

# Handedness and laterality in humans and other animals

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A survey of the developmental, genetic, paleoneurological, comparative behavior, and neuropsychological evidence indicates that the neural organization responsible for handedness and laterality in humans is a heritable, species-specific trait. Handedness and laterality in monkeys, the most intensively studied nonhuman taxon, are not homologous to handedness and laterality in humans. Monkeys learn hand preferences through experience and display no difference in learning by the hemispheres ipsi- and contralateral to the preferred hand. Differences in the functions of the two hemispheres are found in several other nonhuman species, but none has been correlated with paw preferences.

We who studied handedness in nonhuman primates once thought our work might contribute to the understanding of functional asymmetries in the human brain. We hypothesized that handedness in monkeys and apes might be homologous to handedness in humans and that lesions in the hemispheres contra- and ipsilateral to the preferred hand might have differential effects on cognitive behaviors in monkeys, thereby providing a useful model for unilateral cerebral insults in man (Brookshire & Warren, 1962; Hamilton, 1977a, 1977b; Warren, 1958; Warren, Abplanalp, & Warren, 1967; Warren & Nonneman, 1976).

Neither hypothesis compels instant disbelief. Lateralization of the neural control of manipulation could, in theory, have been selected for in much the same way as refinements in the structure of the hand during primate phylogeny (Reynolds, 1975). Prosimians have no differential control of individual digits, only whole-hand control. Old World monkeys have independent control of the thumb and of the fingers collectively, but lack precise and discrete control over individual fingers. Chimpanzees have more exact control of separate fingers. On the assumption that increasing degrees of asymmetrical neural control of hand use accompanied these stages in the evolution of the hand in primates, Reynolds (1975) concluded that "Laterality of function is not necessarily unique to man, but perhaps a human manifestation of processes that began early in primate phylogeny" (p. 499).

Pribram (1977) has suggested a complementary hypothesis regarding the origin of lateralized motor functions. Asymmetrical motor control of the forelimbs in primates arose to direct optimally the use of the arms, hands, and fingers in climbing, brachiating, and other critical arboreal activities, for which

much more variable patterns of coordination are required than are for the stereotyped patterns of locomotion characteristic of terrestrial mammals.

A link between handedness in nonhuman primates and language in humans is suggested by the theories which imply that lateralized control of the hand used preferentially in complex tool making and in gestural language favored lateralization of human speech mechanisms in the same hemisphere (Hewes, 1976; Montagu, 1976; Steklis & Harnad, 1976).

The assumption that handedness in humans and other primates is homologous was not blatantly implausible, nor was the belief that handedness in nonhuman primates might be relevant to understanding laterality in man. Yet both hypotheses have been consistently disconfirmed by the empirical facts, as will be shown by a review of the ontogenetic, phylogenetic, and comparative evidence concerning lateralization of brain functions in primates.

## ONTOGENY

The clinical and experimental evidence indicates that the human brain is laterally differentiated before birth (Wada, Clark, & Hamm, 1975) and that handedness is very probably, like several other traits, subject to strong genetic influences (Levy, 1976).

Anatomic, behavioral, and neuropsychological observations all point to very early cerebral lateralization. The planum temporale and parietal operculum are larger on the left in fetal and neonatal brains, as they are in right-handed adults. Neonates turn their heads and eyes to the right more often than they do to the left, and the direction of the tonic neck reflex at 8 months is predictive of hand preferences at 10 years. When tested as adults, persons subjected to right- and left-hemisphere decortication during infancy are selectively impaired in spatial and verbal performance, much as persons who sustain comparable brain injuries as adults.

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No contemporary genetic model for the inheritance of handedness in humans is in satisfactory agreement with the empirical evidence. This may be because cultural pressures produce sex and class differences in the phenotypic expression of handedness. It is more likely that current theories regarding the transmission genetics of handedness are incomplete or incorrect.

Although the mode of inheritance of handedness remains to be specified, there is no reason to doubt the importance of genetics in the determination of handedness and other lateralized cortical function in humans. Eye dominance, fingerprints, and nose asymmetries are traits subject to little or no cultural influence, and each of these traits is heritable, and each is positively correlated with handedness (Levy, 1976). It is very difficult to imagine a cultural shaping process which could create sex differences in the representation of cognitive processes in the human brain (Dimond, 1977; Witelson, 1976), particularly when a simple genetic correlate is obvious.

Additional support for the participation of genetic factors in the determination of handedness derives from the value of family data in establishing prognoses for patients with unilateral brain damage. Right-handed individuals with lesions in the language areas of the left hemisphere have very different prospects if their families do or do not include left-handed persons. Almost all of the patients with no left-handed relatives are permanently aphasic, but only about one-quarter of the patients with left-handed relatives suffer permanent aphasia after damage to the left hemisphere.

Four lines of evidence thus indicate that handedness and other forms of cerebral laterality are genetically determined in humans: (1) structural and functional asymmetries in neonates; (2) the heritability of lateralized traits correlated with handedness; (3) sex differences in the lateralization of cognitive functions; and (4) the value of pedigree data in predicting the effects of left-hemisphere damage. Since heritable traits arise only as a result of natural selection, the genetic control of human cerebral lateralization indicates that the human pattern of hemispheric specialization is a species-specific trait, correlated with the peculiar life style of humans.

