

# From mouth to hand: Gesture, speech, and the evolution of right-handedness

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**Abstract:** The strong predominance of right-handedness appears to be a uniquely human characteristic, whereas the left-cerebral dominance for vocalization occurs in many species, including frogs, birds, and mammals. Right-handedness may have arisen because of an association between manual gestures and vocalization in the evolution of language. I argue that language evolved from manual gestures, gradually incorporating vocal elements. The transition may be traced through changes in the function of Broca's area. Its homologue in monkeys has nothing to do with vocal control, but contains the so-called "mirror neurons," the code for both the production of manual reaching movements and the perception of the same movements performed by others. This system is bilateral in monkeys, but predominantly left-hemispheric in humans, and in humans is involved with vocalization as well as manual actions. There is evidence that Broca's area is enlarged on the left side in *Homo habilis*, suggesting that a link between gesture and vocalization may go back at least two million years, although other evidence suggests that speech may not have become fully autonomous until *Homo sapiens* appeared some 170,000 years ago, or perhaps even later. The removal of manual gesture as a necessary component of language may explain the rapid advance of technology, allowing late migrations of *Homo sapiens* from Africa to replace all other hominids in other parts of the world, including the Neanderthals in Europe and *Homo erectus* in Asia. Nevertheless, the long association of vocalization with manual gesture left us a legacy of right-handedness.

**Keywords:** cerebral dominance; gestures; handedness; hominids; language evolution; primates; speech; vocalization

## 1. Introduction

Most people are right-handed, whether defined in terms of preference or skill. Just why this is so remains something of a mystery, and there is still argument as to whether the underlying cause is environmental (e.g., Provins 1997) or biological, and more specifically, genetic (e.g., Annett 1995; Corballis 1997; McManus 1999). There is nevertheless general agreement that handedness is a function of the brain rather than of the hands themselves, and that it is related to other cerebral asymmetries of function, including the left-cerebral dominance for speech. For example, Knecht et al. (2000) have recently shown that the incidence of left-cerebral dominance of cerebral activation during word generation is linearly related to the degree of right-hand preference as measured by the Edinburgh Handedness Inventory (Oldfield 1971).

Although there are many examples of population-level asymmetries in nonhuman species (e.g., Bradshaw & Rogers 1993; Rogers 2000), right-handedness itself still appears to be an asymmetry that distinguishes humans from other species, at least in degree. Indeed, if there is a hand preference among nonhuman primates, it may more often favor the left hand, especially for visually guided movement (MacNeilage et al. 1987 – but see also the commentaries on this article). There is some evidence, however, for a slight right-hand preference among the great apes. Although Finch (1941) claimed that there was no systematic popula-

tion-level right-handedness in chimpanzees, Hopkins and his colleagues have shown a right-hand preference among captive chimpanzees for some activities, including bimanual feeding, as in extracting peanut butter with one hand from a tube held in the other (Hopkins 1996). In both cases, the ratio of right- to left-handers appears to be only about 2:1, whereas in humans the ratio is about 9:1. In an extensive review of evidence, McGrew and Marchant (1997) are nevertheless skeptical of most claims of species-level biases in handedness in nonhuman primates, and conclude by stating that "only chimpanzees show signs of a population bias . . . to the right, but only in captivity and only incompletely" (p. 201). In a more recent study of handedness in the chimpanzees of the Mahale Mountains in Tanzania, McGrew and Marchant (2001) again report the absence of

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any population bias and suggest that findings of weak right handedness in captive chimpanzees “may be inadvertently shaped by the routine acts of the humans” (p. 355).

One of the activities in which it is claimed that captive chimpanzees display a population-level bias toward right-handedness is pointing, which suggests that the bias may derive from a left-hemispheric specialization for communication. It is often claimed that great apes do not point in the wild, although there is at least one claim of spontaneous pointing among bonobos (Veà & Sabater-Pi 1998), and Inoue-Nakamura and Matsuzawa (1997) recorded rare pointing among infant chimpanzees as they began to use hammer and anvil stones to crack nuts. In these examples, there is no mention of consistent hand preference. According to Hopkins and Leaven (1998), however, captive chimpanzees can be readily taught by humans to point, and other animals pick up the habit evidently without further human intervention; again, some two-thirds of them point with the right hand. Although this may be taken as evidence for a biologically determined asymmetry for communication, and perhaps a precursor to human right-handedness and left-cerebral control of speech, it might again reflect a subtle influence of human right-handedness on these captive animals.

