

# LANGUAGE IN AN EMBODIED BRAIN: THE ROLE OF ANIMAL MODELS

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The most parsimonious account of language evolution is one where incremental, quantitative changes in primates' vocal tract, fiber pathways, and neuroanatomy converge with social and cultural developments. From this convergence arises the framework upon which complex language skills could build. Such an 'Emergentist' view emphasizes phylogenetic continuity in the neural substrates that mediate language, with language processing embedded in systems with more ancient sensorimotor roots. (Alternatively, 'Mental Organ' theories – such as Chomsky, 1988 – stress the discontinuity of language from all other mental/neural systems in humans and all other species).

Emergentist theories – as represented in developmental dynamical systems models, connectionism, cognitive linguistics, psychology, and cognitive neuroscience – emphasize the "embodied" or sensorimotor nature of brain organization for higher cognitive functions. Following Piaget, complex cognitive operations (grammar, logic, mathematics) are viewed as neither innate nor learned; rather, they emerge (sometimes discontinuously) from interactions between a sensorimotor brain and the constraints of a complex problem space. Language is truly the problem space *sine qua non*, in that it maps high-dimensional thoughts onto a low-dimensional physical channel of sounds or signs. Indeed, it has been shown that some properties of grammar emerge in response to this constraint satisfaction problem (Elman et al., 1996).

Clearly, an understanding of the sensorimotor roots of language is indispensable for emergentist accounts – and here, animal models provide a particularly useful perspective. Recent results from anatomical, behavioral, and electrophysiological studies suggest that much of the neural and cognitive 'scaffolding' upon which language is built also exists in non-human animals. For instance, certain lower-level perceptual mechanisms critical for speech comprehension (and previously thought to be speech-specific) are found not only in primates, but in other mammals and in some birds. As an example, categorical perception of the voice onset times (VOT) that distinguish different phonemes (like 'ta' and 'da') has been documented in such animals as chinchillas and Japanese quail;

electrophysiological studies in macaque primary auditory cortex reveal that this phenomenon may be constrained by the basic physiological response to acoustic transients (Steinschneider et al., 1995).

On a more macroscopic level, structural asymmetry in Broca's area (roughly Brodmann's areas 44/45) and the planum temporale – also cited as evidence for language specialization in humans – has been found in great apes (Cantalupo and Hopkins, 2001; Gannon et al., 1998). Antero- and retrograde tracing of pathways in macaque linking anterior temporal to inferior frontal and prefrontal regions (Brodmann areas 45, 46, and 12) suggests the existence of higher-level audio-motor integration within these regions. This contention is supported by results of a recent macaque electrophysiological study (Romanski and Goldman-Rakic, 2002), where subclasses of neurons in the same inferior and prefrontal regions appeared to code for recognition of complex, meaningful sounds such as environmental sounds and vocalizations. Similar sets of neurons are described by Kohler et al. (2002), as part of the 'mirror' system in the macaque homologue of Broca's; these 'audio-visual' neurons fire not only when the monkey performs a particular action (like cracking a peanut), but when he sees the action performed by the experimenter, or hears the sound that the action produces. In short, we see that the brains of our evolutionary ancestors are already equipped for perceiving complex, meaningful sounds and mapping them onto action, in brain regions that are homologous with those strongly associated with language processing.

A strong prediction of emergentist or embodied theories of language is that the brain regions involved in language also keep their 'day jobs' – e.g., the sensorimotor tasks they evolved to subservise. With regard to the regions discussed above, our own fMRI data appear to bear this out: here, we observed activation in inferior frontal and dorsolateral prefrontal areas (as well as posterior temporal and perisylvian areas) during both environmental sound recognition and a matched language comprehension task (Dick et al., 2002).

Emergentist theories would also predict that if these shared processing regions were damaged, linguistic and non-linguistic skills at least partially mediated by these areas should show similar

patterns of deficit. In this vein, Saygin et al. (2002) compared comprehension of meaningful environmental sounds (e.g., the sound of a cow mooing) with comprehension of short linguistic descriptions of those sounds. Results for 29 aphasic patients revealed extraordinarily high correlations for both accuracy and latencies, and no individual cases of language impairment with spared non-verbal processing. Lesion overlays showed that the areas implicated in both verbal and non-verbal deficits centered around Wernicke's area, the supramarginal gyrus and more anterior regions of the superior temporal gyrus.

A logical outgrowth of this 'shared neural resources' hypothesis is that many seemingly language-specific deficits should be inducible by severely taxing the underlying sensory substrates. In a series of studies involving both aphasic patients and neurologically intact college students, Dick et al. (2001) showed that a hallmark grammatical deficit could be reproduced both qualitatively and quantitatively through parametric imposition of spectral and temporal degradations of the speech signal. Similarly, some of the lexical deficits observed in aphasia can also be reproduced in normals under various kinds of acoustical degradations (Moll et al., 2002), while similar manipulations reveal a gradient of lexical vulnerability that includes patients who appear to have spared lexical comprehension on standard clinical tests (Moineau et al., 2002).

Finally, given the wealth of data on brain plasticity that has emerged from developmental, lesion, and learning-based studies with primates, an emergentist view would strongly predict that language's 'commitment' to a particular set of brain regions would be quite malleable, particularly in the face of early injury. This is exactly what we have observed. Whereas late-onset language deficits are much more pronounced with left rather than right hemisphere damage, children with perinatal focal lesions in either hemisphere tend to fall within the normal range for their age group, in both language production and comprehension measures (Bates et al., 2001).

In short, many of the auditory, motor, and visual resources underlying human language development and processing are also found in non-human primates (and even other animals). When these neural resources are damaged or taxed in adults, the linguistic and non-linguistic processes that rely upon them tend to fall apart in similar ways. And just as in the case of complex skills in other primates, the commitment of language to specific neural processing regions is relatively

unconstrained early on in life, and becomes progressively more fixed in adulthood as these skills increase in number and intricacy.

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