Unfortunately, no statement is possible on the developmental and genetic evidence as to whether or not human laterality is species-unique. There are no adequate ontogenetic data on nonhuman primates.

### PHYLOGENY

The artifacts left by early humans have been studied to answer the behavioral questions: How intelligent was early man? When did humans become right-handed? The archeological evidence consistently indi-

cates a high level of cognitive ability in paleolithic man (Marshack, 1976; Perelló, 1970). For example, Perelló (1970) scored Catalan and Spanish cave paintings as responses to the Draw-A-Person Test, and estimated the mental age of the artists as at least 13 years, with no allowance made for their inferior kit.

Attempts to infer the time at which humans became predominantly right-handed from such material remains as tools, weapons, and paintings have yielded extremely variable estimates. Dart (1949) thought that *Australopithecus* was right-handed, while Blau (1946) and Wile (1934) held that humans were not predominantly right-handed until domesticated as farmers in the Bronze Age.

This literature remains contradictory and inconclusive to the present. Thus, Perelló (1970) observed that contemporary right-handed children draw people and animals facing left, and left-handed persons draw their subjects facing to the right. Since about half the mammals at Altamira and several caves in Catalonia face in either direction, it might be inferred that the paleolithic painters were ambidextrous or equally often right- and left-handed. But graphic artists may be different from ordinary folks and provide misleading information regarding the distribution of laterality. And, indeed, Uhrbrock's (1973) survey of classical, medieval, and modern art works reveals essentially no preponderance of left-facing portraits. Recent artists, like Iberian cave painters but unlike modern children, show little bias in orienting their subjects. Thus, the cave pictures could reflect the peculiarities of painters rather than the distribution of handedness in the general population.

Claims of paleolithic right-handedness are also equivocal inferences from the material evidence. Most tracings of human hands on the walls of Spanish caves are of the left hand. Hicks and Kinsbourne (1976, 1978) infer from this that the population of cave people was right-handed, assuming that each person held his left hand passively against the wall and actively applied pigment with his preferred right hand. But how do we know that the model and the painter were the same person? Paleolithic man had apparently a complex set of religious practices. How can we tell if tracing the left hand was not dictated by ritualistic rather than organismic demands?

Clearly, no conclusion regarding handedness in paleolithic populations is justified by present interpretations of the material remains. There is, however, no serious grounds to doubt that humans have been very largely right-handed for the last 5,000 years. Analysis of 1,180 drawings, paintings, and sculptures of people using tools or weapons shows that about 90% were right-handed, from 3000 B.C. to the present (Coren & Porac, 1977).

Paleoneurology provides more conclusive evidence regarding the history of cerebral laterality and hand-

edness in hominids than does archaeology. Endocasts of fossil human crania show that structural asymmetries like those associated with functional asymmetries in modern humans were present 40,000 years ago. Specifically, the parietal operculum of a Neanderthaler is substantially larger on the left than on the right, strongly suggesting left-hemisphere predominance for speech and handedness (Holloway, 1976; LeMay, 1976; Levy, 1976). Endocasts of older fossil crania do not reveal marked cerebral asymmetries, but they are few in number and badly preserved. It is not possible, therefore, conclusively to deny the possibility that the brains of *Homo* were asymmetrical more than 40,000 years ago.

The discovery of an asymmetrical Neanderthal brain supports the view that lateralization of neural function is a heritable, species-typical characteristic of humans and contradicts environmental explanations of human laterality. The archaeological evidence on the origin of handedness in man is ambiguous, but provides no data adequate to disconfirm the theory that the human pattern of lateralized brain functions is an inherited species-typical trait.

## COMPARATIVE BEHAVIOR

### Distribution of Hand Preferences

Most humans, about 93%, are right-handed, an estimate based upon the median of 48 investigations summarized by Hécaen and de Ajuriaguerra (1964, Table 1). The number of right-handed persons varies somewhat between (Dawson, 1977) and within cultures as a function of sex (Dawson, 1977; Hécaen & de Ajuriaguerra, 1964), educational policies (Levy, 1976), and social class (Falek, 1959).

Although cultural influences complicate research on the genetics of human handedness, they are nowhere strong enough to normalize the asymmetrical distribution of handedness in humans. Differences in the number of right-handed persons in different populations are small, ranging from 90% in permissive hunting and fishing societies to 98% in strict, traditional agricultural societies (Dawson, 1977). The proportion of left-handed students in the United States increased from 2% in 1930 to about 11% in 1970, largely because of the greater tolerance of left-handed persons by teachers. It is, however, apparent from the curve Levy (1976, Figure 1) presents that increases in the number of left-handers have become smaller and smaller with the years since sinistral liberation, and that 11% left-handed persons is the likely empirical asymptote.