It has also long been known that in most people, the left hemisphere is dominant for speech (Broca 1861b; 1865). Insofar as speech itself is uniquely human, this asymmetry might seem to be another distinguishing characteristic of our species. But if we regard speech simply as a means of vocal communication, then it is an asymmetry that appears to be widespread in the animal kingdom. There is evidence of a left-hemispheric bias for vocal production in frogs (Bauer 1993), passerine birds (Nottebohm 1977), mice (Ehert 1987), rats (Fitch et al. 1993), gerbils (Hollman & Hutchison 1994), and marmosets (Hook-Costigan & Rogers 1998). Rhesus monkeys (Hauser & Anderson 1994) and Japanese macaques (Heffner & Heffner 1984) show a right-sided advantage in the perception of species-specific vocalizations, suggesting a left-cerebral specialization that may be associated with left-cerebral dominance for the production of these sounds. These findings suggest that an asymmetry of vocal control may go far back in evolution, perhaps to the origins of the vocal cords themselves some 170 million years ago (Bauer 1993). In this respect, then, left-cerebral dominance for vocalization contrasts with handedness, even though right-handedness in humans also implies a left-cerebral dominance. Hauser and Anderson (1994) found that in rhesus monkeys the orientation asymmetries to vocal calls were not correlated with handedness, whereas cerebral asymmetry for speech and handedness are correlated in humans (Knecht et al. 2000). It might therefore be inferred that right-handedness in humans is a consequence of the left-cerebral dominance for vocalization, given that the latter emerged earlier in evolution.

There have been a number of suggestions as to how the association may have come about in the evolution of our species. One is that a single genetic mutation might have created the left-hemispheric dominance underlying both asymmetries (e.g., Annett 1995; Corballis 1997; McManus 1999). Crow (1993; 1998) has taken this idea further by suggesting that the same genetic mutation was a speciation event that led also to the emergence of *Homo sapiens*, along with such other uniquely human capacities as theory

of mind, a predisposition to schizophrenia, and language itself – which Chomsky (1988, p. 170) has also attributed to “a genetic mutation.” These theories suggest a common cause for the two asymmetries, but overlook the evidence that the asymmetry in vocalization long preceded handedness.

Others have suggested that handedness and speech dominance are causally related, but there is disagreement as to the direction of the causality. Hewes (1973b, p. 9) argued that the origins of left-cerebral dominance lay in the “long selective pressure for the clear separation of the precision grip and the power grip.” Steklis and Harnad (1976) proposed similarly that bipedalism in the early hominids led to increasing specialization of the hands for skilled actions, and that there would be advantages in asymmetrical representation, including systematic separation of the power and precision grip. Like Hewes, they went on to suggest that this asymmetry gave rise to right-handedness for tool making and early gestural language. In the subsequent switch from manual to vocal language, the left hemisphere would then have assumed dominance for speech as well as for manual activities.

Again, this seems at odds with the evidence that it was the left-hemispheric dominance for vocalization, not right-handedness, that arose earlier in evolution. Indeed, this suggests that the causality may go the other way, and that it was the left-cerebral dominance for speech that gave rise to handedness. Brain (1945), for instance, argued that because animals showed no overall preference for one or other hand, it must have been the emergence of a “motor speech center” in the human left hemisphere that created right-handedness. Roberts (1949) argued similarly that right-handedness emerged after the beginnings of speech; “Its essential quality,” he wrote, “is its determination by speech” (p. 567).

In this article, I argue that Brain and Roberts were substantially correct, although the original basis for the asymmetry lay in the left-cerebral dominance for vocalization, not for speech per se. What is missing from their accounts, however, is an explanation of how handedness came to be associated with vocalization. The key to that, I suggest, has to do with the evolution of language itself. Following Hewes, Steklis and Harnad, and others, I shall argue that language emerged in our species, not from primate calls, but from gestural communication. Vocalizations were gradually incorporated into the gestural system, and it was this process that led to the lateralization of manual gesture itself, leading to the right-hand preference. As for the “speciation event,” I suspect that the emergence of our species was not so much an event, genetic or otherwise, as the accumulation of changes that led eventually to the emergence of autonomous speech in our species and thus freed the hands for the advancement of manufacture and material culture.

