

mann (1913/1979) suggested that “the word ‘limb’ here, refers to the tongue, palate, and oral mechanism” (p. 56). In the same tradition, Kimura (1976; 1982; Kimura & Archibald 1974) proposed that the reason for the apparent close relationship between speech and praxic impairment is explained with reference to the finding that speech processing is highly dependent on praxic skills, and that the development of the capacity to speak is built on a phylogenically earlier capacity for action and gesture. Corballis recognises the relationship but sees the causality running in the opposite direction. First there was vocalisation, then gestural communication developed to augment that. A left hemisphere dominance for vocalisation and gesture, the latter controlled by Broca’s area, gave rise over time to right hand dominance for the great majority of us. This contrasts with Rizzolatti and Arbib’s (1998; see also Arbib, submitted) scenario based on mirror neurone research, which sees vocalisation and gestural communication as essentially separate before the development of speech (which they see also as coming predominantly from a preexisting capacity for gestural communication based on Broca’s area). Arbib (submitted) points to the marked relative anatomical distance between the *vocal* anterior cingulate and a *gestural* Broca’s area as supporting this view.

A further issue not considered in Corballis’s target article is the role of the right hemisphere in speech encoding; both hemispheres are engaged in language processing, and even in speech encoding. While it is clear that the left hemisphere is the most important for the mediation of speech encoding, there is a range of evidence from imaging studies and brain damage that the right hemisphere is engaged for most of us in at least the nonpropositional, holistic, emotional, and automatic aspects of speech encoding (Code 1997), and may be dominant for these aspects. Studies of aphasic speech automatism (Code 1994) and the remaining speech of adults who have undergone left hemispherectomy (Code 1996; 1997) provide evidence for right hemisphere engagement in nonpropositional, emotional, and automatic aspects of speech production.

Early studies using regional cerebral bloodflow during automatic counting (Ingvar & Schwartz 1974; Larsen et al. 1978; Skinhoj & Larsen 1980) and recent positron emission tomography scanning during repetition (e.g., Cowell et al. 2000; Wise et al. 1999) show that the right hemisphere is active during automatic and repetitive speech. Larsen et al. (1978) found no significant differences between right and left hemispheres during automatic counting in 18 right-handed volunteers. Bloodflow was predominantly in the upper premotor and sensorimotor mouth areas and the auditory areas of the temporal lobes, with no significant activation of Broca’s areas on either side. More recently, Ryding et al. (1987) examined 15 nonaphasic right-handed volunteers reciting the days of the week and humming a nursery rhyme with a closed mouth. Significantly more activity was observed in the right than left hemisphere during automatic speech, but not for humming, which showed equal bilateral activation. Ryding et al. suggest a left hemisphere control for motoric control of speech but right hemisphere control of vocalisation.

Speedie et al. (1993) described a right-handed Hebrew-French bilingual whose automatic speech was disrupted following haemorrhage involving the right basal ganglia. He was not aphasic but had marked difficulties counting to 20, reciting the Hebrew prayers and blessings before eating that he had recited daily throughout his life, or singing highly familiar songs, although he was able to correctly hum some. His ability to swear and curse was also impaired following the right basal ganglia lesion. This case appears to demonstrate a dissociation between nonpropositional and propositional speech and provide evidence of right hemisphere dominance for automatic and nonpropositional aspects of speech and vocalisation.

This possible right-left dissociation in propositional speech may be more prominent in left-handers than right-handers. Using the Wada technique, Milner and associates (Milner 1974; Milner et al. 1966) showed that seven of 17 left-handed (but neurologi-

cally impaired) volunteers with bilateral representation for speech production made errors in serial counting forwards and backwards, and reciting the days of the week, following right-side anaesthesia. Following left-side injection they made errors in naming, but not automatic speech. For two other participants in the group, naming errors occurred with right hemisphere anaesthesia and automatic speech errors with left hemisphere injection. Corballis cites the research by Graves and others (e.g., Graves & Potter 1988) on asymmetries in mouth opening during speech. What he did not report was that significantly more left-mouth opening is observed during automatic speech.

Does Corballis’s theory predict a possible right hemisphere/left hand engagement in more nonpropositional and automatic aspects of gesture accompanying speech, and in deaf sign language, mirroring the apparent situation for speech production?