No comparably asymmetrical distribution of right- and left-hand or paw preferences has been observed in any other species. The number of right- and left-handed individuals is, within the limits of sampling error, equal in mice, rats, cats, rhesus monkeys, and

chimpanzees (Collins, 1968, 1969; Finch, 1941; Lehman, 1978; Martin & Webster, 1974; Tsai & Maurer, 1930; Warren, 1953, 1958).

Granting that there are equal numbers of animals with right- and left-hand or paw preferences in non-human mammals, primates might still differ from other mammals in the proportion of individuals with strong preferences for either the right hand or left hand. This possibility is tested by comparing the percentage of experimentally naive animals with a 90% preference for one hand, right or left, in reaching for food: mice, 58% (Collins, 1969); cats, 71% (Warren, 1958); rhesus macaques, 47% (Lehman, 1978) and 55% (Warren, 1958); and chimpanzees, 46% (Finch, 1941).

Thus, in regard to the distribution of right- and left-hand preferences and to the number of cases with strong preferences for either the right or the left hand, chimpanzees and rhesus monkeys resemble mice and cats, and differ drastically from humans.

### Temporal and Situational Constancy

Most humans use their right hands for each of the dozen or so manipulations sampled in accepted assessments of handedness, and tend to remain right-handed from later childhood on (Annett, 1972; Briggs & Nebes, 1975; Hécaen & de Ajuriaguerra, 1964; Levy, 1976). The performance of rhesus monkeys on the handedness tests deviates quite markedly from the human pattern of temporally and situationally consistent right-handedness.

Monkeys do not have well-defined hand preferences prior to extended testing on manipulation tasks in the laboratory. Their initial preferences are weak, largely task specific, and unpredictable of later preferences (Warren, 1977). Marmosets are ambidextrous in spontaneous activities like play, feeding, and exploiting materials (Rothe, 1973). Etlinger, Blakemore, and Milner (1968) did not use the early responses of their experimentally naive monkeys to specify their hand preferences because initial responses tend to be atypical. The degree to which the first responses of wild monkeys on laboratory handedness tests are "atypical," or unrepresentative of later performance, has been quantified. The correlation between monkeys' hand-preference scores on their first 500 test trials and scores on the same test replicated 2 years later was  $\pm .10$ , and the correlation between the first test and the average of 14 others 2 years later was  $-.20$  (Warren, 1977).

With continued testing in the laboratory, this picture changes considerably in the direction of increased constancy. Both the split-half and test-retest reliability of the handedness tests increase progressively on successive replications (Beck & Barton, 1972; Warren, 1958, 1977). Increments in the consistency of handedness are also suggested by a rise in the number

of monkeys with statistically significant preferences, in the degree of preference averaged over all monkeys, in the number of significant correlations between tests, and by a decrease in the number of contradictory preferences, that is, when a monkey uses its right on one task and its left on another.

These changes might be construed as indicating that trapped wild monkeys have potentially stable and generalized hand preferences which they are too anxious and apprehensive to show on arrival in the laboratory but reveal after they have become habituated to captivity. This would be wrong. Only the increase in reliability is common to all tasks in a handedness battery; all the other indices vary among the different tests. Some tests continue to elicit weak and sometimes contradictory preference, and remain uncorrelated with one another and with tests that elicit strong and consistent preferences (Warren, 1977).

The central, critical fact about handedness in monkeys is that it is task and situation specific.

Results from *Macaca mulatta* and *M. speciosa* on multiple handedness tests reveal high interest agreement among tasks that acquire common manipulations, but low correlations among tasks that require test-unique hand movements (Beck & Barton, 1972; Deuel, 1975; Warren, 1977). Marmosets also display discrepant hand preferences on different tests of manipulation (Rothe, 1973). The hand preferences of monkeys are also influenced by context effects, in that performance on a specific test, and its correlations with other tests, varies among experiments with different series of monkeys, apparently as a function of which other tests are presented in the test battery, distribution of practice on the several tasks, and other details of experimental procedure.

The argument from correlational analyses is supported by additional evidence of lability in monkeys' manual preferences. Some monkeys use opposite hands in the light and dark, or in the Wisconsin General Test Apparatus and in a primate chair (Deuel, 1975; Ettlinger et al., 1968). Position of the food incentive relative to the monkey and the direction and quality of hand movement required to secure the food also affect the hand preferences of monkeys (Cronholm, Grodsky, & Behar, 1963; Lehman, 1978).

The available behavioral information on handedness in monkeys can be accounted for by a simple model which indicates that the appearance of handedness in monkeys is an artifact produced by the methods that have been used in chronic experiments (Warren, 1977). The first experiment in which trapped wild monkeys fresh from the jungle serve is often a series of handedness tests, since handedness testing is a good way to shape responses that are required in subsequent perception and learning experiments. In such investigations, monkeys typically repeat some of the manipulations elicited in the handedness tests

thousands of times, while other manipulations are not practiced at all. When, after many months or years, the subjects are retested on the handedness test battery, one observes that preferences on tests that require responses that have been highly practiced are stronger and more consistent than in initial testing, but that preferences on tests that require manipulations that were not practiced are no more strong or consistent than in the original tests.

