

Or in the hand, or in the heart? - alternative routes to lateralization.

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The authors' examination of the evidence for primate handedness is extremely thorough, but I do not feel compelled to change the conclusion I drew at the end of the review from which they quote (Walker, 1980), that human handedness is secondary to language (i.e. is not inherited from earlier primate handedness). I have two kinds of reason for not retracting this conclusion: first, despite the thoroughness with which the case is stated, it remains possible to doubt the authors' claim that there are population- level asymmetries of hand-preference of some significance in non- human primates. Second, there are positive reasons for preferring the view that human handedness depends on language.

It does not seem to me that the evidence presented by the authors on primate handedness warrants their conclusion. For instance, they cite a claim (Le Gros Clark, 1927) that one gorilla was observed to be strongly right handed, and add this to various other flimsy claims that gorillas are right handed. In fact the gorilla referred to by Le Gros Clark was intensively domesticated at 15 Sloane Street, London for 2 years from 1918, with such success that his table manners were much admired - he always took afternoon tea, and coffee after dinner (Cunningham, 1921). This animal might be quoted as an example of primate behavioural plasticity, but surely not as evidence for population right- handedness. It is particularly striking that in the next paragraph the authors' give about the same amount of weight to Jane Goodall's quarter century of observations of chimpanzees in the wild, which have revealed many pertinent examples of tool using and social skill, but no sign whatever of group handedness (e.g. Kummer and Goodall, 1985). In the case of more empirical studies, the authors over interpret a non-significant left-hand reaching preference found by Beck and Barton (1977).

I share the authors' concern that an account should be given of the relation between human and other primate behaviours which is not in conflict with the theory of evolution, but do not believe that this demands that all features of human psychology should be directly traceable to traits present in other extant species of anthropoidea. It would not violate evolutionary theory if human handedness is derivative from language, rather than being an adaptation directly affected by Mendelian selection. One reason for asserting this is that the variance associated with human hemispheric specialization for language functions is much less than the variance associated with handedness. Another is the case that the genes are usually left-right agnostic, and that therefore any Mendelian selection can only act on sensitivity to somatic left-right gradients (Morgan and Corballis, 1978; Collins, 1985). As a counter-hypothesis which takes account of both these factors, I suggest that human handedness derives indirectly from a little remarked but quite unequivocal somatic asymmetry in primate (and indeed mammalian) innervation of the vocal apparatus.

1) The intrinsic muscles of the human larynx are innervated by the left and right recurrent laryngeal nerves, which branch off from the vagus. 2) The left branch arises from below the aorta, which it partly encircles, while the right begins below the subclavian artery. 3) Thus, taking into account individual variations, the left branch of the recurrent laryngeal nerve is

considerably longer than the right, and gives off more oesophageal branches . 4) The dependence of voice on these nerves was established in the 16th century by Vesalius, using a pig. 5) The greater length and differing course of the left branch is held to be responsible for the finding that the left vocal cord is affected twice as frequently as the right in human laryngeal palsy (Greene, 1980).

The above facts might suggest so some that, given a degree of crossed-lateral control, there could be natural selection of left hemisphere dominance of laryngeal control. However, it is at least equally plausible that the shorter route to the larynx on the right side should provide an exclusively ontogenetic increase in the probability of left hemisphere control of speech. Indeed this could be deduced as a corollary of the theories presented under the heading of 'The ordering of articulatory events' by Lenneberg (1967), who stressed the complexities of co-ordinating the very rapid and highly ordered muscle movements involved in vocalization, these complexities arising from innervation times being as long, or longer than the duration of some of the articulatory events which they control, and from the differential innervation times for various parts of the vocal apparatus, largely due to the long innervation time for the intrinsic laryngeal muscles, which may be 2 or 3 times longer than innervation times for the oral cavity. Either branch of the recurrent laryngeal nerve is capable of sustaining speech in adult patients, but it is arguable that any problems of co-ordination would be most acute during fine timing operations when left and right laryngeal muscles (in the case of the transverse arytenoid, different sides of the same muscle) require different central initiation times if their peripheral activation is to be synchronous. In any event crossed lateral control in the corticobulbar tract may mean that left hemisphere output reaches the larynx sooner than right, and it is not inconceivable that this could supply a developmental impetus for left hemisphere control of vocalisation in the human species, as an aspect of the more general evolutionary factors that led articulate speech to arise from far more rudimentary forms of vocal expression (Walker, 1986). Once the left hemisphere is dominant for speech, there are various ways in which hand preference could be probabilistically affected - either psychologically via the action-directing properties of inner speech or more physiologically by generalisation in the initiation of complex motor acts.

This alternative may be regarded as even more speculative than the authors' own account, and they may find the details easy to dismiss (e.g. MacNeilage, 1970). But my general point is that features shared by human ancestors and those of living primates could have been selectively important in the human line to the extent that humans and apes are distinctively different: we should not feel obliged to abandon evolutionary accounts if other primates do not share our trait of handedness. However, I agree with the authors that there is a large theoretical gap in explanations of the relation between human and primate cerebral lateralization. If their empirical evidence becomes stronger then in order to fill the gap I will gladly shift my allegiance from an asymmetry within the primate heart to a difference between the primate hands.

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