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Functional Asymmetry in the Light of Human Evolution

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Some functional asymmetries in other species may be evolutionary precursors of human laterality. However, the strong population bias toward right-handedness is uniquely human.

In this article, the most important steps in the increasing of human knowledge about emergence of laterality and evolution of handedness are briefly reviewed. The factors and mechanisms involved in these processes are analyzed, along with the evolutionary advantages of either symmetry and asymmetry.

The author considers that even in the most exhaustive review articles, the genetic bases of handedness and the rest of the factors involved are considered somewhat far apart from each other and proposes two explanations of this fault.

It is emphasized that the only efficient way to further promote our knowledge on this topic is to always presume some mutation(s) and to consider all the other factors and mechanisms simply as instruments by which the natural selection realizes the most appropriate choice.

Key words: asymmetry, laterality, handedness, human evolution.

Dichotomy or Continuity – the Eternal Dilemma

Throughout several centuries, we humans have wondered whether we are set apart by some unique property of mind or deportment, or do we differ from other species only in degree, that is, whether we differ in some fundamental way from other animals. The answer to this question is of vital importance to psychology, because it dictates whether we can create general theories that apply to other animals as well as to humans, or whether we must reserve at least a part of psychological theory for humans only. The question is also fraught with moral and religious implications. Since we have exploited other animals in multifarious ways, we have a strong vested interest in believing ourselves to be fundamentally different and indeed superior, and this makes dispassionate assessment difficult [4].

The origins of discussion of the issue go back to the 17th century philosopher Rene Decartes, who was much impressed by clockwork models of animals that were popular at that time and wondered if it might be possible, in principle, to construct a perfect replica of a human being. He concluded that it was not and this conclusion was later considered as the stage for a dichotomy. Alternatively, it was Charles Darwin with his theory of natural selection as the basis of evolution, who provided the intellectual ground for continuity, considering that the difference in mind between man and higher animals, great as it is, certainly is one of degree and not of kind.

Behaviorism, begun by Watson [35] emphasized continuity between species. The same opinion was supported by the new connectionists of the late 1980's in terms of modern informatics. On the contrary, Chomsky [2] argued that human language, characterized by its generativity and creativity is unmatched by any form of communication between animals and is not amenable to behavioral analysis.

Debates as to whether there is continuity or discontinuity between humans and other species have also centered of the role of consciousness; to some authors [14, 19, 27] it distinguishes qualitatively humans from other species, others (e.g., 15) have argued that animals other than humans are capable of conscious awareness, implying a continuity rather than a dichotomy.

Results of modern biochemical analysis have also been evoked as arguments in this discussion. These results tell us that, at molecular level, humans and chimpanzees are at least 98 % identical, probably close enough to make a hybrid species possible [21, 25]. However, even these data are not convincing enough for some participants in the discussion to definitely resolve the dilemma in question.

Laterality as a Demarcation Line

Rather than rely on subjective criteria, it would clearly be more satisfactory if we could discover some objective framework within which to discuss the issue. One objective characteristic that does seem to distinguish humans from other species is our manifest laterality. Although other mammals and primates may show a preference for one paw or hand over the other, only in humans does there appear to be a marked population bias in favor of one hand. Right handedness is almost certainly universally human, in the sense that it is characteristic of all human cultures [3]. This suggests that it is a biological rather than a cultural endowment. At that, the hands seem to have much to do with the visible signs of human uniqueness, namely the purposeful construction of tools and artifacts and the shaping of the environment toward our own ends. Another aspect of human laterality is the predominantly left-cerebral representation of language and, particularly, of speech.

On the other hand, it is important not to overstate the case. Recent evidence suggests that laterality does not mark humans off from other animals quite so starkly as it was thought. At least some functional asymmetries in other species resemble those in humans, and may be evolutionary precursors of human laterality. Furthermore, not all humans are right-handed and not all have language represented predominantly in the left-cerebral hemisphere. We must be careful to avoid the implication that the 12 % or so who are left-handed or the somewhat smaller minority with bilateral or right-cerebral representation of speech, are somehow throwbacks to a more primitive primate form.

Symmetry and Asymmetry – Evolutionary Advantages

Symmetry is not a natural property of biological matter. The fundamental molecules of living tissue are characterized by asymmetry, not symmetry. Nature has apparently been at some pains to construct organisms that are largely symmetrical out of building blocks that are asymmetrical [4]. It seems reasonable to argue that bilateral symmetry is an adaptation, selected because of its survival value. A primary consideration here may have been locomotion. Linear movement provides the most efficient path between two points and it is best accomplished by limbs that are placed and shaped in symmetrical pairs. To a freely moving animal, moreover, the environment is essentially without left-right bias. An animal needs to be able to react with equal facility in either direction because predators, prey and obstacles are equally likely to appear on either side. If such is the case, the animal must be equally receptive to external events that occur on the two sides, so that sense organs as well as limbs are symmetrically placed. It follows that the external body plan is itself bilaterally symmetrical and that those parts of the brain and nervous system that have to do with sensory and motor functions also tend to be organized symmetrically.