These changes would be expected if one assumes that (1) monkeys learn to prefer one hand for a particular sort of manipulation, and (2) monkeys have a limited range of response generalization. Given a detectable disparity between the hands in skill or the effort required for a given manipulation, or even an environmental asymmetry that militated against equal practice with both hands, a differential delay of reinforcement for responding with the left hand and right hand would develop and monkeys would shape themselves under this contingency to use one hand exclusively to make particular manual responses, such as pushing a block aside and seizing a peanut concealed beneath it. Displacing objects is what monkeys mostly do in the months between series of handedness tests, so it is not surprising that monkeys tend strongly to use the hand preferred to manipulate objects to displace cards, to pick up raisins, and to extract peanuts from a cup; since all these tasks require very similar hand movements, response generalization is anticipated. Pulling in a chain and removing fruit impaled on its end and taking a cereal ring from a wire are manipulations that differ markedly from the well-practiced act of pushing objects about and similar tasks. Persistent failure to observe significant correlations between the two sorts of tasks is compatible with the view that response preferences learned on the object displacement test fail to generalize to chain and wire tests.

This account of the hand preferences of experienced monkeys as the result of task-specific learning and limited response generalization is supported by the findings that the spontaneous hand preferences of squirrel monkeys can be quickly and permanently reversed by contingent reinforcement of the non-preferred hand and that discriminative control of responding by the two hands under the control of visual stimuli can be established by relatively little additional training (McGonigle & Flook, 1978).

## COMPARATIVE NEUROPSYCHOLOGY

The complementary division of special functions between the right and left hemispheres of the human brain (Hécaen & Albert, 1978; Levy, 1977) is well known and the evidence so extensive that an extensive summary would be inappropriate here, where we are concerned with the question of whether there is, as

in man, an essential association between handedness and other lateralized functions in nonhuman primates.

If hand preferences in monkeys were valid indices of an asymmetrical brain organization, with the hemisphere contralateral to the preferred hand predominant for mediating cognitive as well as manual functions, the isolated "dominant" hemisphere (contralateral to the preferred hand) should surpass the "nondominant" hemisphere (ipsilateral to the preferred paw) on learning and performance tasks.

This proposition has been tested by two sorts of experimental designs. Groups of monkeys are tested for handedness and matched groups are subjected to unilateral ablations of association cortex on the apparently dominant and nondominant hemispheres, making it possible to compare the relative capacity of the dominant and nondominant cortical regions that remain on the intact hemispheres. In studies of this kind, all the monkeys with unilateral lesions are, in learning, frequently inferior to unoperated controls, but no significant difference has ever been observed between the effects on lesions contra- or ipsilateral to the preferred hand (Ettlinger & Dawson, 1969; Warren, Cornwell, & Warren, 1969; Warren, Grant, Hara, & Leary, 1963; Warren & Nonneman, 1976).

The second type of experiment provides within-subjects comparisons from split-brained monkeys or monkeys with reversible inactivation of the separate hemispheres. A substantial and significant difference in the rate that the two hemispheres learn discriminations or in the accuracy of performance on such tasks as delayed response would constitute unequivocal evidence of functional lateralization in monkeys. No evidence of this sort is to be found in the literature. All of the properly controlled experiments with a reasonable number of subjects indicate that monkeys' hemispheres are equally proficient in learning on visual cues (Butler, 1968; Downer, 1962; Ebner & Myers, 1962; Fuster & Bauer, 1974; Hamilton, 1977a, 1977b; Hamilton & Gazzaniga, 1964; Lehman & Spencer, 1972).

The complete failure of several investigators to obtain any evidence that the cerebral hemisphere contralateral to the preferred hand differs in any important respect from the hemisphere ipsilateral to the preferred hand is clearly more compatible with the view that "handedness" in monkeys is an artifact of learning in the laboratory rather than a trait that is homologous or analogous to handedness in humans. This interpretation derives additional strong support from Dewson's (1978) discovery that functions may be lateralized in the brains of monkeys, independent of any correlation with handedness. Dewson observed that *M. irus* with ablations of the left superior temporal gyrus and the dorsal bank of the superior temporal sulcus, but not equivalent

lesions on the right, showed a permanent defect in a delayed matching-to-sample task, which required that monkeys press a red key after a tone was sounded and a green key after noise. It is important to emphasize that the locus of the lesion was the determinant of losses on both tasks. Lesions on the left hemisphere impaired both right- and left-handed monkeys, but lesions on the right were ineffective in all monkeys (Dewson, Note 1).

Dewson's demonstration that the processing of complex acoustic signals is lateralized in the left hemisphere in monkeys is corroborated by a behavioral experiment on dichotic listening in *M. fuscata* and three other species of monkeys. The discriminanda were species-specific calls of Japanese macaques with early and late frequency peaks. Five of five Japan macaques made significantly more correct responses with right-ear than with left-ear stimulation. Only one of five representatives of other species showed a significant right-ear advantage. "The results suggest that Japanese macaques engage left-hemisphere processors for the analysis of communicatively significant sounds that are analogous to the lateralized mechanisms used by humans in listening to speech" (Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978, p. 324).

