diamond with a Digitimer, Inc. stimulator in the Laboratories of Clinical Neurophysiology, Mount Sinai School of Medicine, New York.
14. For methods of EP testing with grating stimuli, see I. Bodis-Wollner, C. Hendley, A. Atkin, in *Visual Evoked Potentials in Man: New Developments*, J. E. Desmendt, Ed. (Clarendon, Oxford, 1977), pp. 514-525. The head of the boy was directed toward a screen with a diameter subtending 12° at his eye. When the experimenter watching the child ascertained that he was looking toward the screen, he pushed the "start" button of the averager, and stopped it every time the child seemingly looked away. For control runs, the reverse procedure was adopted.
15. CT scan was performed with an Ohio Nuclear scanner (256 by 256 element matrix). The normal brain section (horizontal section through midlevel of diencephalon) shown for reference on the right in Fig. 2 is redrawn after M. Roberts and J. Hanaway [*Atlas of the Human Brain in Section* (Lea & Febiger, Philadelphia, 1970), p. 49]. An approximation of the boundary between primary and secondary visual cortices was based on figures 289, 290, 293, 294, 296, 300, and 301 in S. Polyak, *The Vertebrate Visual System*, (Univ. of Chicago Press, Chicago, 1957). There is interindividual variability in the location of this boundary [see also G. S. Brindley, *J. Physiol. (London)* **225**, 1P (1972)].
16. It may be logically argued that pattern-evoked potentials in the present case were generated not in area 17 but in nonvisual (cortical or subcortical) areas. There is no experimental support for this supposition [see (*7*)]. The fact that only broadly striped patterns could elicit these potentials, not finer ones, is consistent with the concept of a nontopographically determined specific vulnerability of high spatial frequency channels in cerebral lesions. Cortical neurons with high spatial frequency optima may belong to a class functionally different from those with low spatial frequency optima [H. Ikeda and M. J. Wright, *Exp. Brain Res.* **22**, 363 (1975)]. Those with high spatial frequency optima might be especially vulnerable to hypoxia [I. Bodis-Wollner, *Nature (London)* **261**, 309 (1976)]. Another possible explanation is that the patient's high frequency loss was the result of a partial inclusion of the foveal projection of area 17 in the destroyed cortex.
17. Visual evoked potentials to diffuse light stimuli were registered in some cases of complete blindness due to cerebral lesions: for instance, see K. Kooi and F. Sherborough, *Electroencephalogr. Clin. Neurophysiol.* **20**, 260 (1966); R. Spehlmann, R. Gross, S. Ho, J. Leestman, K. Norcross, *Ann. Neurol.* **1**, 509 (1977).
18. A dissociation between detection and evoked potentials has been noted for somatosensory stimuli in patients with "extinction" due to cortical lesions [A. M. Halliday, *Electroencephalogr. Clin. Neurophysiol. Suppl.* **25**, 178 (1967)]. Dissociation did not occur from lesions of the afferent pathways.
19. M. Mishkin, in *Brain and Human Behavior*, A. H. Karczmar and J. C. Eccles, Eds. (Springer-Verlag, Berlin-Heidelberg, 1972), pp. 187-208.
20. The period of sensitivity of the human for abnormal visual experience has been estimated to be between 1 and 3 years of age for binocularity: M. S. Banks, R. N. Aslin, R. D. Letson [*Science* **190**, 675 (1975)].
21. We thank Dr. A. M. Aron for making the neurological and behavioral evaluation, Dr. H. Nakagawa for interpretation of the CT scans, and H. Morgan and C. D. Morgan of Friendship Ambassadors, Inc., New York, for making these studies possible. Supported in part by NIH grants EY 01867 and EY 01708, and by the Clinical Center for Research in Parkinson's and Allied Disorders, NIH grant NS 11631-03.

