

Continuing commentary on Peter F. MacNeilage, Michael G. Studdert-Kennedy and Bjorn Lindblom (1987) Primate handedness reconsidered BBS 10:247-303.

[Published as Language, handedness and the larynx. *Behavioural and Brain Sciences*, 11, 731-2.]

Stephen Walker Department of Psychology Resource Centre for Life Sciences Birkbeck College, University of London London WC1E 7HX

In their response to commentary on their target article, MacNeilage *et al* (1987; p. 297) agree that “if language originated first, subsequent left-hemisphere control of praxis could easily be motivated”, but resist the suggestion that human handedness is in fact secondary to language, retaining their original hypothesis that human handedness evolved directly from general primate manual and postural asymmetries, with the interaction between language skills and handedness being confined to the sequence of prior left hemisphere specialization for manipulation influencing subsequent hemispheric asymmetries in speech production. Several aspects of the data on both primate handedness and human hemispheric specialization support much more strongly the sequence of speech production specialized in the left hemisphere first, population right handedness second, on either a phylogenetic or ontogenetic dimension.

The authors admit that the evidence for non-human primate population asymmetries in hand usage remains at best ambiguous. If other primate species had clear precursors to human handedness, but no language, this would be strong evidence for the handedness first then language sequence. But at present systematic species handedness, so readily measurable in *Homo sapiens*, remains remarkably elusive in our extant relatives. If other primate species appear to be equally lacking in both handedness and natural language, no conclusions can be drawn about relations between these features in humans. However, there are other reasons for regarding cerebral asymmetries in language skills as being in some sense prior to handedness. One is the greater skew of the statistical distribution of left-hemisphere specialization for language. Estimates vary but, as Annett has emphasized in her commentary on the target article and elsewhere, only at most about 9% of the human population are not “left-brained speakers” (that is would not suffer language impairments from left rather than right unilateral brain damage); and 30-40% have some left hand preferences (Annett, 1985). That is, far more people have some left-hand preferences than have resistance to the effects of left-hemisphere damage on language functions. Direct physiological assessment of speech lateralization has been taken to suggest that more than 90% of right-handers are left-dominant, with 65-70% of left-handers also left-dominant for language (Branch *et al*, 1964; Warrington and Pratt, 1973). It is arguable that manual skills are much more flexible with respect to hemispheric specialization than language skills: relearning manual skills with a different hand is far easier for adults than relearning language skills with a different hemisphere, and many manual skills in bimanual tasks (in particular those of the left hand for the playing of stringed instruments) are clearly performed satisfactorily by the right hemisphere even of those with no left-hand preferences.

These details are more consistent with the view that human population handedness derives from a biasing factor imposed on the random variation in individual limb preferences typically found in mammalian species (Walker, 1980) than with MacNeilage *et al*'s position that manual asymmetries are consistent enough to have been the precursors of other aspects of human hemispheric specialization. Few would wish to introduce anything in addition to a factor which predisposes the left hemisphere to language. Annett (1985) has suggested that

there is a single dominant gene whose possession raises the probability of left-hemisphere language specialization above 50%, but there are several difficulties in supporting a Mendelian account of lateralization, and this theory fails to explain the apparent bias against bilateral language control.

An alternative theory which is based on the completely unambiguous anatomical fact of asymmetrical laryngeal innervation was briefly put forward in my initial commentary (Walker, 1987b), but finessed by the authors' response in favour of a fuller rejection elsewhere, with the comments that the hypothesis would have no implications for behaviour, and is unsupported by neurological evidence. I would wish to add here only a brief response to these comments. First in the context of the contrast between primate grunts and squeals (in anthropoid apes in many cases produced as easily via inhalation as exhalation) and the complexities of articulate speech, and the known bilateral brain control of non-human primate vocalization (see Walker, 1987a for a review), the hypothesis accounts both for a move to unilateral control of speech production, and for a bias towards the left-hemisphere (influenced to some extent by the individual variations which exist for laryngeal innervation). It explains the elusiveness of the behavioural evidence for population handedness in non-human primates by suggesting that this should only be observed in primates with speech, and the variability in human manual preference and skill. Independent neurological evidence for problems produced by left and right output pathways to the larynx being of different lengths is more difficult to come by, but some support may be derived from the literature on stuttering, since this includes suggestions both that stutterers have less complete language lateralization than usual, and that difficulties in laryngeal control contribute to the disorder.

The suspicion that stammerers have incomplete language lateralization has been frequently expressed (e.g. Orton, 1927). It is fair to say that it has been dismissed equally frequently, but evidence has been accumulating recently that there are reliable differences between stutterers and control groups on a variety of measures of laterality (e.g. Sussman and MacNeilage, 1975; Rastatter and Dell, 1987; see Strub, Black and Naesser, 1987 for a review). The idea that laryngeal control (or co-ordination of the larynx with supra- and sub-glottal activities) is problematical in stutterers is equally long standing, since it has always been known that a reduction of voicing variation, as in whispering, singing or mouthing words, radically alleviates dysfluency. Systematic experimentation with speech tasks of varied voicing requirements adds weight to this, and there is increasing confirmation of abnormality from more direct measurement of laryngeal activities in stutterers (Adams and Reis, 1971; Perkins *et al*, 1976; Dalton and Hardcastle, 1977; Shapiro, 1980; Conture *et al*, 1986; Watson and Alfonso, 1987). These findings are consistent with the notion that bilateral control of the larynx causes difficulties which are normally resolved by left-hemisphere specialization.

More generally, the challenge to brain mechanisms presented by the rapid and elaborate serial ordering of human speech has been remarked on by many others apart from Lenneberg (1967), including MacNeilage (1970). It would surely be surprising if asymmetries in output pathways did not complicate this task, especially if, as is probably the case for the larynx, the same pathways contain closed-loop feedback circuits. There is thus ample reason to look to speech itself for the prime mover in the development of human cerebral lateralization, instead of seeking for its origins in a universal primate postural asymmetry, which now, by the very thoroughness of MacNeilage *et al*'s review, seems increasingly chimerical.

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