REVIEW ARTICLE

Understanding Left-Handedness

Stefan Gutwinski, Anna Löscher, Lieselotte Mahler, Jan Kalbitzer, Andreas Heinz, Felix Bermpohl

SUMMARY

Background: The human cerebrum is asymmetrical, consisting of two hemispheres with differing functions. Recent epidemiological and neurobiological research has shed new light on the development of the cerebral lateralization of motor processes, including handedness. In this article, we present these findings from a medical perspective.

Method: We selectively searched the PubMed online database for articles including the terms "handedness," "left handedness," "right handedness," and "cerebral lateralization." Highly ranked and commonly cited articles were included in our analysis.

Results: The emergence of handedness has been explained by physiological and pathological models. Handedness arose early in evolution and has probably been constitutive for the development of higher cognitive functions. For instance, handedness may have provided the basis for the development of speech and fine motor skills, both of which have played a critical role in the evolution of mankind. The disadvantages of certain types of handedness are discussed, as some cases seem to be associated with disease.

Conclusion: The consideration of handedness from the epidemiological, neurobiological, and medical points of view provides insight into cerebral lateralization.

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The left hand has been an object of special reverence ever since the 1986 World Cup match between England and Argentina, if not earlier. When Diego Maradona scored the most famous goal in the annals of soccer, the left hand that did it went down in history as *la mano de Dios,* the hand of God.

Though this hand was not really God's, but only Maradona's, it was surely guided by the latter's right motor cortex. The contralateral cerebral control of movement is a manifestation of the lateralization of human brain function. It presumably redounds to the advantage of the organism by obviating functional redundancy, thereby making neural processes run faster and more efficiently (1, e1, e2).

The fact that either the right or the left hemisphere can be dominant for motor function, resulting in either left- or right-handedness, seems to be a matter of natural variation. It remains unclear, however, why left-handedness is less common than right-handedness. From an evolutionary perspective, if neither of the two variants conferred any greater advantage than the other, a 50:50 distribution in the population would be expected (e3). On the other hand, if either of them were more advantageous than the other, then the less advantageous variant would be expected to decline in prevalence and then eventually die out (e4, e5).

It seems that motor processes in man and the evolutionary predecessors of mankind have been lateralized for more than a million years, and that right-handedness was more common than left-handedness even in our remote forebears (2, e6). According to studies published in the February and October 2010 issues of *Proceedings of the National Academy of Sciences* (PNAS), cerebral motor lateralization may well have laid the basis for the development of language: Vocal speech is thought to have developed out of the lateralized control of communication through hand gestures (3, 4). This idea has lent new significance to lateralization processes in the course of human evolution.

In this article, we will discuss the current state of knowledge concerning the development of motor lateralization with reference to left-handedness. In particular, we will present the medically relevant aspects of handedness.

The publications reviewed here were retrieved by a selective PubMed search based on the terms "handed-

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ness," "left handedness," "right handedness," and "cerebral lateralization." We chose to review the more frequently cited articles and those that were published in high-ranking journals.

Background

Across all human cultures, left-handedness is found in 5% to 25.9% of individuals and is more common in men than in women (5, e4, e7). Its prevalence varies from culture to culture and from region to region (e8), for unknown reasons.

Left-handedness has apparently existed in human beings and their evolutionary predecessors for more than a million years (2, e6), as can be concluded from ancient weapons and tools, unearthed by archeologists and paleontologists, that were apparently made or used by left-handers (e9). Moreover, the technique of some Paleolithic cave paintings points to the early existence of left-handedness, as do direct hand-prints found on cave walls (2). Another line of evidence for early left-handedness comes from the measurement of certain features of the bones of the upper limbs (length, density) in ancient humanoid remains (2, e10).

In summary, the archeological and paleontological findings imply that handedness developed early on in human phylogeny.

As with other natural variants, such as sexual orientation or skin color, handedness has also been an object of stigmatization. In Europe, left-handedness was considered undesirable, and even a sign of inferiority, until well into the 20th century. R. Braun, writing in the German medical journal *Klinische Wochenschrift* in 1941, had this to say: "We can only conclude that the right side generally does correspond to what is right. Physically or otherwise uncoordinated persons are called *gauche* [orig. *linkisch*, 'leftish'], and we may well think that something about them just isn't right." (6)

Until the 1960s, it was common to try to convert left-handers to right-handedness; in particular, children were forced to write with the right hand.