It can be argued further that symmetry is also adaptive in the storage of spatial learning because skills learned in one context may have to be used later in the right-left reversal of that context: for example, an attack from the left may be followed by an attack from the right [6, 7]. The advantages of symmetry might apply to procedural rather than declarative memory [32]. Thus, System I and System II were distinguished [30]: System I refers to memory for skills and habits that involve generalization from one situation to another and codes the invariances between different situations. System II, by contrast, is concerned with memory for particular events, as in remembering where particular things are located, and preserves variances across episodes. In this system, it would be useful to preserve the right-left sense or parity of an event, which requires a structural asymmetry [6].

The internal organs of the body, such as the heart and stomach, are located and shaped asymmetrically, probably because this allows for more efficient packaging.

While the functions for which bilateral symmetry is important are those having to do with reactions to the special surrounds, symmetry is not important with respect to functions that are not tied to or constrained by the spatial environment, including functions that are sequential rather than spatial or functions that are generated internally rather than in response to external events. A prime example is, of course, spoken language. The asymmetrical representation of such functions may have come about simply because there was not advantage to be gained from bilateral symmetry. There may also have been some positive evolutionary pressure toward asymmetry.

Laterality in Other Species

It is commonly supposed that the strong population bias toward right-handedness is uniquely human [4, 5]. Curiously, the only species known to match the population bias that is evident in humans is the parrot. The vast majority of parrots prefer the left foot in picking up objects, and the incidence of right-footed parrots is about 12 to 13 %, which is remarkably close to the incidence of left-handedness in humans. This incidence fits the model in which 25 % of the population is homozygous for a recessive allele in which footedness is determined at random [13, 28].

Mice may evidence strong and persisting preferences for one or other paw but, in the absence of any environmental biases, there are as many left-pawed as right-pawed mice, and the same appears to be true of rats [26].

Finch [11] found that the chimpanzee, humans nearest primate relative, does not show the population-level right-handedness characteristic of humans and his observations have been largely corroborated [23, 17].

MacNeilage et al. [22] have reviewed the evidence on handedness in nonhuman primates and have concluded that there is evidence for a left-hand preference in visually guided reaching in Prosimia, Old World monkeys and New World monkeys. They suggested that the first stage in the evolution of laterality occurred when the early primates used one arm to support themselves in an upright position, so that the other arm and hand became the more specialized in reaching for food and even for catching flying insects. Typically, it was the right arm that was used for support, so that the left arm and right hemisphere was specialized for visually guided reaching, an asymmetry that was a precursor of human right-hemispheric specialization. Later, when the upright posture became less dependent on support from the right arm, a right-hand specialization for manipulation may have evolved from the postural specialization. However, the evidence for left-handed reaching and right-handed manipulation in nonhuman primates is too week to be convincing. It seems more prudent to accept the verdict of Warren [34] that "there is no compelling reason to regard handedness in monkeys as either homologous or analogous to handedness in humans".

On the other hand, Hamilton and Vermeire [16] reported an evidence for a right-hemisphere advantage in monkeys for the discrimination of monkeys faces. Ifune et al. [18] reported that the right hemisphere in monkeys was more responsible than the left one to videotaped recordings of monkeys, people, animals and scenery. These observations are consistent with evidence that perception of faces in humans is largely, although not exclusively, mediated by the right hemisphere [10].

In general, nonhuman primates do exhibit some interesting asymmetries that may have been precursors (although rather week) of human laterality in our common ancestors. In any case, it seems likely that the pattern observed in humans did not emerge until the hominid line split from the other primates.

Why the Right Hand?

A lot of attempts have been made to explain why the right hand was preferred as a dominant to the left one. It was supposed, for instance, that, given the left position of the heart, it was preferable to hold the buckler in the left hand to better protect it and to brandish the sword by the right hand. However, the archaeological findings show that the right hand dominance is much older than the appearance of the first bucklers. Another explanation is based on the link between sympathetic nerves going to the left ventricle and somatic nerves going to the left hand. Reflexes derived from this link (e.g. the sharp pain, propagating along the ulnar axis of the left hand in case of coronary trouble) urged humans to spare the left hand and to assign much bigger efforts to the right one. According to a third hypothesis of this kind, the blood passes through the left carotid artery easier and under a higher pressure than through the right one; the bigger blood supply of the left hemisphere has made it the cerebral basis of language and favoured the hand governed by it, to become the dominant one.

Evolution and Handedness in Hominids

The hominid line diverged from the apes perhaps 5 million years ago [12]. The main characteristic of hominids was bipedalism – they habitually walked upright on their two hind legs. Leakey [20] discovered a set of footprints at Laetoli, in Northern Tanzania, that date from about 3.5 million years B.P. and that had been left there by two hominids who clearly walked upright. They presumably belonged to *Australopithecus afarensis*, the earliest known hominid. The first clearly identified specimen belonging to this species was the famous Lucy, dating from some 3.4 million years B.P.