I begin by reviewing the evidence that language evolved from manual gestures and not from vocal calls.

## 2. The gestural theory of language origins

Although not universally accepted, the idea that articulate language evolved from manual gestures has been proposed many times (e.g., Armstrong 1999; Armstrong et al. 1995; Corballis 1992; 1999; 2002; Givón 1995; Hewes 1973b; Riz-

zolatti & Arbib 1998; Steklis & Harnad 1976). This idea is developed in detail in Corballis (2002), and only the main points will be covered here.

### 2.1. *Manual versus vocal control*

Our primate heritage equipped us with excellent intentional control over the forelimbs and face, a sophisticated visual system, but relatively inflexible vocal control. Other primates, including our closest relatives the chimpanzee and bonobo, certainly vocalize, but their vocal calls are largely under emotional control, more akin to laughing and crying than to articulate speech (Deacon 1997). This is not to say there is no cortical control over primate vocalizations, because there is evidence that vocalization in monkeys is induced by stimulation of the anterior cingulate cortex, and damage to this region impairs the ability of monkeys to produce vocal calls (see Hauser 1996 for a review). Hauser concludes that the cingulate system is not the final motor pathway, but serves to modulate emotively based vocalizations. Bilateral damage to the region corresponding to Broca's area, which is critically involved in speech production in humans, or to surrounding areas, does not appear to interfere with vocalization in monkeys at all (Jürgens et al. 1982). To my knowledge, there is no evidence as to the neural control, cortical or otherwise, of vocalization in the great apes.

Although primate calls appear to be largely automatic, this does not mean that they are invariant. For example, chimpanzee food calls can vary, suggesting a degree of flexibility (Hauser et al. 1993; Hauser & Wrangham 1987), although Tomasello and Call (1997) have suggested that the variation is probably not under voluntary control, and may reflect variation in emotional arousal. There are also regional variations in chimpanzee pant hoot calls (Arcadi 1996; Marshall et al. 1999), although again it is by no means clear that the differences are due to learning. For example, Mitani et al. (1999) have documented geographic variation in the calls of wild chimpanzees, and argued that they can be explained in terms of differences in habitat acoustics, the sound environment of the local biota, and body size.

But even if chimpanzee calls can be modified through learning, there seems no good reason to question the conclusion reached by Goodall (1986, p. 125), on the basis of prolonged and detailed observation, that "[t]he production of sound in the absence of the appropriate emotional state seems to be an almost impossible task for a chimpanzee." Chimpanzee calls surely have little, if any, of the voluntary control and flexibility of human speech. This presumably explains why attempts to teach chimpanzees to actually talk have been futile (Hayes 1952), whereas there has been at least modest success in teaching great apes to communicate using manual signs (Gardner & Gardner 1969; Miles 1990; Patterson 1978), or a system of visual symbols on a keyboard that they can point to (Savage-Rumbaugh et al. 1998). These enterprises have so far fallen well short of establishing true syntactic language in great apes (Pinker 1994), but clearly have gone well beyond what was apparently achievable through vocalization.

It is also clear that chimpanzees and other apes make extensive use of gestures in the wild. De Waal (1982) noted that chimpanzee gestures often start out as actions on objects, but become "conventionalized" for the purposes of communication – just as the signs in the signed languages of the deaf lose their iconic form and become convention-

alized. Gestures are often subtle and difficult for human observers to discern, but at least some of them have been identified and documented. For example, Tanner and Byrne (1996) itemized some 30 spontaneous gestures developed by lowland gorillas in the San Francisco Zoo, where the animals are enclosed in a large, naturalistic area; and Tomasello et al. (1997) also have also identified 30 different gestures from the repertoire of free-ranging chimpanzees at the Yerkes Regional Primate Center Field Station. Tomasello et al. also make the point that these gestures are typically dyadic, involving exchanges between individuals, and are in this sense more "language-like" than the vocalizations of chimpanzees, which are typically not directed to specific others.