Petersen et al. give no information regarding the hand preference of their monkeys. Given, however, the symmetrical distribution of hand preferences in monkeys, the probability is low ( $\pm .03$ ) that their five Japanese macaques were all right-handed as well as right-eared and left-brained. The results of the dichotic tests provide additional evidence for the lateralization of some auditory processes in monkeys, and suggest that this sort of functional asymmetry is independent of hand preference in monkeys.

The studies of handedness and auditory functions in monkeys reveal an important fact about lateralization in the primate nervous system: The close link between handedness and other lateralized functions characteristic of human persons is not inevitable. In monkeys, the mechanisms for processing some kinds of auditory information are lateralized, even though monkeys lack the stable handedness seen in humans. The neural bases of functional lateralization are organized in fundamentally different ways in monkeys and men. Macaques are not little men in brown fur suits, whose cerebral dominance is revealed by their hand preferences, since handedness and other lateralized traits appear to be correlated only in humans.

Although it now seems unlikely that homologues of human handedness and laterality will be found in other taxa, several sorts of spontaneous and induced lateralized functions have recently been demonstrated in experimental animals. The following phenomena may reasonably be regarded as analogues of lateralized neural functions in humans.

(1) Section of the left hypoglossal nerve or destruc-

tion of the left hypoglossal nucleus disrupts singing in canaries, chaffinches, white-crowned sparrows, and white-throated sparrows much more severely than do identical injuries on the right (Nottebohm, 1977).

(2) Rats that can escape shock in a T-maze running to either the right or left arm manifest strong preferences for turning in one direction. Post mortem determinations showed that the concentration of dopamine in the striatum contralateral to the side preferred by each rat was significantly higher than on the ipsilateral side (Zimmerberg, Glick, & Jerussi, 1974).

(3) Mice, like monkeys, display lateralization of brain function independent of paw preferences. DBA mice develop audiogenic seizures significantly sooner with monaural stimulation of the left ear than with the right. Yet, paw preferences in DBA mice are symmetrically distributed (Collins & Ward, 1970).

My last two examples of laterality in nonhuman animals were induced, not spontaneous as those described above. The lateral asymmetries are not seen in untreated populations, but are created by the experimenter in the laboratory.

(4) Monkeys trained on a delayed response task with one hand restrained in a cuff develop significantly larger steady potential shifts in the frontal granular and precentral cortex contralateral to the active hand than they do in the same areas ipsilateral to the active hand. Later, when the initially restrained hand is freed and the previously active hand is chained, the steady potential shift in the precentral region becomes larger on the hemisphere contralateral to the currently active hand, but the steady potential shift in the frontal granular cortex, which is associated with the mnemonic traces that mediate successful delayed response, remains larger on the hemisphere contralateral to the first-trained hand. Unilateral training has thus induced a persistent interhemispheric asymmetry that was not present before training. The subjects in this experiment were tested for hand preferences prior to the beginning of unimanual restraint. Apparent handedness had no effect upon the genesis of the differences in steady potential shifts between hemispheres (Stamm, Gadotti, & Rosen, 1975).

(5) An investigation of interaction of preweaning handling, postweaning exposure to an enriched environment, and unilateral cortical lesions in adulthood on open-field activity in rats reveals a curious new form of cerebral lateralization which few of us would have predicted (Dennenberg, Garbanati, Sherman, Yutzey, & Kaplan, 1978). Differential effects were obtained from the animals handled from birth to 20 days. Rats with lesions in the left hemisphere, whether provided environmental enrichment or not from Day 21 to Day 50, did not differ from the appropriate intact controls. Rats that had been handled in infancy and suffered right-hemisphere damage had higher scores in the open field than any

other group if they had been denied experiences in the enriched environment, while handled and enriched rats with right cerebral insults had the lowest activity scores of any group. As measured by activity levels, handling and enrichment experiences affect the right hemisphere more than the left in rats. Since emotional states strongly influence rats' activity in an open field, the results of Dennenberg et al. inevitably remind one of the findings that the right hemisphere is more consequential than the left for the expression and evaluation of emotions by humans (Sackheim, Gur, & Saucy, 1978).

More recent works demonstrate that the right and left hemispheres of rats handled in infancy are functionally asymmetrical in their control of taste aversion learning, spatial turning preferences, and mouse killing behavior (Sherman, Garbanati, Rosen, Yutzey, & Dennenberg, 1980). The neurological bases of hemispheric asymmetries in rats are unknown. It seems probable, however, that interhemispheric differences in catecholamine levels (Robinson, 1979; Zimmerman et al., 1974) are importantly involved.

These experiments obviously indicate that lateralization of neural functions occurs in animals other than man. The induction of lateral asymmetries in the monkeys of Stamm et al. (1975) and in the rats of Dennenberg and his colleagues is a particularly significant observation, since it tells that there is a latent capacity for lateralization within the brains of nonhuman animals, and a lateralized system can be generated by appropriate experiences. The processes that underlie the experimental induction of lateralized functions in monkeys and rats may resemble, in some ways, those which permit the right hemisphere in humans to mediate linguistic functions after damage to the language areas on the left hemisphere in infancy and childhood.