Even today, the left hand is considered impure in some cultures, being the hand that is used for wiping one's behind, while all other tasks are assigned to the right hand (e8).

Genetic aspects and frequency distribution of handedness

Handedness is thought to be partly hereditary (5, e7). Left-handers are more likely to have left-handed parents, particularly left-handed mothers; this indicates possible maternal transmission (e7, e11). Twin studies also point to a possible genetic component, as the handedness concordance rate of identical twins is higher than that of fraternal twins (81.2% vs. 73.3%) (7). The handedness of adopted children corresponds more closely to that of their biological parents than to that of their adoptive parents (8, e12).

Moreover, the intensity of handedness varies: Some activities are performed with the non-dominant hand. The tendency toward ambidexterity is more pronounced among left-handed persons (e13, e14). The frequency of "pure" ambidexterity is hard to assess. It seems to be low, with estimates ranging from 0% to 2%, because, even when the two hands are equally adroit in motor skills, one hand nonetheless tends to dominate in the actual performance of motor activities (e15, e16). There is also an extreme form of right-handedness in which practically all activities are carried out by the right hand and the left hand is only minimally involved.

The origins of handedness

Handedness probably begins to develop in the uterus: Fetuses suck the right thumb more often than the left (e17), move the right arm more (e18), and lie more often with the head turned to the right (e19). The handedness arising in fetal life is thought to persist as the individual's postnatal handedness (e20).

In most cases, left-handedness appears to be the result of natural variation, but some types of handedness may be the expression of an early developmental disturbance or genetic defect (e21, e22). This is implied by the observation that left-handedness and extreme right-handedness are more common among persons with certain diseases and developmental abnormalities.

This phenomenon is seen, for example, in epilepsy, schizophrenia, and autism (9, 10, e23, e24). Moreover, neural tube defects and some types of cleft lip and palate that are thought to be due to intrauterine disturbances are also associated with left-handedness (e25, e26). Left-handedness is reportedly 1.2 to 2 times more common among schizophrenics than in the normal population (e27, e28).

A possible explanation for the more common prevalence of certain diseases among left-handers and extreme right-handers is that intrauterine or perinatal disturbances such as infections or brief phases of hypoxia alter cerebral development. Thus, it has been found that the differentiation of interhemispheric connections such as the corpus callosum can be affected in certain developmental phases, leading to extreme right-handedness (9, e23, e29).

The development of the left cerebral hemisphere, which probably takes longer to mature than the right hemisphere, might be affected in other phases of brain development. This would result in a transfer of motor functions from the otherwise dominant left hemisphere to the right hemisphere, leading to left-handedness (11, 12, e30–e32).

Further evidence suggests that elevated testosterone concentrations during intrauterine life can affect handedness by promoting the loss of callosal axons or by inhibiting the development of the left hemisphere during certain phases of cerebral maturation (9, 12, e23, e29, e33– e36). The testosterone hypothesis is controversial, however, as it is mainly based on observations from animal experiments.

There are several genetic explanatory models for the development of handedness. Annett's right-shift hypothesis postulates the existence of a gene encoding the necessary information for a shift of functions such as language and manual skills into the right hemisphere (e37).

Certain types of developmental disturbance also seem to be linked to the distribution of handedness. Their relation to left-handedness has been more extensively studied than their relation to extreme right-handedness.

Left-handedness is significantly more common in persons who were born in the spring or early summer (March to July) (e38). Perhaps, in such persons, intrauterine cerebral development during the winter months has been affected by altered vitamin D metabolism owing to the lack of sunlight; immune mechanisms related to the higher incidence of viral infections in winter might be another cause (13, e39).