It seems reasonable to conclude that the common ancestor of humans and chimpanzees would have had a repertoire of fixed calls perhaps similar to those of present-day chimpanzees, but that these calls would not have provided a basis for intentional communication. Their arboreal heritage, however, would have provided them with a gestural system on which flexible communication might be built. This is not to say that gestural communication would have been particularly adaptive in an arboreal setting itself, because arboreal life keeps the hands occupied with climbing, grasping, clinging, and so forth. Rather, the manual flexibility that evolved in this environment could later have been exapted for communication after our bipedal forebears descended from the trees and occupied more open territory.

### 2.2. *"Mirror neurons" and the role of Broca's area*

Recording from single cells in area F5 of the monkey brain indicates that these cells have to do with manual gestures rather than vocalization, even though this region is thought to be the homologue of Broca's area in the human brain. These neurons are selective for particular reaching movements made by the animal, but some of them, dubbed "mirror neurons," also respond when the monkey observes the same movement carried out by another individual (Rizzolatti et al. 1996a). This 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 (Rizzolatti & Arbib 1998). Further, there appears to be a mirror-neuron system for the perception, imaging, and execution of manual action, also involving Broca's area, in humans (e.g., Nishitani & Hari 2000).

Eventually, of course, Broca's area became involved in the organization of articulate speech. This is discussed further in a later section, but the point to be noted here is that this area appears to have been involved in manual action well before it was involved in vocalization.

### 2.3. *Bipedalism*

The hominids split from the line leading to modern chimpanzees and bonobos around six million years ago, and the main characteristic distinguishing them was a bipedal posture. Bipedalism would have freed the hands and arms from locomotion, creating increased opportunity for manual expression. Chimpanzees have an extensive range of gestures in the wild (e.g., Tomasello & Call 1997), and one can only conjecture that this range would have been increased with the emergence of bipedalism, perhaps to the point that effective communication was achieved through mime (Don-

ald 1991). This is not to say that it was the adaptive advantages of manual communication that led to selection for bipedalism, and true syntactic language probably did not evolve until after the emergence of the genus *Homo* around two million years ago. This genus is associated with the emergence of stone tool technologies and increase in brain size (Wood & Collard 1999), and a little later with migrations out of Africa (Tattersall 1997), all of which may reflect increasingly sophisticated communication.

#### 2.4. Adaptations for articulate speech

The fossil evidence suggests that the adaptations necessary for articulate speech occurred only recently in hominid evolution. P. Lieberman (e.g., 1998; Lieberman et al. 1972) has long argued, largely on the basis of the inferred location of the larynx, that even the Neanderthals of 30,000 years ago would have suffered speech defects sufficient to keep them separate from *Homo sapiens*, leading to their eventual extinction. This work remains controversial (e.g., Gibson & Jessee 1999), although it has been recently supported by evidence that the facial structure of *Homo sapiens* might have been uniquely adapted to speech (D. Lieberman 1998). A further clue comes from inspection of the thoracic region of the spinal cord, which is relatively larger in humans than in nonhuman primates, probably because breathing during speech involves extra muscles of the thorax and abdomen. Fossil evidence indicates that this enlargement was not present in the early hominids or even in *Homo ergaster*, dating from about 1.6 million years ago, but was present in several Neanderthal fossils (MacLarnon & Hewitt 1999).

Yet another fossil clue comes from the hypoglossal canal at the base of the tongue. The hypoglossal nerve, which passes through this canal and innervates the tongue, is much larger in humans than in great apes, probably because of the important role of the tongue in speech. Fossil evidence suggests that the size of the hypoglossal canal in early australopithecines, and perhaps in *Homo habilis*, was within the range of that contained in modern great apes, whereas that of the Neanderthal and early *Homo sapiens* skulls was well within the modern human range (Kay et al. 1998).