Perhaps mammals and birds have generally been preadapted to develop lateralized control systems for a long time. If so, it is not hard to imagine that, at different times and in the phylogeny of different and unrelated species, circumstances arose in which animals with more lateralized functions enjoyed a selective advantage over less lateralized conspecifics; continued selection pressure would lead to progressively more highly lateralized populations.

Functional lateralization may thus have arisen independently in several lines of descent in response to a variety of species-specific problems in adaptation; expressions of laterality in different species are therefore probably best regarded as analogous. The history of research on other problems in neuropsychology strongly encourages the belief that neurological analyses of analogous types of functional lateralization in other animals will significantly aid us in our efforts to understand cerebral lateralization in humans.

The nervous system is more conservative than the

behavior it mediates (Warren & Kolb, 1978). The positive reinforcement system is in essentially the same place and the effects of stimulating it electrically are very similar in goldfish, pigeons, chickens, rats, rabbits, guinea pigs, cats, dogs, monkeys, porpoises, and humans (Valenstein, 1973), in spite of the fact that vertebrates differ substantially in respect to which naturally occurring stimuli act as reinforcers. Likewise, mammalian species differ from one another in almost every measurable dimension of their sex behavior (Dewsbury, 1972, 1975), but sex behavior in all species depends on the integrity of the preoptic nucleus. Destruction of the ventromedial nucleus in the hypothalamus makes mammals fat and mean, no matter what their species-specific patterns of eating and fighting behavior may be.

By analogy, it seems sensible to speculate that, although different functional lateralizations arose in different species to solve different problems in adaptation, all arose from the same sort of preadapted neural mechanism and all operate in basically very similar ways.

### SUMMARY

Developmental and genetic data indicate that handedness and associated functional asymmetries in the human brain are heritable, species-specific characteristics. Paleoneurological evidence shows that the left and right parietal opercula were structurally differentiated in humans 40,000 years ago.

Comparative behavioral and neuropsychological findings very strongly suggest that the human pattern of handedness and cerebral laterality is species-unique and that no truly homologous traits are to be found in nonhuman mammals. Handedness has been most extensively studied in macaque monkeys. An equal number of monkeys are right- and left-handed. Their hand preferences are initially weak, inconsistent over tasks requiring different kinds of manipulations, and strongly influenced by learning and experience. The cerebral hemispheres contra- and ipsilateral to the preferred hand contribute equivalently to visual learning by monkeys. The left hemisphere is superior to the right in processing acoustic signals in both right- and left-handed macaques; the hemispheres function asymmetrically, but independently of hand preference.

Although the human pattern of lateralization of function is species-unique, apparently analogous forms of lateralization of function have been observed in the brains of several nonhuman species. For example, the motor control of singing by canaries, chaffinches, and white-crowned sparrows is mediated exclusively by the left cerebrum, and early experience preferentially affects the right hemisphere in rats.

Functional lateralization in the central nervous

system is not unique to humans, and is perhaps not extremely rare in mammals and birds. Functional lateralization seems now to have evolved independently in a number of species whenever lateralization of a specific function afforded a selective advantage.

The several types of cerebral laterality observed in nonhuman species are most probably analogous rather than homologous to the functional specification of the hemispheres in man.

However heterogeneous the origins of species-specific forms of functional asymmetries in the nervous system may be, there is reason to believe that studies of laterality in other animals may illuminate the mechanisms of laterality in humans. Although species differ in the particular functions that are lateralized in their brains, the molecular and neural bases of laterality are probably very similar in different species. The copulatory and feeding behaviors in mammals are highly variegated, but all are regulated by common neural mechanisms.

### REFERENCE NOTE

1. Dewson, J. H. Personal communication, 1976.

### REFERENCES

- ANNETT, M. The distribution of manual asymmetry. *British Journal of Psychology*, 1972, **63**, 343-358.
- BECK, C. H. M., & BARTON, R. L. Deviation and laterality of hand preference in monkeys. *Cortex*, 1972, **7**, 339-363.
- BLAU, A. *The master hand*. New York: American Orthopsychiatric Association, 1946.
- BIGGS, G., & NEBES, R. Patterns of hand preference in a student population. *Cortex*, 1975, **11**, 230-238.
- BROOKSHIRE, K. H., & WARREN, J. M. The generality and consistency of handedness in monkeys. *Animal Behaviour*, 1962, **10**, 222-227.
- BUTLER, C. R. A memory-record for visual discrimination habits produced in both cerebral hemispheres of monkey when only one hemisphere has received direct visual information. *Brain Research*, 1968, **10**, 152-167.
- COLLINS, R. L. On the inheritance of handedness: I. Laterality in inbred mice. *Journal of Heredity*, 1968, **59**, 9-12.
- COLLINS, R. L. On the inheritance of handedness: II. Selection for sinistrality in mice. *Journal of Heredity*, 1969, **60**, 117-119.
- COLLINS, R. L., & WARD, R. Evidence for an asymmetry of cerebral function in mice tested for audiogenic seizures. *Nature*, 1970, **226**, 1062-1063.
- COREN, S., & PORAC, C. Fifty centuries of right-handedness: The historical record. *Science*, 1977, **198**, 631-632.
- CRONHOLM, J. N., GRODSKY, M., & BEHAR, I. Situational factors in the lateral preferences of rhesus monkeys. *Journal of Genetic Psychology*, 1963, **103**, 167-174.
- DART, R. A. The predatory implement technique of *Australopithecus*. *American Journal of Physical Anthropology*, 1949, **7**, 1-38.
- DAWSON, J. L. M. B. An anthropological perspective on the evolution and lateralization of the brain. *Annals of the New York Academy of Sciences*, 1977, **299**, 424-447.
- DENNENBERG, V. H., GARBANATI, J., SHERMAN, G., YUTZEY, D., & KAPLAN, R. Infantile stimulation induces brain lateralization in rats. *Science*, 1978, **201**, 1150-1152.
- DEUEL, R. K. 30 monkeys without cerebral dominance. *Neurology*, 1975, **25**, 389.

