cal gestures in Broca's area of the prefrontal cerebral cortex. Both types of gesture probably have something to do with mirror neurones. This is almost certainly true, but is it useful or reasonable to try to determine whether asymmetries of vocal control, or of hand control, evolved first?

Evolutionary scenarios can be fascinating, but so can the myths of first cause told in all human societies. The argument that vocalisation came first and right-handedness was secondary depends on evaluating evidence of these asymmetries in other species. The upshot of Corballis's appraisal is that there is better evidence for early asymmetries in the control of vocalisation in nonhumans than for asymmetrical control of the limbs. Undoubtedly there are asymmetries of vocal control in some song-birds, but there is also footedness in parrots (Bradshaw & Rogers 1993). Questions about the origins of human handedness and speech require evidence for nonhuman primates. All primates vocalise and all have handedness, but in none other than humans is there unequivocal evidence of species asymmetry. It is the *divergence* of humans from apes in these respects that is most impressive. Asymmetrical control of vocalisation in humans, birds, and marine mammals is more likely to depend on convergent evolution than descent. The similarities suggest the importance of unilateral control for complex vocal output. They suggest why nature came up with a similar strategy for human speech. But the mechanisms involved are not likely to have been preserved through intervening species that do not have these adaptations.

The nature and quality of the evidence cited here for asymmetries in nonhuman species is debatable. Independent replication must be the criterion. In the published literature, negative evidence tends to be neglected in favour of positive findings. Similarities with humans are likely to be stressed in applications for funding. To be fair to Corballis, it must be acknowledged that almost every sentence in the target article includes a "may be" or a "perhaps," but I still find speculations woven from doubtful evidence. This is not to deny that there must be an important role for "mirror neurones" in the story of primate and human evolution. Beyond their role in manual gestures, they are likely to be involved in the production and interpretation of other nonverbal behaviours in primate social interactions. Both frontal and temporoparietal areas were aroused in a study of theory of mind awareness (Gallagher et al. 2000). Much more than vocalisation and hand use may be involved. To assert a link between handedness and vocalisation is not the same as specifying what it might be. The jump from vocalisation to speech is barely touched upon.

The target article lacks a clear account of human individual differences for brain asymmetry or handedness. Pathology remains the implicit default explanation, in the absence of a theory of natural variation. Corballis's estimates of the prevalence of right brain speech (sect. 5.2) neglect evidence from a population representative series of dysphasics (Annett 1975; Annett & Alexander 1996). Estimates from these sources were confirmed by a community survey (Pederson et al. 1995), with an incidence of just over 9% in the general population. The incidence tends to be underestimated by arguments from Wada tests on epileptic patients classified as right- or left-handed. If cerebral asymmetries for human vocalisation truly have the ancient lineage argued here, why should any modern humans be right-brained or left-handed? Was there a period when everyone was left-brained and right-handed? Was a new genetic mutation required to re-introduce variability? Where was this supposed universally right-handed species? Corballis seems ambivalent about these ideas.

The right shift (RS) theory (see Annett 2002 for a review) agrees with the thesis that the human bias toward right-handedness depends on the bias toward left-hemisphere speech, but it is as fruitless to ask which came first here, as it is with the chicken and the egg. The theory suggests that a single gene promotes left-cerebral dominance for speech by weakening speech related cortex in the right hemisphere. An incidental weakening of the left hand displaces a chance distribution of hand skill asymmetry in favour of the right. The chance distribution depends on nongenetic accidental variation in the growth of every individual. The right shift gene (RS +) evolved in early humans to facilitate the amazing process by which human infants acquire the speech sounds of their native tongue. However, the gene did not become universal or fixed in humans, because it is associated with risks to other functions, and possibly with mental illness (Crow 1997). Whether RS + is present or absent, the universal and natural determinant of asymmetries of hand and brain is a chance variation. There is no need for a gene for chance, or complicated rules about when it is expressed. Corballis is mistaken in suggesting that other theories are equivalent. Annett (2002) argued that supposed alternative theories are variations on a similar theme, but quite out of tune with the facts.