Perhaps the most critical adaptation necessary for the evolution of speech was the change in brain organization that resulted in the intentional control of vocalization. One of the key areas involved in this change was undoubtedly Broca's area, which is further discussed in later sections. The important point for the present is that all of these changes occurred fairly late in hominid evolution. This could simply mean that language itself evolved late, as some authors have indeed proposed (e.g., Bickerton 1995; Chomsky 1988; P. Lieberman 1998). But, given the intricate nature of syntax, it is much more likely that language itself evolved gradually through natural selection (MacNeilage 1998; Pinker & Bloom 1990). If speech itself emerged late, then we might conclude that language itself has deeper roots. Those roots may therefore lie in gesture rather than in vocalization.

#### 2.5. Gesture and modern language

People commonly gesture as they speak. McNeill (1985) has shown that gestures are precisely synchronized with speech, arguing that they together form a single, integrated system. Goldin-Meadow and McNeill (1999) suggest that

speech carries the syntactic component, whereas gesture carries the mimetic, iconic component, although if people who normally communicate with speech are instructed to communicate using gestures alone, then the gestures also assume syntactic elements (Goldin-Meadow et al. 1996). More compelling, though, it is now clear that the sign languages invented by the deaf have all the essential properties of spoken language, including a sophisticated syntax (Armstrong et al. 1995; Neidle et al. 2000). Children exposed only to sign language go through the same stages of language acquisition, possibly reaching each stage slightly earlier than their vocal peers (Meier & Newport 1990), and children exposed to crude forms of signing actually create systematic syntax (e.g., Goldin-Meadow & Mylander 1998; Senghas & Coppola 2001). There is also evidence that sign language is represented primarily in the left cerebral hemisphere in the majority of individuals, and involves the two major areas usually associated with vocal language, namely Broca's and Wernicke's areas (Neville et al. 1997).

Armstrong et al. (1995) have made the further point that syntax could have emerged from the structure of individual gestures themselves. Some gestures can be interpreted equally as morphemes or as sentences. Armstrong et al. give the example of the gesture of swinging the right hand across to grasp the raised forefinger of the left hand. This gesture can be interpreted either as the verb "to grasp" or as the sentence "I grasp it." In fact there are many gestures in common use that can be understood as a simple sentence, such as the shrug, or the dismissive wave of the hands that says, in effect, "forget it." Nevertheless, this argument for the origin of syntax is perhaps not definitive, because Carstairs-McCarthy (1999) has argued in somewhat similar fashion that basic sentence structure might have been exapted from the structure of the syllable in speech. I find this less convincing than the gestural argument because syllables typically do not convey meaning by themselves, whereas individual gestures do.

Taken together, these various sources of information reveal a close association between speech and manual gestures, and they are consistent with the view that the dominant mode has shifted from manual gesture to speech.

### 3. An evolutionary scenario

As Hewes (1973b) recognized, one of the problems to be surmounted when proposing the gestural theory, is that of explaining why vocalization eventually predominated – a point also raised by MacNeilage (1998). In the following sections, I suggest a scenario as to how, when, and why vocalization became part of language.

#### 3.1. The role of visuofacial movements

It is perhaps important to note first that gestures involve movements of the face as well as of the hands. With the emergence of bipedalism some six million years ago, gestural language may have been predominantly manual, but around two million years ago there were a number of changes that may have led to an increasing involvement of the forelimbs in other activities. Stone tool cultures date from some 2.5 million years ago (Semaw et al. 1997), suggesting increasing involvement of the hands in manufacture. There appears to be growing evidence that the early hominids

lived in forested environments, near water, and not, as previously supposed, in savanna-like conditions (Gibbons 2002; Tobias 1998). The shift to open savanna may have occurred more recently, perhaps from around two million years ago (Wood 1992), leading to increasing use of the hands for defensive actions, such as throwing and the use of weapons, and for carrying. Further, migrations out of Africa appear to have begun around two million years ago (Tattersall 1997), again suggesting the forelimbs would have been adapted for carrying. These various factors suggest that a shift to increasing involvement of the face in communication may have occurred from about two million years ago.

One clue that this may be so comes from the structure of the eye. We are exceptional among primates in having eyes in which the sclera is white rather than pigmented, and much more of it is visible in humans than in other primates. The human eye is also exceptionally elongated horizontally (Kobayashi & Kohshima 2001). The dark color of the exposed sclera in nonhuman primates may be an adaptation to conceal the direction of eye gaze from other primates or predators, whereas the human eye seems to have evolved to enhance communication rather than to conceal it.