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## Hemispheric dominance has its origins in the control of the midline organs of speech

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**Abstract:** Unlike all other lateral specializations, the necessity for unilateral dominance is clear only for the case of the motor control of the speech organs lying on the midline of the body and innervated from both hemispheres. All functional asymmetries are likely to be a consequence of this asymmetry of executive control.

As always, Michael Corballis demonstrates in the target article that he has his finger on all of the important issues in human laterality; but I think that he has built the causality story back-to-front in an effort to upgrade the handedness issue to the level of importance of the cerebral asymmetry for language. The crucial question that he does not address is: Of what possible value (evolutionary significance) could unequal hemispheric capabilities have for *Homo sapiens* – and possibly other species? Although he briefly reviews the literature indicating degrees of laterality in diverse species for diverse tasks, without a fundamental reason why some cortical functions should be asymmetrical, the causality arguments dissolve into a mass of possible scenarios supported by whispers of fossil evidence and unconvincing statistics on captive versus noncaptive monkeys, chimps, and frogs.

The evolutionary argument has been most clearly stated by Passingham (1981). That is, in considering why cerebral lateralization is unambiguously strongest for speech functions, Passingham noted that, unlike all other lateral specializations, there is the potential for real conflict only in the motor control of organs that lie on the midline of the body and are innervated from both hemispheres. In other words, only for motor speech acts is it clear why unilateral cerebral control would have been selected for in evolution. For the hands, there may be some mild advantage to a precision-versus-power or stabilization-versus-execution specialization of the hemispheres, but such a division of labor is empirically rather complex in humans and takes various forms in other species. The presence of similar motor control programs in both hemispheres for the control of the separate hands is theoretically possible and poses no greater problem than one of slightly inefficient cortical storage. As demonstrated by several of the split-brain patients and individuals with callosal agenesis, conflicting commands coming from the two hemispheres can lead to an incoordination where the two hands are not pursuing the same goal; but for the control of the organs of speech in the intact brain, conflicting motor commands sent from both hemispheres to one-and-

the-same speech organs would inevitably imply a dysfunction that would make coherent speech impossible. Left-right functional asymmetry (~dominance) for speech is more accurately described as a motoric necessity than a luxury of efficient storage.

Passingham's theoretical argument has found empirical support in brain imaging studies on chronic stutterers. Unlike the relatively strong unilateral left hemispheric activation seen in normal speakers, stutterers exhibit an abnormal pattern of bilateral activation. Moreover, training to reduce the stuttering is associated with the emergence of left dominance (Fox et al. 1996). The underlying neurophysiological mechanisms remain unclear, but the bilateral activation in stutterers (and unilateral left activation in stutterers who aren't stuttering) is direct evidence that a behavioral disorder can result from a failure to achieve unilateral dominance.

What the argument concerning the "necessity of unilateral dominance for speech" means is that the underlying reason for human functional asymmetries is grounded in comprehensible issues of behavior. For vocal communication, unilateral dominance will be favored to the degree that the phonological message is a complex sequence of motor commands that cannot be coherently delivered from two quasi-independent cerebral hemispheres. For the highly complex behavior of human speech, the need for precise, millisecond control is clear, but the same advantage of unilateral control should also hold for other species, insofar as their vocalizations imply relatively complex motor sequences (e.g., the song of songbirds). At the other extreme, where the barking of dogs and the screeching of monkeys has little temporal organization and is not informationally complex, the need for unilateral control is less critical (and, in fact, empirically ambiguous). Insofar as fear, anger, and mating vocalizations of many species are a consequence of bilaterally symmetrical limbic activations, unilateral motor control is simply unnecessary as both hemispheres holler their similar messages.