Moreover, left-handedness is associated with perinatal stress (e30–e32): Left-handed persons are more likely to have had Rh incompatibility and to have been born prematurely, and their Apgar scores are lower on average (11, e40). (The Apgar score for neonates was devised by Dr. Virginia Apgar; a mnemonic "backronym" is Apgar = **a**ppearance [skin color], **p**ulse [heart rate], **g**rimace [reflex irritability], **a**ctivity [muscle tone], and **r**espiration.) More than half of all children of very low birth weight (under 1000 g) are left-handed; this finding is statistically significant (14).

Certain types of left-handedness also display a statistically significant association with developmental delays in childhood, of various kinds (15, e41–e43):

- The onset of sexual maturity is later, on average, among left-handers than among right-handers.
- Secondary sexual characteristics (pubic hair, deepening of the voice in boys) appear later, on average, in left-handers.
- Left-handers tend to be shorter.

Dyslexia has also been reported to be more common in left-handers (e44).

In summary, neither left-handedness nor extreme right-handedness can be considered a sign of increased vulnerability to disease, as both are normal variants. In rare cases, however, either one can be the expression of a cerebral developmental disturbance and can thus be associated with other, related disease manifestations.

Handedness and lateralization in evolution

There are multiple indications that left-handedness is associated with more pronounced bilaterality of cognitive processing (e13). 97% of right-handers have their motor speech area located exclusively in the left hemisphere (19, 20, e45, e46), but only 60% of left-handers have it exclusively in the left hemisphere; in 30%, motor speech processing is bihemispheric, while, in 10%, it is localized to the right hemisphere.

Multiple studies have also revealed that the corpus callosum of left-handers tends to be larger (21, e47, e48). This may be a sign of greater interhemispheric connectivity and may be associated with certain cognitive skills, such as language fluency and retentiveness (e49, e50).

Greater interhemispheric connectivity in left-handers might account for the reported findings that left-handers are more likely to have an IQ score above 131 and to have exceptional mathematical ability (e51–e53).

Left-handedness is also more common among proficient musicians (e54, e55), perhaps partly because left-handers are better at using both hands at once (e13). There is also some controversy over a possible connection between mainly right-hemispheric language processing and high creativity (e56).

Furthermore, left-handedness is unusually common among successful high-performance athletes, particularly in one-on-one sports such as tennis, boxing, and judo (e4, e57). Left-handers in these sports might benefit not only from their greater dexterity with both hands, but also from a potential surprise effect on their opponents when they strike a ball or land a blow from the left side instead of the right. Many examples from sporting history might be adduced on this point, e.g., Andreas Brehme's goal scored with the left foot in the 1986 World cup quarter-final (Germany vs. Mexico) or Maradona's *mano de Dios,* mentioned above.

Such phenomena provide an interesting counterpoint to the so-called right-sided world hypothesis (e58), which concerns the disadvantages of left-handers in a world where right-handedness is the rule. For example, non-right-handers are at greater risk for accidents, because many of the machines that they use (e.g., automobiles) are constructed for right-handers; "emergency buttons," too, tend to be located on the right side (16, e59). It has even been reported that left-handers tend to die a few months or even years younger than right-handers; the potential causes that have been considered include a variety of extrinsic factors (e.g., a higher accident rate) and intrinsic ones (e.g., a higher rate of certain diseases) (17, 18, e60).

Left-handedness thus seems to confer advantages and disadvantages whose net result is a relatively stable distribution of left- and right-handedness. This is an example of continuous polymorphism, i.e., the persistence of multiple types in a population (e61, e62). Game theory has been adduced to explain how continuous polymorphism is possible (22, e63): for example, the surprise effect of left-handedness on opponents in one-on-one confrontations might give left-handers an evolutionary advantage (e4). This might be called "survival of the unexpected," rather than "survival of the fittest": Left-handedness is advantageous in such situations only because it is rare.

On the societal level, left-handers might enjoy a selective advantage because of their increased interhemispheric connectivity, possibly leading to enhanced cognitive abilities, such as creativity and language skills.

The lateralization of brain function was long considered an exclusively human phenomenon. It was even viewed as a feature acquired at the moment when evolution began to differentiate mankind from prehuman creatures and as a prime cause of the development of higher cognitive functions. When such functions are impaired, lateralization can be viewed as a predisposing factor for the development of psychosis (3, 4, e64, e65).

