handedness. The crux of the matter is that the ventromedial pathways develop before the direct corticospinal system (Kuypers 1985). These pathways contain the vestibulospinal tract which projects bilaterally to the spinal cord and controls the proximal muscles of the arm.

Therefore, when a goal directed arm-hand movement first emerges, it would be subject to ipsilateral control, with subsequent contralateral control of the fingers being dependent on the establishment of direct corticospinal connections. Hence, the initial manifestations of lateral biases in reaching should be regarded as primarily indicative of an arm rather than a hand preference (Hopkins & Rönnqvist 1998). In line with a proximal-distal trend in motor development, the neural systems controlling the head, the trunk, and the proximal arm movements develop before the systems controlling the distal arm and hand movements involved in manual gestures. Therefore, the initial manifestations of hemispheric dominance related to gesture communication and later vocalization should be regarded as primarily the development of a trunk, head, and arm preference rather than a hemispheric dominance for vocalization. This suggests that we should also start to look for signs of a right-arm preference in our ancestors and closely related species rather than a hand preference.

Primates such as capuchins and chimpanzees do not make high-speed accurate throws and neither do they seem to have any consistent side preference when "tossing" an object forward (Calvin 1983b; Watson 2001), even if they are relatively good at manipulating objects with their hands. Of course, we should be happy that this is not the case when we visit the zoo. Calvin (1983b) has further proposed that the timing mechanism involved in throwing has subsequently been co-opted into motor sequencing more generally, particularly in speech.

Indeed, a major problem in evaluating the evolutionary depth of human handedness is that artifacts indicative of tool use in the earliest hominids may have been made from wood and so are not preserved in the fossil record. *Homo habilis* (Leakey et al. 1964; Steele 1999), who was perhaps the first to develop refined and successful throwing, would definitely have had the prerequisites for hunting and fighting. Throwing involves a complex chain of coordinated movements (and activation of the motor cortex) and not only the position and regulation of the speed of the hand movement and its location in space, but also the regulation of head, shoulder, and arm.

There is evidence that mirror neurons in the monkey's premotor cortex discharge both when the monkey makes a particular action and when it observes another individual, monkey or human, making a similar action (Rizzolatti & Arbib 1998). Learning by imitation may also play an important part in the acquisition of motor skill during infancy (e.g., Meltzoff & Moor 1992). According to Kohler et al. (2002), these mirror neurons may be a key to gestural communication. In monkeys, the mirror neuron system appears to be bilateral, whereas in human adults it is largely located in the left hemisphere. However, little is known about the developmental processes of mirror neurons in relation to the early development of hand preference in humans.

Hence, we should not underestimate the difficulty of learning to execute rapid, precise, aimed movements of the arm and the hand such as those needed for successful throwing. In human infants at about two to three years of age, throwing is one of the most prominent and consistently lateralized behaviors, although far from an adult's precision. Even if a ball or a stone is grasped with the left (nonpreferred) hand, most children move it over to the right (preferred) hand for executing the action of throwing.

Our understanding of the evolutionary and developmental origins of hemispheric specialization will probably come only from process-oriented models on the developmental and evolutionary origins of laterality which can illustrate how early (motor) asymmetries may be linked to later functional and structural specialization. The development of human right-left asymmetry should be regarded as a complex, multidimensional trait involving different developmental processes. Proper understanding of the developmental processes of handedness may be attained only when it is theoretically dissociated from issues surrounding the origins and acquisition of language.

The left hemisphere as the redundant hemisphere

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Abstract: In this commentary we argue that evolution of the human brain to host the language system was accomplished by the selective development of frontal and temporal areas in the left hemisphere. The unilateral development of Broca's and Wernicke's areas could have resulted from one or more transcription factors that have an expression pattern restricted to the left hemisphere.

In the target article, Corballis summarizes several intriguing findings in monkeys, apes, hominids, and humans. He succeeds in incorporating them into a theory of the evolution of human speech and right-hand preference from animal gestures. A central statement is that communication by manual gestures evolved to a more vocally based language.