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Fifty Centuries of Right-Handedness: The Historical Record

Abstract. *A survey of more than 5000 years of art works, encompassing 1180 scorable instances of unimanual tool or weapon usage, revealed no systematic trends in hand usage. The right hand was used in an average of 93 percent of the cases, regardless of which historical era or geographic region was assessed.*

It is common knowledge that contemporary man prefers to use his right hand when performing unimanual tasks; however, little evidence exists as to whether this has always been so. To embark on such an investigation is theoretically important because it could possibly elucidate the adequacy of competing explanations of the etiology of hand preference. Basically, there are two types of theories that attempt to explain the development of handedness in man. The first maintains that there are physiological predispositions, possibly heritable in nature, which lead to the favoring of one hand over the other (*1*). This position is supported by reports of familial similarities in handedness patterns (*2*). The second type of theory suggests that social or environmental pressures (or both) lead to the high incidence of dextrality in man. This position is supported by human and animal work that has attempted to alter limb preference through behavioral manipulations (*3*). The social pressure position is summarized by Wile (*4*) who stated: "There arose, not so much a decline in the hereditary presence of left-handedness but rather a suppression of it under the demand for adaptation to changing principles of social organization, preservation and advancement."

Given these different viewpoints, one might be led to different predictions about the distribution of handedness if it were measured at different points along the historical continuum. The social pressure theory would predict an increase in the percentage of human dextrality coincident with the development of more formalized societies with more complex patterns of tool use. In contrast, the physiological theory, which views handedness as being independent of these influences, should presume a relatively constant distribution of manual preference regardless of historical period measured. Unfortunately, these predictions are difficult to test since written references to the distribution of lateral preferences are rare. Perhaps the earliest quantitative account of handedness appears in the Bible, Judges **20** : 15-16, where 700 left-handed or ambidextrous men were counted against 26,000 right-handed individuals. Thus, this biblical population was 97 percent dextral. However, unhappily, such written reports are too rare to be useful in systematic investigations of the history of handedness. There are, however, other archival sources which can be used to assess historical trends in the distribution of manual preference. Nearly all cultures have art forms that depict human beings engaged in various activities. To the extent that such artistic efforts are an attempt to describe reality, one might expect that such drawings and paintings would mimic the distribution of hand use which the artist actually observed. If so, then manifestations of lateral preference in works of art could serve as a record of the handedness pattern within the culture which produced them. Although this has been suggested before (*5*), no systematic studies of handedness over the broad range of eras and cultures using this data base have as yet been attempted.

The history of manual preference was assessed from works of art from various cultures and times. More than 12,000 photographs and reproductions of drawings, paintings, and sculpture were examined. The earliest sample included was dated at approximately 15,000 B.C., the latest in A.D. 1950. Items were drawn from European, Asian, African, and American sources. Each plate or reproduction was examined for figures displaying a clear hand preference. Only unambiguous instances of unimanual tool or weapon use were scored. Instances of mirror image symmetry (such as are common in some urn patterns) were excluded from the sample. For

Table 1. Historical distribution of handedness as manifested by works of art.

Time	Sample size	Right-handed (%)
Pre 3000 B.C.	39	90
2000 B.C.	51	86
1000 B.C.	99	90
500 B.C.	142	94
~0 B.C.	134	97
A.D. 500	42	93
A.D. 1000	64	89
A.D. 1200	41	98
A.D. 1400	50	88
A.D. 1500	68	93
A.D. 1600	72	94
A.D. 1700	71	93
A.D. 1800	101	94
A.D. 1850	39	97
A.D. 1900	77	92
A.D. 1950	90	89
Summary	1,180	92.6

works containing more than one instance of hand preference, only one example was counted and scored. The case to be scored was selected by means of a random number table that was used to determine the quadrant (or subquadrant) within the picture to be searched and recorded.

By means of these selection procedures, 1180 scorable instances were found. Of these, 92.6 percent depicted the use of the right hand. There is no systematic trend toward increasing dextrality over the more than 50 centuries represented by this sample ($\chi^2 = 17.04$; d.f. = 15). To further demonstrate this point, our results were compared to a sample of contemporary laboratory and survey research on handedness. Hecaen and de Ajuriaguerra (*6*) have reviewed 48 such studies which yield a mean incidence of dextrality of 90.6 percent (median 93.4 percent) and a standard deviation of 7.5 percent. None of the historical periods shown in Table 1 deviate significantly from these values.