In terms of human evolution, it is clear that increased manual dexterity in general would be advantageous, but it is not obvious how the very slight asymmetries of precision-versus-power (etc.) of the hands in primates or early *Homo sapiens* could have had evolutionary significance. In contrast, a severe impediment of stuttering or the confusion created by both hemispheres simultaneously attempting to convey different vocal messages using the same organs of speech would be socially disadvantageous. For this reason, it seems likely to me that the traditional argument advocated by Brain (1945) (and supported by Corballis, sect. 1), that is, that modern human laterality is first and foremost an issue of the motor control of speech, is correct for the evolutionary reasons given by Passingham. However, the evolutionary argument implies – contrary to Corballis's gestural argument – that, as a consequence of the executive dominance required for speech acts, a host of asymmetries subsequently evolved with one hemisphere becoming dominant for executive control (Goldberg 2001). These include the asymmetries of handedness and footedness, and the emergence of the paralinguistic functions of the right hemisphere (Cook 2002). The many known lateral asymmetries might be generalized into some overarching duality of fine-motor-control versus "support" functions, but the underlying behavioral necessity of unilateral motor control arises initially from the problem of control of the midline organs of speech. Nothing comparable is known in the realm of gestures and handedness.

I conclude that the flip-flop causal chain advocated by Corballis (manual gestures à speech asymmetry à handedness) is less plausible than the traditional view (animal vocalizations à speech asymmetry à handedness), but I fully agree that a combination of evolutionary speculations, modern neuropsychological data and backward extrapolation from current genetic data (e.g., Crow 2002) will remain the main tools for explaining the remarkable switch from the relative symmetry of the primate brain to the functional asymmetry of the human brain.

## Right-handedness may have come first: Evidence from studies in human infants and nonhuman primates

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**Abstract:** Recent studies with human infants and nonhuman primates reveal that posture interacts with the expression and stability of handedness. Converging results demonstrate that quadrupedal locomotion hinders the expression of handedness, whereas bipedal posture enhances preferred hand use. From an evolutionary perspective, these findings suggest that right-handedness may have emerged first, following the adoption of bipedal locomotion, with speech emerging later.

Corballis proposes an evolutionary scenario in which gesture, speech, and right-handedness have emerged in that order in the course of human evolution, with each capability perhaps setting the foundations for the next one to follow. However, this ordering, stipulating that right-handedness may have evolved last, emerging from speech lateralization, may not be warranted. Here, I report some developmental and evolutionary evidence indicating that handedness may have made its appearance much earlier in time and followed closely the transition to bipedalism. Such evidence would be in favor of a different scenario, that handedness may have preceded the emergence of speech.

Some archeological artifacts, for example, suggest that small brain asymmetries and possibly the existence of right-handed patterns were already present in the australopithecine lineage (Holloway 1996). Furthermore, the oldest prehistoric stone tools, which were dated around 2.6 million years ago, not only required considerable motor skills to be manufactured (Lewin 1998), but also, in all likelihood, were fabricated using already lateralized motor functions (Steele 2000). Clearly, additional research is needed to strengthen and verify such preliminary archeological evidence. Nonetheless, if the evidence is corroborated, one can begin to consider the possibility that the evolution of right-handedness might have preceded the emergence of speech, rather than the contrary, as proposed by Corballis.

Following up on this alternate scenario, that right-handedness did not evolve from vocalization and speech, but rather formed prior to them, what then could have been another important and earlier trigger to the emergence of right-handedness in human evolution? Recent work with human infants and nonhuman primates suggests that manual preference may have evolved closely after the emergence and adoption of upright bipedal locomotion. In human development, it is well known that generally, before the age of three, infants do not display clear patterns of preferred hand use (McManus et al. 1988). As reported by several studies, before the age of three, infants' patterns of hand use fluctuate frequently between right, left, or both hand use (Carlson & Harris 1985; Corbetta & Thelen 1999; Gesell & Ames 1947). Recently, however, colleagues and I discovered that infants' early fluctuating patterns of hand use were not occurring randomly, but rather were shifting in concert with the development and adoption of new postural motor milestones, as infants learned to sit, crawl, and walk (Corbetta & Bojczyk 2002; Corbetta & Thelen 1999; 2002). In all these studies we followed infants longitudinally during their first year. Every week, we screened their postural motor milestones and assessed their preferred hand use in reaching and object retrieval tasks. We observed that at the youngest age, prior to developing any form of self-produced locomotion, infants displayed stable forms of preferred hand use. When they began to crawl on hands-and-knees, however, these preferred patterns of hand use dissipated (Corbetta & Thelen 1999; 2002). During the crawling period, infants used either hand interchangeably to reach for or to retrieve concealed objects, as if the previously displayed lateral biases never existed. Another change in preferred hand use