regarded as a fundamental prerequisite for attaining spoken language. The implication is that the presence of mirror-neurones in humans may be irrelevant to our faculty of language, despite being associated with Broca's area.

Corballis is impressed by the suggestion (Holloway 1983) that there was an anatomical asymmetry in Broca's area in *Homo habilis* (see also Falk 1983). I am less convinced. Given the individual variability of gyral morphology in extant brains, any inferences (e.g., Falk 1983) made from patterns on endocasts of fossil skulls to underlying cortex must be regarded with caution, if not downright scepticism, and are, according to Oakley (1972), "no more reliable than any other form of phrenology" (p. 48).

Even if we accept the evidence concerning Broca's area, there remains the possibility that an asymmetry in this region, as with the planum temporale (Annett 1992; Beaton 1997), relates to handedness (see Foundas et al. 1998) rather than to speech. Toth's suggestion, based on examination of ancient stone tools and modern tool-making experiments, that *Homo habilis* was largely right-handed as long ago as 1.9 to 1.4 million years ago, is well known, although not without its critics (see Marzke & Shackley 1986; Noble & Davidson 1996). It is conceivable that some even earlier ancestor of modern humans was right-handed – perhaps for such actions as throwing sticks or stones (Calvin 1983a).

The claims that *Australopithecus (Ardipithecus) ramidus* (White et al. 1994) and *Australopithecus anamensis* (Leakey et al. 1995), not to mention *Orrorin tugenensis* (Senut et al. 2001) and *Sahelanthropus tchadensis* (Brunet et al. 2002), were bipedal raise the possibility (see, for example, Previc 1991) that handedness emerged more than four million, and possibly more than six million, years ago. The available fossils do not provide relevant evidence, but it may be appropriate to note that the *Homo erectus* (or *H. ergaster*) specimen referred to as Nariokotome boy shows certain features, such as a longer right than left ulna bone (Walker & Leakey 1993), which are found on the skeletons of modern, and therefore predominantly right-handed, humans (Steele 2000). If this was also the case for any of the other putative hominid species, it might indicate that a right-hand superiority for most actions, not just gestures, was present much earlier than Corballis proposes.

Regardless of when language or handedness evolved, it is a mistake, in my view, to think of handedness purely in categorical terms. Most discussions of laterality tend to ignore its variability (see Beaton 2003). With regard to preference, there is no clear dividing line between right- and left-preferent individuals when a range of manual activities, rather than a single task such as writing, is considered (Annett 1970). Thus, mixed- and left-handedness have to be explained as well as right-handedness. Those genetic theories which introduce an element of chance or randomness into their postulates (Annett 2002; Laland et al. 1995; McManus 1985a) can cope with this, but theories such as the one under scrutiny here have difficulty in accounting for the discrepancy that sometimes occurs between laterality of speech and the side of the preferred hand.

Corballis refers to the possibility that "one allele of a handedness gene codes for some underlying gradient to be expressed whereas the other essentially leaves handedness to chance" (sect. 5.3, last para.). It is thus not clear that his theory differs in principle from theories such as those of Annett and McManus. The only issue that distinguishes his evolutionary theory from the genetic theories concerns whether handedness should be considered a byproduct of speech lateralization or of an earlier lateralization for vocalization and gestures.

In speculating on the origins of laterality, it may be misleading to concentrate on handedness, albeit this is the most conspicuous behavioural asymmetry exhibited by humans. There are many other kinds of lateral preference – of which the preference for one or other foot is perhaps the strongest. There is no obvious connection between meaningful gestures and footedness, eyedness, or various other forms of side preference. If only these aspects of laterality, rather than handedness, were to be under consideration, it is unlikely that any causal link with vocalization or language would be postulated by Corballis or by anyone else.

Gesture in language evolution: Could I but raise my hand to it!

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Abstract: An intervening gestural stage in language evolution, though seductive, is ultimately redundant, and is not necessarily supported by modern human or chimp behaviour. The findings and arguments offered from mirror neurones, anatomy, and lateralization are capable of other interpretations, and the manipulative dextrality of chimps is under-recognized. While language certainly possesses certain unique properties, its roots are ancient.

A strong, if intuitively somewhat implausible, form of Corballis's admittedly seductive hypothesis appears as: "the precursors of *Homo sapiens* had evolved a form of signed language similar in principle, if not in detail, to the signed languages that are today used by the deaf" (Corballis 2002, p. 125). Were there really troupes of silent, rapidly signing prehominids? Indeed, given how speech came to supersede gesture, and given left hemisphere (LH) mediation of communication in so many "lower" animals, as Corballis explains and reviews in his 2002 book, the insertion of an extra, gestural stage seems gratuitous and redundant. Our capacity to spontaneously develop signs, if deaf, no more supports an evolutionary primacy of sign in language development, than does the fact that we can read much faster than we can speak suggest that speech may have originated from some early analog of reading. An example maybe of evolutionary over-engineering, it is reminiscent of the discredited thesis that phylogeny necessarily recapitulates ontogeny. Nor is there evidence, in any case, that infants substantively gesture before speech unfolds; or that blind infants, or those born without forelimbs, have fewer problems in language acquisition than those born deaf. True, chimps exhibit many commonalities with our own gestures, but biomechanical and situational constraints may limit the range of options, with analogy rather than homology operating. The anatomical adjacency of cortical regions mediating speech and praxis (gesture) may merely reflect commonalities of seriality and generativity, whereby the two capacities may, admittedly, have interacted autocatalytically in their respective, or mutual, evolution.

Mirror neurones may certainly have played a key role in language evolution and may continue to do so in its acquisition, but they could be far more pervasive than just mediating, prefrontally, the sensorimotor correlates of gesture (Bradshaw & Mattingley 2001). Indeed, Hauser et al. (2002) claim that in macaques mirror neurones are *not* sufficient for imitation – a capacity which is necessary for a common, shared language, and which, while highly developed in parrots and dolphins, is, in fact, poorly developed in chimps and monkeys. At a more peripheral level, DeGusta et al. (1999) find that hypoglossal canal size is of little functional significance. Likewise, was a size increase in the thoracic region of the spinal cord – said by Corballis to occur late in our evolution – really necessary for better breathing during speech, given, for example, the articulatory capabilities of the African grey parrot?

The proposal that a left-hemisphere dominance for vocal communication emerged earlier than dextrality, with the latter a consequence of the former, does not necessarily follow; both may stem from another, prior, asymmetry (recursive seriality? – though I would opt also for a very early, initial, determining right-hemisphere preemption of emotional and/or spatial processing). Similarly, I feel that Corballis downplays recent findings of dextrality in chimps, which is especially prominent with the precision grip. Hopkins et al. (2002) make the important distinction (often overlooked) between hand *preference* and *performance,* and also conclude that language is *not* a necessary condition for the expression of hemispheric specialization. Indeed, they say it seems unlikely 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

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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.

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