Commentary/Corballis: From mouth to hand: Gesture, speech, and the evolution of right-handedness

been less than convincing. The lateralization of language functions is often thought of as a uniquely human trait, but as Corballis points out, lateralization for vocalization is far from unique; in fact, it is quite common in the animal kingdom. What probably is unique is the consistent, population-level handedness seen in human beings. What is new here is Corballis's assertion that the initial step was the introduction of a gesture-based language, followed by the recruitment of vocalization by a developing gesturelanguage capability. If there is some inherent tendency for vocal functions to be lateralized to the left side of the brain, then, as speech came to predominate, it could have influenced the development of handedness first for gesture, later more globally.

The correlation between left cerebral hemispheric lateralization for language and for handedness makes sense if we assume that it is communication-through-gesture that underlies both functions. In support of this assertion, Corballis mentions the fairly well-known association of sign language functions with Broca's area in deaf native signers. This association has been taken as evidence of an abstract linguistic function for Broca's area (see Emmorey 2001, p. 292); that is, if Broca's area can deal with language in such divergent modalities, then it must function linguistically at a highly abstract level. Corballis offers us an alternative explanation. If his hypothesis is correct, then Broca's area has been built up from a practical action/recognition system.

How, then, can we account for Broca's area as a "syntax" or grammatical processing center? First, we can repeat that this area in the human brain may be homologous with the seat of mirror neurons in the brains of nonhuman primates. Second, we could repeat a suggestion of Armstrong et al. (1995) (noted by Corballis) that syntax evolved through a series of stages in which hominids "parsed" grammatical elements out of meaningful but potentially componential manual gestures. The appearance of syntax has generally been construed as a "chicken and egg" problem how can you have the grammatical components of a sentence without first having a sentence, but how can you have a sentence without first putting together a string of components that have grammatical roles? (In this regard, see Jackendoff 2002.) One solution has been to assume that syntax arrived all at once, perhaps enabled by a genetic mutation. Stokoe (1991) proposes an alternate solution to this problem in terms of what he calls *semantic* phonology, which was elaborated on by Armstrong et al. (1995). In this formulation, an iconic manual gesture, such as the "grasp" gesture described by Corballis, is seen as having an agent/action semantic structure built into its physical expression. This structure is also "parsable" into a primitive noun phrase and verb phrase – for example, a hand and its movement. So, if we assume that, instead of having to build up sentences from elementary components that could only be identified within the context of existing sentences, early hominids could have seen the components as parts of already meaningful wholes, we can see a way for grammar to develop gradually. Incidentally, Stokoe also saw elements of the phonological system of an incipient sign language in these iconic manual structures. Hence, there would have been the possibility for "carving" the combinatorial elements of the phonological, syntactic, and semantic systems out of these elementary, transparently meaningful structures.

Another source of support for Corballis's hypothesis comes from the observation that hand preference appears in signing before it does for object manipulation in young children (Bonvillian & Richards 1993). This original preference in signing is then highly correlated with the hand that eventually becomes the child's dominant hand for other purposes. I have suggested elsewhere (Armstrong 1999, p. 122) that a tight linkage between handedness and signing might help to solve the mystery of the linkage between lateralization for language and for handedness. By proposing his current hypothesis, Corballis has proposed a plausible mechanism for the manner in which this association developed phylogenetically.

Perhaps harder to support is Corballis's notion that a shift from gestural (or signed) to spoken language was the key to the rapid expansion of *Homo sapiens* out of Africa, replacing earlier hominids in other parts of the world. It seems likely that there was a lot more to it than this, given that perfectly serviceable signed languages exist today among deaf people and others for whom speech may be impossible or inconvenient. Simply freeing the hands for manufacture or increasing the capacity for instruction while in the act of manufacturing don't seem sufficiently powerful causal agents. But that may be the topic for another discussion. In general, Corballis succeeds admirably in presenting his major argument.

Going for Broca? I wouldn't bet on it!

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Abstract: The role of Broca's area is currently unclear even with regard to language. Suggestions that this area was enlarged on the left in certain of our hominid ancestors are unconvincing. Broca's area may have nothing to do with a lateralized gestural or vocal system Handedness may have evolved more than four million years ago.

In the target article, Corballis has proposed a theory of how handedness arose in humans. Other authors have proposed similar evolutionary scenarios. What is novel in Corballis's proposal is the idea that vocalization was lateralized before language and that lateralized gestures preceded, rather than followed, a right hand superiority for skilled action.

Considerable theoretical weight is attached to the role of Broca's area in the target article. However, despite more than a century of research, we are still not entirely clear as to the significance of this area in humans (Bub 2000). In discussing the celebrated case of Leborgne, Broca (1861b) dismissed the significance of neighbouring areas of damaged cortex, thereby inviting a strict localisationist view of the role of the third frontal convolution. In a later publication, he drew attention to the fact that in each of the eight patients discussed in the 1861 paper, the damage also involved this area (Broca 1865). Although Broca himself was cautious about drawing any conclusion therefrom, the critical role of the inferior frontal gyrus in "language articulé" became widely accepted by many (Pierre Marie was a notable exception). However, damage to this convolution alone does not appear to produce a permanent Broca's aphasia (Mohr et al. 1978), notwithstanding the confident assertions of generations of neuropsychologists and neurologists.

Broca was uncertain about whether patients who have lost the power of speech should be regarded simply as having forgotten how to articulate (*"ont seulement oublié l'art de l'articulation"*), which Broca thought of as an intellectual or cognitive deficit, or whether the impairment constituted a type of motor deficit confined to speech sounds (*"d'une ataxie locomotrice limitée à la partie de l'appareil nerveux central qui préside aux mouvements de l'articulation des sons"*), which he considered to be a somewhat lower-level deficit. Either way, the essential nature of Broca's aphasia, and hence the role of the inferior frontal gyrus, has been obscure ever since.

Another reason the role of Broca's area is obscure, arises from the discovery of "mirror-neurones." Corballis argues that "mapping of perception onto execution seems to provide a natural starting point for language and supports the idea that language originated in gesture, not in vocalization" (sect. 2.2). However, not all manual movements should be considered gestures (a concept that is somewhat underspecified in the target article). In both humans and monkeys, mirror neurones appear to be related to actions related to object manipulation (Rizzolatti et al. 1996b). In any event, the presence of mirror-neurones in monkeys does not seem to support an ability in these animals to mirror or reflect, that is, to imitate, actual manual behaviour (see Hauser et al. 2002). Vocal imitation, too, appears to be absent in monkeys, yet this might be 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 righthanded 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