These data can also be evaluated for evidence of social pressures which might manifest themselves as cross-cultural rather than historical differences. Table 2 shows the division of the sample into geographical regions with the data collapsed across the temporal dimension. Once again, no clear differences emerge among the various cultural subgroupings ($\chi^2 = 8.14$, d.f. = 6).

Table 2. Geographical distribution of handedness as manifested by works of art.

Region	Sample size	Right-handed (%)
Central Europe	335	93
Mediterranean Europe	317	95
Middle East	89	96
Africa	117	90
Central Asia	101	92
Far East	139	91
Americas	82	88
Summary	1180	92.6

If this apparent absence of any systematic changes in the distribution of hand preference over the past 50 centuries is considered in conjunction with the uniform distribution of dextrality regardless of geographical region, these results seem to support a physiological theory of handedness rather than one which proposed cultural and social determinants of handedness. Thus, as far as the historical record takes us, man appears to have always been right-handed.

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Behavioral Choice: Neural Mechanisms in *Pleurobranchaea*

Abstract. *In the marine mollusk* Pleurobranchaea, *it is known that feeding occurs and withdrawal from tactile stimuli is suppressed when the sensory stimuli for feeding and withdrawal are presented simultaneously. This "dominance" of feeding behavior over withdrawal behavior occurs because the central nervous network controlling feeding inhibits the central nervous network controlling withdrawal. The inhibition is mediated by a bilaterally symmetrical pair of reidentifiable feeding neurons that are members of the "corollary discharge" population in the buccal ganglion. This study supports the hypothesis that inhibitory interactions between competing motor systems are responsible for the "singleness of action" that characterizes animal behavior.*

Sherrington observed that certain spinal reflexes are prepotent over others that employ the same motoneurons and concluded that the resultant "singleness of action" is the keystone to coordinated movement (*1*). Ethologists have since recognized that singleness of action applies also to the integrated behavior of the whole organism; indeed, a major issue in the study of behavior is the methods by which animals "decide" to perform a single behavioral act to the partial or complete exclusion of others (*2*). In the carnivorous marine gastropod *Pleurobranchaea*, such decisions are made in accord with a behavioral hierarchy (*3*), defined as the organization of unrelated acts of behavior into a priority sequence that governs behavioral choices. For example, when *Pleurobranchaea* is touched vigorously on the anterior oral veil, it withdraws from the tactile stimulus; when presented with squid extract, *Pleurobranchaea* exhibits a stereotyped, rhythmic feeding response (*3, 4*). When touch and food are presented together, feeding is normally elicited and withdrawal is suppressed (*4*). Therefore, feeding is "dominant" over withdrawal in the behavioral hierarchy of *Pleurobranchaea*, an evolutionary adaptation that presumably prevents withdrawal from food.

Previous behavioral experiments (*4*) suggested that feeding dominates withdrawal because neurons that are part of the feeding system inhibit the withdrawal behavior. We have confirmed this hypothesis by identifying the inhibitory neurons that mediate the effect. Our study indicates that inhibitory interaction between different motor systems represents one neural mechanism underlying behavioral hierarchies.

Three types of preparations were employed in these experiments: the whole animal, the semi-intact animal, and the isolated central nervous system. Whole-animal preparations were made by exposing the cerebropleural ganglion (brain) by a 2-cm incision and suspending the animal in seawater by hooks attached to the margins of the opening (*5*). The brain was stabilized on a micromanipulated platform with small pins passed through the marginal connective tissue. Sensory and motor connections remained intact and operational for one to several hours in such preparations. Semi-intact preparations consisted of eviscerated animals whose nervous systems remained intact and connected as usual to feeding and withdrawal muscles (Fig. 1A). Such preparations were anchored to a base (Sylgard) by pins that passed through the foot. Isolated nervous systems (Fig. 1B) were prepared as detailed previously (*6*). All preparations were made from medium-sized specimens (volume, 100 ml) and submerged in filtered seawater at 13°C during experiments. Extracellular stimulation and recording from nerves mediating feeding and withdrawal was accomplished with glass capillary suction electrodes. Intracellular recording and stimulation of single neurons was accomplished with glass capillary microelectrodes filled