Although the emphasis on the face may have occurred fairly recently in hominid evolution, many of the gestures made by primates are also visuofacial rather than manual, and some of these, such as lip smacks, tongue smacks, and teeth chatters, also create distinctive sounds, although they do not involve voicing. Further, the posterior part of the homologue of Broca's area in monkeys is involved in the movements of the mouth and jaw involved in mastication (Luschei & Goldberg 1981), and stimulation of the area immediately posterior to Broca's area in humans elicits chewing movements (Foerster 1936). These observations have suggested to MacNeilage (1998) that speech itself might have evolved from the repetitive movements involved in mastication. Whereas there are some difficulties with this argument (see commentaries to MacNeilage's 1998 article), the proximity of areas associated with manual and facial control make it highly likely that manual and facial gestures came to comprise an integrated gestural system. Integration may have also come about partly through the mechanics of eating. Among primates, at least, food is brought to the mouth by hand, and eating often requires integrated movements of the hands and mouth.

In the sign languages of the deaf, facial movements and expressions often serve syntactic functions. For example, in American Sign Language, a declarative sentence is converted into a question if accompanied by a forward movement of the head and shoulders, and a raising of the eyebrows. Relative clauses are signaled by a raising of the eyebrows and upper lip, with the head tilted back. An affirmative sentence becomes a negative one if accompanied by a shaking of the head. (Examples are from Neidle et al. 2000.) Of course, sign language does not necessarily resemble any gestural language that our ancestors, such as *Homo erectus*, may have used. It is nevertheless interesting that facial gestures should generally convey syntax, whereas manual gestures supply content. As suggested earlier, syntax may have been grafted onto gestural communication from around two million years ago with the emergence of the genus *Homo*. If syntax was predominantly facial, this suggests a progression from manual to facial gesture in the emergence of language.

The next step may have been to add voicing.

### 3.2. Adding sounds to gestures

The addition of vocal sounds to facial gestures would have enhanced their accessibility and created distinctions between otherwise identical gestures, thereby increasing the repertoire. For example, the voiced plosives [b], [d], and [g] are distinguished from their unvoiced counterparts [p], [t], and [k] by the addition of voicing. Voicing is therefore a feature that serves to double up many of the possible sounds of speech. The visual element persists, however, as illustrated by the McGurk effect: If you dub a sound such as *ga* onto a video recording of a mouth that is actually saying *ba*, then you hear the syllable *da*, which is a sort of compromise between the sound itself and what the lips seem to be saying (McGurk & MacDonald 1976). Once the principle of adding vocal sounds is established, gestures that are barely distinguishable visually become easily distinguishable acoustically, although a skilled lip reader can extract a good deal of the message without access to the voiced sounds. Some of the sounds of speech are not voiced, as is the case with some of the click sounds of the Khoisan languages of Africa or even the unvoiced aspirated sounds of our own speech.

Vocal elements may have occurred first as emotional accompaniments. Great apes certainly vocalize, and it is likely that emotional cries would have accompanied early gestural communication, perhaps to provide emphasis or convey urgency. Kanzi, the bonobo studied by Savage-Rumbaugh et al. (1998), vocalizes freely while communicating gesturally or via the keyboard, to the point that some observers have wondered whether his vocalizations might be interpreted as words. It is more likely, I think, that they are emotional cries, without semantic or syntactic content. Vocalization may also occur as an involuntary part of action itself. Diamond (1959) suggested that speech originated in the release of air that follows action, as in the grunting of tennis players when they play a shot. Speech may therefore have evolved as modulated grunts, which might explain why it is generated from the exhalation of air and not from inhalation.

The selective pressure to add vocalization to the articulatory repertoire was no doubt strong, as indicated by the cost it inflicted. The lowering of the larynx meant that breathing and swallowing must share the same passage. Humans, unlike other mammals, cannot breathe and swallow at the same time, and are therefore especially vulnerable to choking. Even so, vocal speech essentially replaced gestures of the face and hands as the primary language medium, and became autonomous to the point that we can communicate without visual contact, as on radio or telephone. And yet we continue to gesture, redundantly, even when using these devices.