It has been hypothesized that the lateralization of language in (usually) the left hemisphere is a consequence of the lateralization of motor function that appeared earlier on in human evolution. According to this hypothesis, manual gestures were originally the main mode of human communication, and were then gradually supplemented and replaced by language (e66, e67).

Another hypothesis postulates the reverse sequence of events (first language lateralization, then motor lateralization). This issue has not yet been resolved.

In any case, recent research has shown that lateralization pervades the animal kingdom and is certainly not a human particularity. Birds, for example, grasp mainly with the left leg, and their song system is lateralized to a single hemisphere (e68).

Cerebral lateralization is also found in dogs (e69), chimpanzees (e70), and horses (e71). Clapham et al. examined whale jaws and found a greater degree of erosion on the right side than on the left (e72).

Lateralization of other functions

Other aspects of motor control are lateralized as well, including the control of the lower limbs, although "footedness" is less marked than handedness (e73, e74). Right-handedness is more commonly associated with right-footedness; left-handedness is more commonly associated with either right-and-left-footedness or right-footedness (e73, e74). One side also appears to be dominant for the perception of visual stimuli. "Eyedness" (e.g., the eye with which one looks through a telescope) is correlated with handedness (e73, e74, e75). In general, visual stimuli that are presented to the left hemifield, and are thus processed in the right hemisphere, seem to be perceived more strongly, while there is a "pseudoneglect" for right-sided stimuli (e76).

Further lateralizing tendencies have been described for the senses of hearing, taste, and smell (e73, e77).

Research on emotion has yielded evidence of lateralizing tendencies in emotional processing. In general, positive emotions seem to be processed mainly in the left hemisphere, negative ones mainly in the right hemisphere (23, e78). Whether the reverse situation obtains among left-handers is currently debated (e79). These general observations provide the motivation for the imbalance hypothesis of affective diseases (e80), according to which the left hemisphere is less active in depression, the right hemiphere in mania. This idea is supported by a number of lesional (e81, e82) and functional-imaging studies (e83, e84), but a meta-analysis failed to reveal any asymmetry of brain activity in depressed patients (e85).

Differential processing of emotions and sensations on the two sides seems to occur in other areas as well. In 2003, Güntürkün found in a field study that 64.5% of people turn their head to the right while kissing (24). In 2009, Marzoli found that cadging cigarettes in a discothèque is more likely to succeed if the request is whispered into the right ear rather than the left (25).

In general, motor functions seem to be more strongly lateralized than sensory, emotional, and cognitive functions. For example, speech production seems to be more strongly lateralized than the understanding of speech (e62).

Overview

The two hemispheres of the human cerebrum are not symmetrical and possess different functions and specializations. Cerebral lateralization apparently arose early in the course of human phylogeny and may have been a decisive factor in the development of complex cognitive control processes.

Human cerebral lateralization is most evident, firstly, with respect to language, and, secondly, with respect to handedness and the exceedingly fine motor skills that go along with it—two aspects of brain function that are intimately linked to human evolutionary development. Fine motor control provides the basis for our access to the modern world; it enables us to manipulate not only tools and weapons, as our remote ancestors did, but also computers and medical devices.

KEY MESSAGES

- Handedness has probably existed for more than a million years and was a precondition for the evolutionary development of language and fine motor function.
- Left-handedness and extreme right-handedness usually occur as normal variants but, in rare cases, can be an expression of disturbances of cerebral development.
- Lateralizing tendencies are seen for other cerebral functions as well, including language and emotion.
- Understanding the origin of handedness helps us understand the evolutionary development of the brain.

Conflict of interest statement

Dr. Gutwinski has received reimbursement of participation fees for scientific meetings and continuing medical education seminars from the Janssen-Cilag und Biogen Idec companies.

Dr. Löscher has received reimbursement of participation fees for scientific meetings and continuing medical education seminars, as well as travel and accommodation expenses, from the UCB and EISAI companies.

Prof. Heinz has received lecture honoraria and unrestricted grants from Eli Lilly, Janssen-Cilag, and Bristol-Myers Squibb.

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