- DEWSBURY, D. A. Patterns of copulatory behavior in male mammals. *Quarterly Review of Biology*, 1972, **47**, 1-33.
- DEWSBURY, D. A. Diversity and adaptation in rodent copulatory behavior. *Science*, 1975, **190**, 947-954.
- DEWSON, J. H. Some behavioral effects of removal of superior temporal cortex in the monkey. In D. J. Chivers & J. Herbert (Eds.), *Recent advances in primatology* (Vol. 1). London: Academic Press, 1978.
- DIMOND, S. J. Evolution and lateralization of the brain. *Annals of the New York Academy of Sciences*, 1977, **299**, 477-501.
- DOWNER, J. L. Interhemispheric integration in the visual system. In V. B. Mountcastle (Ed.), *Interhemispheric relations and cerebral dominance*. Baltimore: Johns Hopkins Press, 1962.
- EBNER, F. F., & MYERS, R. E. Corpus callosum and the interhemispheric transmission of actual learning. *Journal of Neurophysiology*, 1962, **25**, 380-391.
- ETTLINGER, G., BLAKEMORE, C., & MILNER, A. Opposite hand preferences in two sense-modalities. *Nature*, 1968, **218**, 1276.
- ETTLINGER, G., & DAWSON, R. F. Hand preferences in the monkey: The effect of unilateral cortical removals. *Neuropsychologia*, 1969, **7**, 161-166.
- FALEK, A. Handedness, a family study. *American Journal of Human Genetics*, 1959, **11**, 52-62.
- FINCH, G. Chimpanzee handedness. *Science*, 1941, **94**, 117-118.
- FUSTER, J. M., & BAUER, R. H. Visual short-term memory deficit from hypothermia of frontal cortex. *Brain Research*, 1974, **81**, 393-400.
- HAMILTON, C. R. An assessment of hemispheric specialization in monkeys. *Annals of the New York Academy of Sciences*, 1977, **299**, 222-232. (a)
- HAMILTON, C. R. Investigations of perceptual and mnemonic lateralization in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krautheimer (Eds.), *Lateralization in the nervous system*. New York: Academic Press, 1977. (b)
- HAMILTON, C. R., & GAZZANAGA, M. Lateralization of learning of colour and brightness discriminations following brain bisection. *Nature*, 1964, **201**, 220.
- HÉCAEN, H., & ALBERT, M. L. *Human neuropsychology*. New York: Wiley, 1978.
- HÉCAEN, H., & DE AJURIAGUERRA, J. *Left-handedness*. New York: Greene & Stratton, 1964.
- HEWES, G. W. Current status of the gestural theory of language origin. *Annals of the New York Academy of Sciences*, 1976, **280**, 482-504.
- HICKS, R. E., & KINSBOURNE, M. On the genesis of human handedness: A review. *Journal of Motor Behavior*, 1976, **8**, 257-266.
- HICKS, R. E., & KINSBOURNE, M. Human handedness. In M. Kinsbourne (Ed.), *Asymmetrical function of the brain*. New York: Cambridge University Press, 1978.
- HOLLOWAY, R. L. Paleoneurological evidence for language origins. *Annals of the New York Academy of Sciences*, 1976, **280**, 330-348.
- LEHMAN, R. A. W. Hand preference and cerebral predominance in 24 rhesus monkeys. *Journal of the Neurological Sciences*, 1970, **10**, 185-192.
- LEHMAN, R. A. W. The handedness of rhesus monkeys—I. Distribution. *Neuropsychologia*, 1978, **16**, 33-42.
- LEHMAN, R. A. W., & SPENCER, D. D. Hand preference and hemispheric learning in the monkey. *Experimental Neurology*, 1972, **36**, 88-100.
- LEMAY, M. Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primate. *Annals of the New York Academy of Sciences*, 1976, **280**, 349-366.
- LEVY, J. A review of evidence for a genetic component in the determination of handedness. *Behavior Genetics*, 1976, **6**, 429-453.
- LEVY, J. The mammalian brain and the adaptive advantage of cerebral asymmetry. *Annals of the New York Academy of Sciences*, 1977, **299**, 264-272.
- MARSHACK, A. Some implications of the paleolithic symbolic evidence for the origin of language. *Annals of the New York Academy of Sciences*, 1976, **280**, 289-311.
- MARTIN, D., & WEBSTER, W. G. Paw preference shifts following forced practice. *Physiology & Behavior*, 1974, **13**, 745-748.
- MCGONIGLE, B., & FLOOK, J. The learning of hand preferences by squirrel monkeys. *Psychological Research*, 1978, **40**, 93-98.