Evidence for this theory is derived from the function of the inferior frontal area in monkey and man. The mirror neurons, located in the monkey's homologue of Broca's area and its contralateral homotope, can initiate a grasping movement, but can also recognize the same movement performed by another animal. These cells may have provided the essential neurological basis on which language developed. The dual function of these mirror neurons guarantees the necessary parity between speaker and listener, which requires that the two parties have a common understanding of the communicative elements. This parity is essential to account for the human ability to perceive the invariant articulatory units, despite great variability in the acoustic signal (i.e., pitch, loudness, velocity, and emotional color). This dual function of the neurological substrate for language is the core premise of one of the most influential theories of language: "the motor theory of speech perception" (Liberman & Whalen 2000). This theory assumes that the basic phonetic elements of speech are not the sounds but the articulatory gestures that generate these sounds. This assumption is supported by the finding of functional imaging studies, that listening to speech activates the frontal areas of the brain (the "motor lobe") much more than the temporal areas (the "sound lobe") (Bookheimer 2002). Hence, part of the frontal neurons that represented the production and perception of gestures in monkeys, may have gradually acquired the ability to generate and recognize facial mimicry and eventually speech.

However, basic language functions in human are generally lateralized to the left hemisphere, whereas the monkey's mirror neurons appear to be bilaterally similar. Whatever evolutionary mutation took place, it appears to have particularly affected the left hemisphere.

An explanation for this "unilateral evolution" could be found in an evolutionary principle in molecular genetics. At the molecular genetic level, an evolutionary change often starts with the duplication of a gene (Cooper 1999). One gene copy maintains functioning as before, thereby preventing loss of a vital protein, while the redundant copy is free to mutate into a potentially useful variant. The latter gene copy may accumulate formerly lethal mutations and in some instances acquires a hitherto nonexisting function.

Evolution of the human brain may have progressed parallel to

this molecular principle. The left cerebral hemisphere could be viewed as the redundant copy, the one that gradually adopted a new function – language – while the right hemisphere warranted the continuation of conventional attainments – the production and perception of automatic emotional utterances.

The monkey's vocal productions are characterized by Corballis as automatic, emotional utterances without semantic or syntactic content. This description bears close resemblance to the speech of aphasia patients who have suffered severe left-hemispheric stroke. These patients can hardly produce any intentional speech but can sometimes produce unexpected automatic speech (frequently curses) in emotional situations. As in the monkey, this speech is not under voluntary control and most likely originates from the right hemisphere, because it is lost after a second infarction at the right side (Kinsbourne 1971). It could thus be hypothesized that the verbal capacity of the human right hemisphere is the homologue of the monkey's vocal system.

Evolution of language areas in one hemisphere only could result from a new gene (or genes), most likely a transcription factor, which has an expression pattern restricted to the left hemisphere. Such unilateral expression patterns have previously been discovered for transcription factors that induce asymmetric development of the heart and great vessels (Levin & Mercola 1998). Parallel to asymmetry of the heart, asymmetry of the brain may also result from an asymmetric expression pattern of certain gene products (discussed by Sommer et al. 2002).

Presently, only one gene has been identified as having a major role in human language: the transcription factor FOXP2 (Enard et al. 2002). However, the importance and the uniqueness of this gene for human language capacity have yet to be established.

If we accept that FOXP2 or other language-related genes enable language functions in the brain, then the human variance in language lateralization could be explained as a genetic polymorphism that affects not the function but only the expression pattern of these genes. Aberrant expression patterns of the hypothesized language genes would cause the language areas to develop normally but at a different location (i.e., bilaterally or in the right hemisphere).

According to our view, motor dominance is not likely to result from the same gene or genes as language dominance, because 70% of left-handed subjects have left cerebral language dominance (Knecht et al. 2000). However, genetic and environmental factors that disrupt the unilateral left-sided expression pattern of the language gene or genes, may also disrupt unilateral expression of the gene or genes that supports the development of manual dexterity. This could explain why deviant language lateralization is more common but not standard in subjects with deviant motor dominance.

