

BOOK REVIEW

Comparative Vertebrate Lateralization. Edited by Lesley J. Rogers and Richard J. Andrew. (Cambridge University Press, 2002). [661 pp.]. ISBN: 0521781612, £90.00 hbk.

The human brain is asymmetric, 90% of people being right-handed, and a similar proportion having language in the left hemisphere. A battle is currently raging in the literature about where, how and when that asymmetry arose, and this book provides detailed communiqués from the forces of one side, which perhaps we can call the ‘Universalist’ camp. To somewhat oversimplify the story, this book is packed with 600 pages of detailed evidence from 20 contributors; the Universalists believe that behavioural asymmetries occur in many species of vertebrates, and that by implication there is nothing very special about humans having asymmetric brains and behaviours.

Across the academic trenches lie the forces of the other side, perhaps most strongly represented by Tim Crow, whose recent book (Crow 2003) puts forward the strong suggestion that human functional asymmetry is unique to man, that it provides the neural underpinning for language itself, and that the evolution of language was the key ‘speciation event’ that made man what he is today—and in particular made us the only species on Earth to communicate symbolically, either by spoken sounds, or, as in the case of this review, by the strings of differently shaped little black symbols that we call letters and words. Human culture is unimaginable without language, and Crow argues that humans are unimaginable without cerebral asymmetries. Let us call this the ‘Speciationist’ camp.

This war started, as do many others, with a small skirmish, which concerned handedness in chimpanzees, the closest living relatives to humans. Marchant and McGrew (1996) suggested that free-living chimps in Africa were equally likely to use the right and left hands in complicated and skilled activities such as ‘fishing’ for ants and termites. In contrast, Bill Hopkins and his colleagues have championed the idea, based on data collected with a more experimental paradigm in captive chimps in Atlanta (Hopkins 1995), that the proportion of right-handed chimps is closer to 65%, or about two-thirds. Still nothing like 90%, but very different from the precise 50% expected from fluctuating asymmetry. Whether the differences between these groups reflects differences in testing protocols, task differences, statistical artefacts, or even undue exposure to right-handed human role models, is still being debated.

The chimpanzee battle has now been put somewhat into the shade by the broader Universalist position which says that almost all parts of the vertebrate family tree show behavioural asymmetries, be they fish, amphibia, reptiles, birds or mammals. Recent newspaper stories have described how walruses are ‘right-handed’, and there have been similar accounts of whales showing asymmetries, and this book describes undoubted asymmetries in chicks, frogs and fish. Work has even discussed the possibility of handedness in snakes. This book wisely restricts itself to vertebrates, but there are no doubt similar phenomena in invertebrates (with perhaps the most ancient asymmetry being reported in trilobites (Babcock 1993)), and also in plants, which show phyllotactic and other asymmetries, as were described long ago (Ludwig 1932). All such asymmetries are potentially grist to the Universalist mill. Certainly the research findings are robust, and therefore require explanation.

Although so far a non-combatant, having no research data to contribute, I cannot be entirely neutral in this war, and indeed in *Right Hand, Left Hand* (McManus 2002) I might have seemed to take the view that handedness is unique to humans. In what was, of necessity, a popular book, I purposely avoided discussing the many subtleties of non-human asymmetry, restricting myself to Marchant and McGrew’s study as it made the clear point that there are advantages to being lateralized, although not necessarily to being lateralized in a particular direction—Adam Smith’s point that it always pays to specialize.

When any war is over, it is usually easy to see that the two sides had more in common than they would ever have thought. Let us see how a negotiated peace might possibly arise.

The Universalists and the Speciationists agree that it is evolutionarily and functionally important that the brain is asymmetric. Given that it was only 15 or so years ago that biologists became interested in the mechanisms by which vertebrate *bodies* become asymmetric (Brown and Wolpert 1990)—heart on the left, liver on the right, etc.—this is substantial common ground. Both sides also agree that individual organisms inevitably have a tendency to become asymmetric—due ultimately to complex symmetric systems having an inherent instability, which is resolved by becoming asymmetric. The bones of contention all centre on whether the right–left mixture in the population is 50:50, 65:35 or 90:10.

Both sides also seem implicitly to agree that functional asymmetries in frogs or walrus are of fundamental importance, potentially vindicating the Universalists or fatally undermining the Speciationists. Here I think the two sides also share something, but only perhaps because both may well be wrong.

The fundamental problem in any evolutionary argument—and this argument is ultimately to do with phylogeny—is deciding whether characters are similar because of homology or analogy.

Homology occurs because of the common descent of an ancestral trait, whereas analogy occurs because of a shared functional adaptation. Frogs and ducks both have a notochord because of homology, having common chordate ancestors, whereas frogs and ducks have webbed feet by analogy because of their use in swimming, although their immediate common ancestors do not have the trait, as neither do many of their close relatives such as salamanders and eagles, respectively. The argument becomes more complex, however, as the deep mechanism for generating webbed feet in frogs and ducks is probably a shared embryological mechanism common to limb formation in all the vertebrates.

The key question then is whether the myriad asymmetries in vertebrates are analogous or homologous to one another, and whether in particular they are homologous to human handedness. My current view is that analogy is the most parsimonious explanation. Symmetry readily breaks into asymmetry, and in organisms whose bodies are also asymmetric it is hardly surprising if exactly equal proportions do not break to right and left. The real test of vertebrate asymmetries being homologous has to be in the phylogenetic details. I know of only one detailed phylogenetic tree, published by Vallortigara *et al.* (1999), who looked at turning tendencies in 20 species of fish. This tree is of great interest because although some species show systematic biases, some being to right and some to left, and some show no biases, there is no evidence in the phylogenetic tree of common descent—closely related species are no more similar than more distant species. This is the signature of analogy not homology (and it contrasts with the flatfish, whose anatomical asymmetry is homologous, the Achiridae, the most primitive flatfishes, being a racemic mixture, and the two great families, the Soleidae and the Bothidae being right-turning and left-turning, respectively (Norman and Greenwood 1963, Hensley 1997)).

If a peace treaty is to be signed in this dispute, then its preamble should perhaps require the signatories to accept that the Universalists are correct that behavioural asymmetries are very common in the animal kingdom, but that the Speciationists could be correct that humans are humans because of a particularly extreme degree of cerebral asymmetry, which might well have caused the novel neural architecture underpinning the uniqueness of language. Both sides could then collaborate in finding whether there may be deeper level homologies, perhaps in neurotransmitters or other neural functions, which acted as precursors for human cerebral asymmetry. Either way, many of the disputes would be settled if only we knew the molecular genetic basis for human handedness. Whatever the outcome of the war, this book will be a key starting point for those trying to understand it (or perhaps to fight in it).

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