By about 2 million years B.P. there were several species of australopithecines, including *A. africanus, A. robustus* and *A. boisei*, as well the first species identified as belonging to the homo line, *Homo habilis*. The last was distinguished from the australopithecines by having a larger cranial capacity, although it was still only about one half that of modern humans (21).

The next step occurred some 1.5 million years B. P., with the emergence of *H. erectus*, whose brain was still larger than *H. habilis,* and who showed the beginnings of organized society and developed tools with some sort of design specification. It is the first hominid whose remains have been found outside of Africa and who may have taken variable forms of which only one led to *H. sapiens* [12]. The archaic *H. sapiens* (the Neanderthals) date from some 300 000 years and become extinct some 35 000 years B.P. The line that survived to become anatomically modern humans, *H. sapiens sapiens,* appears to have evolved from a taxon of *H. erectus,* that remained in Africa (about 200 000 years ago) and subsequently radiated to other parts of the globe.

The predominance of right-handedness goes back at least 5000 years [8]. But the analysis of tools takes it back considerably further than that. Microscopic analysis shows that tools used in the upper Paleolithic, dating from about 35 000 to about 8 000 B.C., were predominantly worn on the right side, indicating that they were mostly held in the right hand [29]. Tools recovered from Clacton in England, and dating from the Lower Paleolithic some 50 000 to 100 000 years ago, also seem to have been used predominantly by right-handers. And going back even further, T o t h [33] has examined flakes formed from the manufacture and sharpening of tools, recovered from sites at Koobi For a in Kenia, and dating from the time of *H. habilis* some 1.4 to 1.9 million years ago; the majority of users were right-handed. Even the australopithecines may also have been right-handed. D a r t [9] examined the fossil remains, dated as some 2 million years B. P. Many of the specimens had evidently been clubbed to death by the murderous australopithecines, and the location of the skull fractures indicated that the majority of attackers were right-handed.

Genetic Background

Several generations of Soviet authors (e.g. 36, 37), following E n g e l s [38], supported and overestimated his conception about "the role of labor in transformation of monkey in man", "the human hand as organ of labor and its product", etc. Such a "transformation of monkey in man" is not only impossible. Even if we accept to impart an evolutionary meaning to this expression, the general scheme remains very elementary: when the labor "appeared", it developed progressively the hand (mainly the right one, it is not known why) and the improved hand, in its turn, gradually improved the manufacture skills.

According Annett's theory [1], cerebral asymmetry and handedness are determined by a single gene locus. The dominant, right-shift allele produces right-handedness and left-cerebral control of speech in the great majority of those who carry it, either homozygous or heterozygous. Among those homozygous for the recessive allele, there is no overall disposition to be right- or left-handed and they are randomly distributed between the two categories. In fact, the proportion of left-handedness in societies in which the cultural pressure toward right-handedness is minimized, does seem to asymptote at about 12.5 %, that is, one half of those homozygous for the recessive allele. Mc M a n u s's [24] model is somewhat similar; it postulates the incidence of right-handedness to be 100 % among DD homozygotes, 75 % among heterozygotes DC and 50 % among CC homozygotes.

The most probable evolutionary scenario is that the D allele emerged at some point of hominid evolution as a mutation in a single individual, and spread through the population over succeeding generations, raising the incidence of right-handedness to about 90 %. Had this allele simply conferred an advantage on those inheriting it, it would have replaced alternative alleles and this would be simply a matter of time. However, it is at odds with the apparent stability of handedness ratios. The only way in which two alleles could be maintained in the population in stable proportions would be through the balanced polymorphism due to heterozygotic advantage. That is, CD individuals must have greater fitness than either DD and CC homozygotes, "fitness" referring to the relative number of offspring contributed by an individual to the next generation [31]. Fitness is a probabilistic concept and depends on a number of factors, such as survival rate in infancy or childhood, probability of finding a mate, age at which sexual maturity is reached, and number of offspring produced.

Conclusion

As a whole, publications on the appearance and development of the brain asymmetry and handedness in hominids allow to reconstruct integrally (although rather approximately at some points) the succession of these processes, along with the factors and mechanisms involved.

However, it is our impression that, even in the most exhaustive review articles, the genetic bases of handedness and the rest of the factors involved are considered somewhat far apart from each other. We could suppose a twofold explanation of this fault. First of all, the unconscious influence of ancient "teleological" beliefs that necessity may generate changes in living beings and that changes, acquired during individual life under the pressure of necessity, could be inherited. Second possible reason is that the problem about the genetic background of human laterality is still far from being definitely clarified though there are several quite satisfactory hypotheses about it.

It follows that the only efficient way to further promote our views on this topic is to always presume some mutation(s) and to consider all the other factors and mechanisms simply as instruments by which the natural selection makes the most appropriate choice.

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