that captivity, or any subtle effects of human handedness, would cause a systematic bias absent in the wild, though it may unmask or release latent effects.

Corballis claims that, unlike our speech, vocal control is relatively inflexible, involuntary, and emotional – though he also, separately, argues that manual gesture progressed to facial gesture, and thence to speech proper, by the addition of voicing, perhaps initially as *emotional* accompaniment; and that, therefore, chimps cannot be taught to speak. However, that bonobos do understand quite complex *spoken* commands, suggests that the problem for apes may be more in the realization of speech sounds than in their comprehension.

As Hauser et al. (2002) note, animal communication, though sharing many features with human language, lacks its rich expressiveness and open-ended recursive and re-combinatory power. We cannot yet conclude whether the evolution of the latter was gradual or saltatory; and if gradual, whether it extended pre-existing primate systems, or whether important features such as recursion were exapted away from other, previous, irrelevant but adapted functions like tool-making or social behaviour, and then made available for language. Thus, certain features of language may be spandrels, *by*-products of pre-existing constraints, rather than *end*-products of a history of natural selection.

In conclusion, I applaud Corballis's ingenious and seductive hypothesis, but I dispute whether "handedness would have emerged as vocalization was progressively incorporated into gestural language" (sect. 6, para. 3); the roots of both are surely far older than the latter.

Lateralisation may be a side issue for understanding language development

Caterina Breitenstein[a], Agnes Floel[b], Bianca Dräger[a], and Stefan Knecht[a]

[a]*Department of Neurology, University of Muenster, 48129 Muenster, Germany;* [b]*Human Cortical Physiology Section, National Institute of Neurological Disorders and Stroke, National Institutes of Health, Bethesda, MD 20892-1430.*
{caterina.breitenstein;dragerb;knecht}@uni-muenster.de
http://neurologie.uni-muenster.de/ger/mitarbeiter/breitenstein
http://neurologie.uni-muenster.de/ger/mitarbeiter/knecht
floela@ninds.nih.gov

Abstract: We add evidence in support of Corballis's gestural theory of language. Using transcranial magnetic stimulation, we found that productive and receptive linguistic tasks excite the motor cortices for both hands. This indicates that the language and the hand motor systems are still tightly linked in modern man. The bilaterality of the effect, however, implies that lateralisation is a secondary issue.

In attempting to construe a biological model for language, the issue of lateralisation cannot be ignored. The long-known correlation between manual dexterity and language lateralisation certainly was a starting point for the development of a gestural theory of language. Furthermore, language lateralisation is the single most critical factor for determining whether an ischemic stroke will lead to aphasia (Knecht et al. 2002). At this point, however, focusing on lateralisation issues may not be of additional help. It may simply distract from more important issues in enhancing language recovery. A comprehensive neurobiological understanding of the human language system will aid in the development of effective treatment options for language disorders, the most prevalent being stroke-related aphasia.

One methodological problem is that the evidence put forward with respect to language development is necessarily circumstantial, because of the retrospective character of the study designs. The gestural theory of language, as eloquently outlined by Corballis, has nevertheless substantially contributed to the construction of such a biological model of language. It relates language to aspects of other complex motor behaviors. The theory predicts that the activation of "gestures" comprising spoken language is functionally linked to and should thus coactivate an extended network of manual actions. In concert with this view, treatment strategies adapted from motor rehabilitation have already been effectively applied in aphasia therapy (Pulvermüller et al. 2001; for a summary, see Breitenstein & Knecht 2003). Here we argue that the effectiveness of the motor-theory approach may be independent of lateralisation.

Recent data from our laboratory demonstrate that the hand motor cortex, as assessed by transcranial magnetic stimulation, is activated by a variety of linguistic tasks (Floel et al. 2001; 2002; 2003) – that is, during speaking, covert reading, and listening to sentences. The degree of motor system activation was comparable in both hemispheres, and the effects were independent of the side of language dominance or of handedness. Listening to nonspeech auditory stimuli (white noise, tones), viewing nonlinguistic visual materials, or listening to meaningless phonemes (Sundara et al. 2001) did not coactivate the hand motor cortices. In a just-completed follow-up study, we examined whether presentation of the prosodic component of sentences in isolation, without semantic and grammatical information, suffices to activate the bodily action system. The results replicated and extended our previous findings: Both listening to sentences and to variable prosodic contours (matched in duration and pitch variation with the sentences) bilaterally activated the hand motor cortex (Rogalewski et al. 2003).

The specificity of the effect for language perception underlines that it is not an unspecific effect of covert rehearsal. Furthermore, speech perception activates not only the hand motor system, but also the cortical motor representations of the orofacial "gesture" systems (Fadiga et al. 2002). This indicates a direct link between the language and the manual/facial action systems, which is far more extensive than previously assumed and which might still be functionally relevant in modern man. For example, motor cortex activation, as part of a widely distributed cortical network, might contribute to the implementation of word meanings (Pulvermüller 1999). Our findings provide support for Corballis's view that today's language has developed from a gestural system of communication. Although yet to be developed, the close bilateral association between the language and manual motor systems could inform aphasia therapy, in that, for example, preactivation of the (manual) motor system of the undamaged side could facilitate language processing. The rationale is supported by preliminary evidence that (a) patients with aphasia improve on naming objects when pointing to objects (Hanlon et al. 1990) and (b) stutterers benefit from hand gestures (Mayberry et al. 1998). Additionally, a recent magnetoencephalographic study demonstrated that a wide-spread bilateral cortical network, including Broca's area and its homologue, were activated by the observation and imitation of orofacial gestures (Nishitani & Hari 2002).

In summary, the empirical database establishes a close link between the language and the motor systems. Within this framework, it may be possible to develop more systematic therapeutic strategies for language disorders. Future studies are required to examine the outcome of concomitant motor activation in language therapy in a larger group of aphasic patients in a more systematic manner.

Last but not least, future research should be directed toward both the relation of language faculties to other cognitive domains, as well as to the relation of language associated brain activity to brain activity related to other brain functions. Corballis's theory and data from different laboratories working on the link between the language and the motor systems imply that at least some aspects of language are part of a domain-general system (Hauser et al. 2002). This domain-general system is most likely represented bilaterally.

ACKNOWLEDGMENT
Work is supported by the NRW Nachwuchsgruppenförderung (awarded to Stefan Knecht).