The Origin of Broca's Articulate Speech.

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Abstract

Paul Broca's discovery, in the early 1860s of a region of left inferior frontal cortex crucial to speech production (Broca, 1861/1960) was an epoch-making event in what later came to be called cognitive neuroscience. It was the first evidence suggesting that a higher human mental function could be both localized and lateralized in the brain. However, 150 or so years later we find that Broca's faculty of "articulate speech" is out of the spotlight of cognitive neuroscience. It is the focus of various disparate subgroups with virtually no conceptual overlap and therefore no agreed-upon conceptual core. As a result, we don't yet have an accepted neuroscientific theory regarding the nature of Broca's articulate speech. In conformity with Dobzhansky's (1973) dictum that "Nothing in biology makes sense except in the light of Evolution", I present here a unified Neodarwinian framework for approaching the question, focusing explicitly on the issue of descent with modification, a central topic, neglected from the anthropocentric perspective that uniqueness of speech encourages. The approach focuses on the ultimate (evolutionary) causes of speech.

Little help regarding the ultimate causes of articulate speech is available from the dominant generative school of linguistics. Chomsky has been a negative force with his essentialistic anti-evolutionary view that language is "just there", and no phonologist has attempted to produce the necessary descent with modification view of the origin of sound patterns whereby they evolved from simple nonspeech capabilities to complex speech patterns.

Let us begin with the basic properties of the target form—modern speech. Adult segmental speech errors suggest that speech has evolved a Frame/Content mode of organization whereby segmental content elements—consonants and vowels—are inserted into syllable structure frames. The frame may have evolved from cycles of mandibular oscillation associated with mammalian ingestive behaviors, (a motor frame) via an intermediate stage of visuofacial communicative cyclicities (e.g., "lipsmacks") before being paired with phonation to form protosyllables. (MacNeilage, 1998).

What the first sound patterns of speech were like, and something about how they subsequently developed can be surmised from the modern process of speech acquisition (MacNeilage & Davis, 2000). The initial "Frame Dominance" of babbling and early speech is primarily characterized by biomechanical inertia, as the earliest hominin speech must have been. Subsequent speech development, basically from intersyllabic reduplication to intersyllabic variegation, presumably also mirrors the progression from frames to frame/content in ancestral hominins, driven by culturally selected capabilities for transmission of an increasing message set.

The role of Broca's area, broadly defined, in these developments is elucidated by the fact that this region is the main cortical site of ingestive control, including ingestive cyclicities, in mammals (Woolsey, 1958). The recent discovery of mirror neurons in this region (including auditory, ingestive and lipsmack neurons) by Rizzolatti and colleagues helps us to understand its key role in the evolution of the vocal learning capacity that separates us from other primates.

Evidence from psychopathology suggests that the primary role of Broca's region in speech is, as Broca initially surmised, the generation of motor algorithms for consonant and vowel content elements. The cerebellum is also involved in these algorithms. A few years after Broca's discovery, Wernicke identified another speech area, in the posterior superior temporal lobe with a primary role in speech perception, and, as it subsequently turned out, the organization of the mental lexicon.

More recent work makes it clear that at least two additional cortical regions with their attendant connectivities, one in anterior and one in posterior cortex, need to be added to the classical Broca-Wernicke model. In anterior cortex, the role of generation of rhythmic syllabic frames, initially in Broca's region, has passed to another premotor region in medial frontal cortex, the Supplementary Motor Area (in concert with the basal ganglia) (MacNeilage & Davis, 2001) Electrical stimulation and the presence of irritative lesions in this region give rise to involuntary production of rhythmically repeated strings of a single CV form (e.g. "bababababa"). In addition, patients with global aphasia in which the typical destruction of perisylvian cortex is accompanied by damage to the basal ganglia also produce, sometimes as their only utterance, repetitive strings of a single CV form. In fact, Broca's most famous patient "Tan" (whose sole utterance was "tantantan…"—with a nasalized vowel) was such a patient.

The fundamental importance of this rhythmic syllabic form in the evolution of learnable vocalization is indicated by the convergent evolution of a similar form in songbirds. "Syllables" in birdsong are characteristically accompanied by a beak open-close cycle, and electrical stimulation of the telencephalic nucleus HVC in zebra finches and canaries elicits rhythmic syllable production (Vicario and Simpson, 1995). Even electrical stimulation of the HVC in vitro elicits discharges at the typical syllable rate.

The second additional region, in posterior cortex, is the posterior inferior parietal lobe. This region has been firmly established as a locus associated with the phonological loop of working memory for speech (see Arboitiz and Garcia, l997). Presumably it is involved in specification of spatial targets (MacNeilage, 1970) and/or sensory goals for speech.

Important recent anatomical evidence of perisylvian connectivities provided by Catani et al (2005) is consistent with the tripartite (temporal, parietal, frontal) perisylvian control structure suggested here. In addition to classical temporo-frontal arcuate fasciculus, perhaps primarily involved in repetition, there are temporoparietal and parietofrontal circuits perhaps more involved in spontaneous generation of speech partially involving somatic representations.

It is important to note here that there is no evidence in cognitive neuroscience for a locus of an abstract mental representation of phonology of the kind required by modern generative phonology. Instead, the findings are consistent with an embodiment perspective in which control is vested in centers and pathways associated with the physically based actions of the body in speech—auditory, somatic and motor— and their physical consequences. Instead of an abstract master controller, there is a distribution of loci of control between the four cortical regions discussed here—posterior temporal cortex, posterior parietal cortex, inferior frontal cortex, and medial premotor cortex changes depending on the speech task.

References

Arboitiz, F. & Garcia, R.V. (1997) The evolutionary origin of the language areas in the human brain: A neuroanatomical perspective. *Brain Research Reviews*, 25, 381-396.

Broca, P. (1861/1960) Remarks on the seat of the faculty of articulate language followed by an observation of aphemia. In G. von Bonin (Ed.) *Some papers on the cerebral cortex*. Springfield Ill.: C.C. Thomas.

Catani, M.C., Jones, D.K., & Ffytche, D.H. (2005) Perisylvian networks of the human brain. *Annals of Neurology*, 57, 8-16.

Dobzhansky, T. (1973) Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher*, 35, 125-129.

MacNeilage, P.F. (1970) Motor control of serial ordering of speech. *Psychological Review*, 1970, 77, 182-196.

MacNeilage, P.F. (1998) The frame/content theory of evolution of speech production. *Behavioral and Brain Sciences*, 21,499-546.

MacNeilage, P.F. & Davis, B.L. (2000) Origin of the Internal Structure of Word Forms, *Science*, 288, 527-531.

MacNeilage, P.F. & Davis, B.L. (2001) Motor mechanisms in speech ontogeny: Phylogenetic, neurobiological and linguistic implications. *Current opinion in neurobiology*, 11, 696-700.

Vicario, D.S. & Simpson, H.B. (1995) Electrical stimulation in forebrain nuclei elicits learned vocal patterns in songbirds. *Journal of neurophysiology*, 73, 2602-2607.

Woolsey, C.W. (1958) Organization of somatic sensory and motor areas of the cerebral cortex. In H.F. Harlow and C.N. Woolsey (Eds) *Biological and biochemical bases of behavior*. Madison WI: University of Wisconsin Press.