Protosign and protospeech: An expanding spiral

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Abstract: The intriguing observation that left-cerebral dominance for vocalization is ancient, occurring in frogs, birds, and mammals, grounds Corballis's argument that the predominance of right-handedness may result from an association between manual gestures and vocalization in the evolution of language. This commentary supports the general thesis that language evolved "From hand to mouth" (Corballis 2002), while offering alternatives for some of Corballis's supporting arguments.

The numbered passages in italic below are based on the corresponding sections of the target article; unnumbered paragraphs convey my comments.

1. Human language emerged from gestural communication. Vocalizations were gradually incorporated into the gestural system.

I agree with this statement but note the problem that it might be taken to suggest that a complete human language in gestural mode existed prior to the incorporation of vocalization. I offer instead "The Doctrine of the Expanding Spiral": that is, that our ancestors had a form of "protosign" (a manual precursor of language) that provided essential scaffolding for the emergence of "protospeech," but that the hominid line saw advances in both protosign and protospeech, feeding off each other in an expanding spiral.

2.3. True syntactic language probably did not evolve until after the emergence of the genus Homo around two million years ago.

I would speculate, to the contrary, that the protosign and protospeech of early *Homo,* and even of *Homo sapiens* until perhaps 50,000 years ago, had little or no syntax. However, contrary to Bickerton (1995) and in agreement with Wray (1998), I would argue that such protolanguage did not consist primarily of words akin to today's words, only lacking syntax, but rather was *holophrastic* – that is, consisting primarily of utterances without internal syntax but whose translation into English, say, would require several words and the syntax to combine them. I speculate that the transition from protolanguage to modern human language with syntax and a compositional semantics was the result of cultural innovation across many millennia of the history of *Homo sapiens* (Arbib 2002). Protosign had the great advantage over protospeech in that it could convey many meanings by pantomime, with far greater richness than protospeech could gain from expressive grunts or onomatopoeia.

> [A] third person sees you and a companion together, leaves for a moment, returns, and shows surprise at seeing you alone. You immediately . . . make a gesture [that means], "She went that way." But your gesture [also] shows which way she went . . . [Y]our hand pointed out the direction of your companion's departure, but your hand also stands for her, the one who departed. (Stokoe 2001, pp. xii–xiii)

2.4. Given the intricate nature of syntax, it is likely that language itself evolved gradually through natural selection.

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Against this, I offer the hypothesis that syntax is more a cultural than a biological phenomenon – and therefore speak of a *language-ready brain* as one that can acquire language in a modern human society, while denying than human brains have syntax "biologically precoded."

2.5. Sign languages invented by the deaf have all the essential properties of spoken language, including a sophisticated syntax.

Indeed. But it may be asked whether full sign language was a necessary precursor to spoken language or whether an Expanding Spiral of protosign and protospeech provided early *Homo sapiens* with a language-readiness that fell short of full language, signed or spoken. In many cases, "full" sign languages reflect, in part, the attempt of deaf people to import the richness of spoken or written language back into sign.

2.5. Syntax could have emerged from the structure of individual gestures themselves.

In similar vein, Stokoe (2001; continuing the quote from Stokoe above) asserts that: "The gesture also has . . . syntax because the hand for the person and its movement telling what she did are subject and predicate (or noun phrase [NP] + verb phrase [VP])."

I think this is a mistake. It is true that a linguist can *sometimes* dub the hand shape of a sign as denoting an object and the movement of the hand as denoting an action, but these are not necessarily separable. And if they are not separated, they do not need syntax to put them together again. It is only the *translation* to, for example, English that has this syntax. Moreover, *airplane* is signed in ASL with tiny repeated movements of a specific handshape, while *fly* is signed by moving the same handshape along a trajectory (Supalla & Newport 1978). Here, both verb and noun combine handshape and motion. For me, the import of the airplane/fly distinction is that, while a "natural" gesture is unitary, extending the range of discourse requires distinctions that cannot be mimed directly. Thus, early humans might have developed a natural pantomime which stood equally for "a bird is flying," "the flying bird," "flying," or "bird" – relying on the "listener" to interpret the sign correctly in context. As it became useful to distinguish these meanings, a community had to develop conventions to mark them, initiating the transition from pantomime to a conventionalized system of signed communication (Arbib 2003b).

3.1. Facial gestures generally convey syntax, whereas manual gestures supply content, suggesting a progression from manual to facial gesture in the emergence of language.

