

## **Brain circuits ancient and modern**

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*Abstract: I support the application of the 'evolution as tinkering' idea to vocalization and emphasize that some of the subcortical parts of the brain circuits used for speech organs retain features common to non-primate mammals and in some cases common to lower vertebrates, pointing up the importance of cortical evolution as suggested by McNeilage.*

No one can disagree that the articulatory organs (tongue, jaws, lips, larynx) are also used in eating. The more peripheral organization of neuromuscular control of these organs (e.g. the functions of the cranial nerves: Lazar et al, 1992; Hamdy et al, 1997) is relatively conservative in vertebrate evolution and therefore some aspects of the neural control of speech can be related not only to brain mechanisms common to humans and non-human primates, but also to non-primate and even non-mammalian cross-species comparisons.

There is for instance a paradox in the fact that comparison of musculotopic organization of the hypoglossal nucleus in the grass-frog (Sokoloff 1991) and a macaque monkey (Sokoloff & Deacon 1992) suggests a high degree of evolutionary conservatism in this part of the control of tongue movement, while the use of the tongue in human speech is sufficiently distinctive to have given rise to the theoretical problem for which McNeilage offers a solution.

It would be consistent with his theme to try to resolve this paradox partly by appealing to a process of corticalization of vocalization, with language evolution being seen as the addition of voluntary and learned cortical control of vocal communication to the fixed subcortical or limbic cortical elicitation of innate acoustic signals (Walker 1994). The hypothesis would have to be that voluntary and learned cortical control of eating and some forms of head and limb movement is characteristic of mammals, but that these aspects of neocortical potential only became fully applied to vocalization at some point during specifically human evolution. Modern brain imaging techniques should allow hypotheses about human cortical and subcortical function to be tested (e.g. Urban et al, 1996)

In cats (Zhang et al, 1995) as well as monkeys (Jurgens 1994) much of the muscular co-ordination required for vocalization is subcortical, involving circuits through the midbrain periaqueductal gray (PAG) and brain-stem nuclei. Davis et al (1996) have recently proposed that the PAG can be classed as a universal brain site for mammalian voice production, generating respiratory and laryngeal motor patterns both for emotional and involuntary sounds and for human speech and song. Jurgens & Zwirner (1996) however suggest that the PAG is a relay station for limbic or emotional vocal expression but is not part of route for neocortical output from facial motor cortex.

There is evidence that control of some kinds of oral activity was a very early feature of the functions of mammalian cortex, because multiple somatosensory cortical representation which includes orofacial regions has been demonstrated in monotremes (Krubitzer et al, 1995) and marsupials (Beck et al, 1996). Dual pathways of output from orofacial motor cortex are observed in guinea pigs (Enomoto et al, 1995) and rats have a specialized “jaw, lips and tongue” region of motor cortex (Ebrahimi et al, 1992). Macaque monkeys can be trained in a variety of tongue-protrusion tasks, and the participation of individual neurons in both sensory and motor cortex in these tasks can be monitored (Lin et al, 1994; Murray and Sessle 1992). This is consistent with the notion that there is voluntary cortical control of the tongue and lips for ingestive movements in non-human primates, but not fine cortical control of the co-ordination of the articulators within vocalization (Hayes and Nissen, 1971). Tongue movements in the above studies appear to be localized in motor cortex separately from jaw movements (Murray and Sessle 1992). It supports McNeilage’s thesis that, within cingulate cortex, recording of single unit activity suggests that some neurons relate to both jaw-opening and vocalization, and there are also neurons that specialize in just one of these activities (West and Larson 1995).

How the flexible control of ingestive tongue and jaw movements in primates with fixed patterns of vocalization developed into human speech remains a puzzle, and the suggestion that lipsmacks and teeth chattering provide intermediaries is at least as well supported as the alternative of hand and arm gestures (Wilkins & Wakefield 1995).

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