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

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occurred when infants began to stand up and perform their first independent steps. Initially, when infants began to walk, and their upright balance was quite precarious, they increased their rate of two-handed responses for reaching and retrieving concealed objects. Yet, as soon as they developed relatively steady gait patterns and gained better upright balance, stable one-handed lateral responses reemerged (Corbetta in press; Corbetta & Bojczyk 2002).

Converging observations have been reported in studies aimed at assessing the role of posture on handedness in nonhuman primates (Spinozzi et al. 1998; Westergaard et al. 1998). Similar to human infants, and as reported by Corballis, nonhuman primates do not display clear hand preference at the population level. However, evidence shows that it depends – the strength of hand preference in nonhuman primates can be altered by task and postural constraints, just as in humans. In particular, Spinozzi et al.'s (1998) and Westergaard et al.'s (1998) research revealed that when subjects were asked to retrieve food from a quadrupedal posture, no clear pattern of hand preference emerged. In contrast, when the same subjects were constrained to adopt a bipedal posture to solve identical manual tasks, preferred biases in hand use increased significantly.

Together, these studies with human infants and nonhuman primates confirm the existence of a close interaction between posture and the lateral organization of the upper limbs. Moreover, these studies suggest that the adoption of the upright posture contributes significantly to enhance and stabilize the expression of manual preferences. Based on this evidence, it seems plausible that when bipedalism emerged in human evolution, about six to four million years ago, the progressive anatomical and neurophysiological changes that such adaptation incurred, entailed and facilitated the formation of right-hand use and brain lateralization. Moreover, based on the above-mentioned evidence, it is conceivable that the emergence of right-handedness might have come before the emergence of speech in human evolution, as handedness would have emerged closely aligned with the evolution of bipedalism. Our alternate proposal, however, would still be compatible with part of Corballis's scenario that gesture – and supposedly, in our account, lateralized forms of gesture – may have been associated with vocalizations and may have subsequently led to the evolution of congruent lateralized speech functions.

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Pumping for gestural origins: The well may be rather dry

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Abstract: Corballis's explanation for right-handedness in humans relies heavily on the gestural protolanguage hypothesis, which he argues for by a series of "intuition pumps." Scrutinizing the mirror system hypothesis and modern gesture as components of the argument, we find that they do not provide the desired evidence of a gestural precursor to speech.

Corballis traces gestural protolanguage in earlier hominids to vocal protolanguage in later hominids, giving rise to a legacy of overwhelming right-handedness in humans. His argumentation follows an extended path, one that is unfortunately more frequently based on appealing to intuitive plausibility than providing a critical evaluation of data. Here, we will be working the handles on two of Corballis's "intuition pumps," arguing that neither the mirror system nor human gesturing produce the flow of evidence he desires.

A recent version of the mirror system hypothesis argues that "Broca's area in the human contains a mirror system for grasping that is homologous to the F5 mirror system of [the] monkey, and this provides the evolutionary basis for language parity; i.e., an utterance means roughly the same for both speaker and hearer" (Arbib 2003a, p. 609). The central component of this hypothesis is simply a system that integrates perception and motor control. Corballis and Arbib go significantly further, however, drawing drastic evolutionary conclusions based on the link between skilled manual action in a nonhuman primate, sharing of intentional states, and a brain region that in humans is specifically involved in language production. The discovery itself is clearly important – neurons in primate F5 provide a substrate for integrating perceptual processing with motor activity, thereby potentially making manual tasks subject to joint attention among different individuals. Nevertheless, using the phenomenon as a pillar of language evolution is taking a long step beyond the data, where simpler interpretations are also available.

For example, there is ample and growing evidence that perceptual and motor systems routinely interact in the brain, working together in creating and shaping cognitive processes (e.g., Barsalou 1999; Hommel et al. 2001). The mirror system may be a powerful [instead of "prototypical"] example of such convergence, but is unlikely to be unique. Perceptuo-motor integration demonstrably plays a role in other aspects of human language and cognition, more likely traceable to activity in distributed networks than being restricted to Broca's area alone. Corballis appeals to the reader's evolutionary intuition by invoking the mirror system findings, the importance of which depends largely on assuming that perceptual and motor integration is playing a special, language-specific role. Our intuition is the opposite, that it would be surprising if such integration were not found to be a basic function of multiple brain areas underlying cognition. Finding that joint attention can play a role, is already implied by imitative, observational, or simply socially facilitated learning that both humans and nonhuman primates can show to varying degrees. Those phenomena are not specifically linked to F5 or Broca's area, which suggests that the integrative processing strategy involved is basic and widespread.

Taken at face value, the discovery of mirror neurons can lead one in many possible directions, and it does not specifically support a gestural-origins hypothesis of language. Unfortunately, speculation seems particularly prone to run roughshod over available data when language evolution becomes the topic of discussion. Rizzolatti and Arbib's (1998) argument that mirror system function can instantiate an elementary case grammar is a case in point. Both these authors and Corballis attach very specific evolutionary hypotheses to a neural phenomenon whose implications are as yet just beginning to be explored. It seems wiser to exercise more restraint, until there is at least some sense of the many different roles that mirror neurons, or something like them, may be playing in various brain regions across species.

Gesturing in modern humans is another of the intuition pumps Corballis invokes. Here, the data do convincingly show that gesture is an important partner to normal speech, and that it develops into a full-fledged linguistic system when the vocal-auditory channel is unavailable. Once again, however, implications for the evolutionary emergence of human language are much less clear. Gestures observed in conjunction with modern speech are largely not linguistic in nature, being iconic instead and lacking the requisite complex structure (Goldin-Meadow & McNeill 1999). Contrary to intuition, in fact, gesturing does not necessarily further the talker's linguistic goals (Krauss et al. 1995). In addition, the fact that manual signing can develop into an explicitly linguistic system demonstrates only that critical aspects of the human capacity for language are likely modality-independent. Rather than specifically implicating gesture as the origin of spoken language, this outcome readily suggests other interpretations – for example, that increasingly complex general sequential-learning capacities played a critical role (Christiansen et al. 2001; Conway & Christiansen 2001).