The first statement is false, thus invalidating the second. Emmorey et al. (2002, Fig. 1) show how a sequence of hand movements may employ classifier constructions to express spatial syntax. But note, too, that signers make fuller use of the facial musculature than speakers do. Is this because protosign evolved the appropriate muscle control, or because signers can exploit a more generic human capacity for fractionation of motor skills? Recent modeling of the development of manual skills seems to suggest the latter (Oztop et al. 2003). And consider learning to play the piano (surely not part of the experience of early *Homo*!) – with its cumulative mastery of finger exercises and the hierarchical progression from note to chord to phrase and on to syncopation.

3.1. The next step may have been to add voicing.

Since other primates have vocalization, we can expect that some voicing was always present. I suggest that the development of conventionalized gestures in protosign, rather than any syntactic structure in sign, provided the "evolutionary drive" for the development of a rich protospeech and the concomitant neural apparatus to control the articulators. The Expanding Spiral then allowed the expressiveness of protosign and protospeech to feed off each other to yield the evolution of the language-ready brain. By contrast, I find the frame/content theory of MacNeilage (1998) unconvincing because it grounds the syllable in mastication with no indication of how evolving modes of communication could provide the selection pressure for relevant changes in the articulators and their neural control.

3.3. In view of the longstanding involvement of Broca's area in manual activity, its enlargement in Homo habilis, *nearly two million years ago, may reflect the incorporation of syntax into gestural communication.*

Again, why posit syntax this early? The switch from a closed repertoire to the ability to create, learn, and use an open set of holophrastic utterances would possibly have been enough for this. The stasis of tool use in *Homo habilis* argues for a long period of stasis in protolanguage (cf. Noble & Davidson 1996), which might be more consistent with a limited stock of holophrastic utterances than with a flexible syntax. This would seem to accord better with Corballis's later statement (sect. 3.6) that autonomous speech may have emerged gradually in Africa over the period from 170,000 to 50,000 years ago. I would suggest that language (as distinct from protolanguage) and rich systems of syntax also emerged, postbiologically, during this period.

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Is gestural communication more sophisticated than vocal communication in wild chimpanzees?

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Abstract: The communicative behavior of chimpanzees has been cited in support of the hypothesis that language evolved from gesture. In this commentary, I compare gestural and vocal communication in wild chimpanzees. Because the use of gesture in wild chimpanzees is limited, whereas their vocal behavior is relatively complex, I argue that wild chimpanzee behavior fails to support the gestural origins hypothesis.

Corballis argues that manual gesturing was the mediating factor in the evolution of handedness in humans. As he points out in the conclusion of his article, the key issue in his argument, therefore, is whether language evolved from gesture. To support the gestural origins hypothesis, Corballis uses the communicative behavior of wild chimpanzees to speculate about the communicative repertoire of a human/chimp common ancestor. He concludes that wild chimpanzee gestural communication provides a more plausible hypothetical substrate for the evolution of an intentional communication system than chimpanzee vocal communication does. In this commentary, I will compare what is known about gestural and vocal communication in wild chimpanzees. Leaving aside the significant problems associated with using modern apes to model the behavior of human ancestors (Marks 2002), I will argue that Corballis has overestimated the role of gestural communication in wild chimpanzee interactions while simultaneously underestimating the complexity of their vocal behavior. I suggest that wild chimpanzees offer little support for the idea that language evolved from a structured system of gesture, or, by extension, that manual gesture led to handedness.

Is it true, as asserted in section 2.1, that "chimpanzees and other apes make extensive use of gestures in the wild"? In an effort to support this claim, Corballis reviews three different studies of *captive* apes: de Waal (1982) and Tomasello et al. (1997) on chimpanzees, and Tanner and Byrne (1996) on gorillas. However, the behavior of captives, who are influenced by human caretakers and artificial environments, is irrelevant here. Moreover, published reports of wild chimpanzee behavior do not support Corballis's representation of wild chimpanzee gestural communication. In Table 1, I have listed the gestures so far documented for wild chimpanzee communicative interactions. The evidence to date shows clearly that wild chimpanzees rarely use manual gestures, and that the vast majority of gestures they do use are employed in the context of