Misleading asymmetries of brain structure

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Abstract: I do not disagree with the argument that human-population right-handedness may in some way be a consequence of the population-level left-lateralization of language. But I suggest that the human functional lateralization is not dependent on the structural left-right brain asymmetries to which Corballis refers.

There are two separate sources of evidence for this. First, as discussed by Corballis, great apes and possibly other large primates such as baboons (Cain & Wada 1979) have left-right asymmetries in homologues of the human language areas, but evidence for either population-handedness or language capacities in apes remains extremely weak. Second, although there is a weak associa-

tion between handedness and language lateralization, recent data suggest little correlation between functional lateralization and human anatomical left-right brain asymmetries.

In addition to the studies by Gannon et al. (1998) and Cantalupo and Hopkins (2001), Pilcher and colleagues (2001) have reported volumetric studies of nonhuman primates which have revealed a pattern of rightward frontal and leftward occipital structural asymmetries similar to that observed in humans (known as "torque" or the frontal and occipital petalia). However, although some, such as Bodamer and Gardner (2002), continue to suggest that great apes may have precursors to human conversational ability, the content of the conversations is entirely consistent with the conclusions of Premack (1986) and Terrace et al. (1979) that the linguistic capacities of even extensively trained apes are best regarded as nonexistent. Humanlike structural left-right brain asymmetries are therefore present in great apes without any related functional specializations for language.

Corballis proposes that there should be some degree of association between handedness and degree and direction of language lateralization, and he is able to cite the study by Knecht et al. (2000) in support of this long-held view. That a small but otherwise normal fraction of the population is nevertheless expected to have language in a different hemisphere from that which is used for the preferred hand suggests a rather indirect association. Knecht et al. (2001) have emphasized that atypical language lateralization is not necessarily pathological, and they found no relation between the direction or degree of language lateralization and a variety of measures such as academic achievement and language fluency, whereas strong lateralization has the potential disadvantage of increasing susceptibility to unilateral capacity decrements (as tested with transcranial magnetic stimulation; Knecht et al. 2002).

Given the variability in functional specialization, it is perhaps less surprising than the authors suggest that Good et al. (2001) did not detect any correlation whatsoever between handedness and features of brain structure in a voxel-based study of cerebral asymmetry which was sensitive enough to reveal significant sex differences. Language lateralization was not assessed in this study, and it would be interesting to see if statistically significant results would emerge for anatomical correlates of language dominance with this fully automated procedure, which is less sensitive to bias than postmortem or "region of interest" methods.

The study by Good et al. (2001) used a large sample (465 normal brains). The report by Kennedy et al. (1999) involved only three subjects but is useful because it demonstrated a dissociation between functional and structural brain asymmetries, measured using magnetic resonance imaging (MRI) techniques. The subjects had mirror-image reversal of the internal organs (*situs inversus totalis*) but were in normal health. Anatomically, left-right brain asymmetries followed the mirror reversal of the internal organs – there were reversed frontal and occipital petalia in all three subjects. Inspecting the details of the Sylvian fissure revealed that two thirds of participants with SI (*situs inversus*) had a larger planum temporale on the left, with an earlier Sylvian fissure upturn on the right (i.e., not reversed). However, in the 15 normal controls in this study, only eight had a larger left planum temporale, and so it is difficult to draw firm conclusions about the degree of association between "typical" planum temporale differences and frontal and occipital petalia. The measurement of language lateralization via functional magnetic resonance imaging (fMRI) during behavioral tasks such as word-stem completion disclosed that all three SI individuals had normal left-side language dominances as well as strong right-handedness assessed by questionnaires.

Kennedy et al. (1999) concluded that the factors responsible for typical brain petalia are not the same as those that govern the lateralization of language. This report is consistent with others that have suggested that SI individuals are usually right-handed and show a "right ear advantage" in dichotic listening tasks (used as a measure of left-hemisphere dominance of language before brain-