- MONTAGU, A. Tool making, hunting and the origin of language. *Annals of the New York Academy of Sciences*, 1976, **280**, 266-274.
- NOTTEBOHM, F. Asymmetries in neural control of vocalization in the canary. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krautheimer (Eds.), *Lateralization in the nervous system*. New York: Academic Press, 1977.
- PERELLÓ, J. Digressions on the biological foundations of language. *Journal of Communication Disorders*, 1970, **3**, 140-149.
- PETERSEN, M. R., BEECHER, M. D., ZOLOTH, S. R., MOODY, D. B., & STEBBINS, W. C. Neural lateralization of species-specific vocalizations by Japanese macaques (*Macaca fuscata*). *Science*, 1978, **202**, 324-327.
- PRIBRAM, K. H. Hemispheric specialization: Evolution or revolution. *Annals of the New York Academy of Sciences*, 1977, **299**, 18-22.
- REYNOLDS, P. C. Handedness and the evolution of the primate forelimb. *Neuropsychologia*, 1975, **13**, 499-500.
- ROBINSON, R. G. Differential behavioral and biochemical effects of right and left hemispheric cerebral infarction in the rat. *Science*, 1979, **205**, 707-710.
- ROTHER, H. Handedness in the common marmoset (*Callithrix jacchus*). *American Journal of Physical Anthropology*, 1973, **38**, 561-565.
- SACKHEIM, H. A., GUR, R., & SAUCY, M. C. Emotions are expressed more intensely on the left side of the face. *Science*, 1978, **202**, 434-436.
- SHERMAN, G. F., GARBANATI, J. A., ROSEN, G. D., YUTZEY, D. A., & DENNENBERG, V. H. Brain and behavioral asymmetries for spatial preference in rats. *Brain Research*, 1980, **192**, 61-67.
- STAMM, J. S., GADOTTI, A., & ROSEN, S. C. Interhemispheric functional differences in prefrontal cortex of monkeys. *Journal of Neurobiology*, 1975, **6**, 39-49.
- STEKLIS, H. D., & HARNAD, S. R. From hand to mouth: Some critical stages in the evolution of language. *Annals of the New York Academy of Sciences*, 1976, **280**, 445-455.
- TSAL, L., & MAURER, S. Right handedness in white rats. *Science*, 1930, **72**, 436-438.
- UHRBROCK, R. S. Laterality in art. *Journal of Aesthetics and Art Criticism*, 1973, **32**, 27-35.
- VALENSTEIN, E. S. *Brain control*. New York: Wiley, 1973.
- WADA, J. A., CLARK, R., & HAMM, A. Cerebral hemispheric asymmetry in humans: Cortical speech zones in 100 adult and 100 infant brains. *Archives of Neurology*, 1975, **32**, 239-246.
- WARREN, J. M. Handedness in the rhesus monkey. *Science*, 1953, **118**, 622-623.
- WARREN, J. M. The development of paw preferences in cats and monkeys. *Journal of Genetic Psychology*, 1958, **93**, 229-236.
- WARREN, J. M. Handedness and cerebral dominance in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krautheimer (Eds.), *Lateralization in the nervous system*. New York: Academic Press, 1977.
- WARREN, J. M., ABPLANALP, J. M., & WARREN, H. B. The development of handedness in cats and rhesus monkeys. In H. W. Stevenson, E. H. Hess, & H. Rheingold (Eds.), *Early behavior: Comparative developmental approaches*. New York: Wiley, 1967.
- WARREN, J. M., CORNWELL, P. R., & WARREN, H. B. Unilateral frontal lesions and learning by rhesus monkeys. *Journal of*



- Comparative and Physiological Psychology*, 1969, **69**, 498-505.
- WARREN, J. M., GRANT, R., HARA, K., & LEARY, R. W. Impaired learning by monkeys with unilateral lesions in association cortex. *Journal of Comparative and Physiological Psychology*, 1963, **56**, 241-253.
- WARREN, J. M., & KOLB, B. Generalizations in neuropsychology. In S. Finger (Ed.), *Recovery from brain damage*. New York: Plenum, 1978.
- WARREN, J. M., & NONNEMAN, A. J. The search for cerebral dominance in monkeys. *Annals of the New York Academy of Sciences*, 1976, **280**, 732-744.
- WILE, I. S. *Handedness: Right and left*. Boston: Lathrop, Lee & Shepard, 1934.
- WITELSON, S. F. Sex and the single hemisphere: Specialization of the right hemisphere for spatial processing. *Science*, 1976, **193**, 425-426.
- ZIMMERBERG, B., GLICK, S. D., & JERUSSI, T. P. Neurochemical correlate of a spatial preference in rats. *Science*, 1974, **185**, 623-625.

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