### 3.3. Going for Broca

The key to adding sounds to gesture lies, at least in part, in the development of Broca's area, which in monkeys has to do with manual activity but in humans has added speech to its portfolio. On the basis of endocasts made from fossil skulls, Holloway (1983) has claimed that *Homo habilis*, dating from nearly two million years ago, possessed a prominent asymmetry of the left frontal lobe in the region corresponding to Broca's area, and there is also evidence for an enlargement of the inferior parietal lobule, which overlaps

with Wernicke's area. This has led Tobias (1987), among others, to proclaim that the origins of language date from *Homo habilis*. As we have already seen, there are other reasons to suppose that syntactic language may have emerged with the genus *Homo*.

But does the appearance of Broca's area necessarily signal the origins of speech, as distinct from language? In view of its longstanding involvement in manual activity, its enlargement may reflect the incorporation of syntax into gestural communication. What may signal the beginnings of vocal control, however, is the evidence that Broca's area in *Homo habilis* appears to be enlarged in the left hemisphere. This theme is explored later.

### 3.4. Speech itself as gesture

According to the scenario outlined here, speech itself might be regarded as composed of gestures, albeit vocal ones, rather than of abstract phonemes. Studdert-Kennedy (1998, p. 207) has maintained that "the basic particles of speech are not, as generally assumed, phonetic segments (consonants and vowels) or their descriptive features, but the gestures that form them." These gestures are made up of the movements of six different articulators, namely, the lips, the blade of the tongue, the body of the tongue, the root of the tongue, the velum (or soft palate), and the larynx, which are combined in various ways to produce syllables and words. Liberman and Whalen (2000) argue that the same gestural system underlies the perception as well as the production of speech, presumably through a system resembling the "mirror-neuron" system described earlier. Browman and Goldstein (1991), who developed a gestural theory of speech, based their work on a theory previously developed to describe skilled motor actions in general, and note that the preliminary version of their theory was "exactly the model used for controlling arm movements, with the articulators of the vocal tract simply substituted for those of the arm" (p. 314). This underscores the possibility of a continuous transition from manual gesture through facial gesture to vocal speech.

### 3.5. Autonomous speech as an invention

It is possible that the mechanisms for autonomous vocal speech were in place well before it was realized. It is important to recognize that even today, normal speech is accompanied by manual and facial gestures that modulate meaning, and these gestures readily assume dominance in the deaf, or if vocalization is for some other reason prevented. Gesture remains close to the surface. Nevertheless, fully autonomous speech is normally possible and little is lost if accompanying gestures are not available to the listener. However, the realization of a language that could function through speech alone may have been an invention rather than a biological necessity, and transmitted culturally rather genetically.

Even Darwin (1904, p. 60) seems to have anticipated this possibility:

Man not only uses inarticulate cries, gestures and expressions, but has invented articulate language; if, indeed, the word invented can be applied to a process, completed by innumerable steps, half-consciously made.

Some have claimed that language itself is essentially a cultural invention – Lock (1980), for example, refers to the de-

velopment of language in children, in the very title of his book, as "the guided reinvention of language." However, the evidence is overwhelming that both the structure of language itself and the modification to the vocal tract and control of breathing necessary for articulate speech are biological adaptations (e.g., Pinker 1994). It is the autonomy of speech that may have been a cultural invention – the realization that visible gestures could be largely dispensed with and that the message could be carried by vocalization alone.

Another example of a cultural invention that is dependent on prior biological adaptations is writing. Writing as a codified system is thought to have been developed in the Fertile Crescent only around 5,000 years ago (Gaur 1984), and for much of the intervening period the great majority of humans have been illiterate. Even today, some 10 to 20% of the U.S. population are said to be functionally illiterate, and the percentage may be well over 50% in some African countries (Crystal 1997). Yet, the biological capacities required for reading and writing must have been in place well before that and probably date at least to the origins of our species some 170,000 years ago. Of course, writing is not as "natural" as either spoken or signed language, in part because it is normally dependent on the prior acquisition of spoken language; but this nevertheless illustrates the point that the precise forms that language can take have a strong cultural component.

### 3.6. On the recency and impact of autonomous speech

It is possible that autonomous speech was invented, in Africa, some time after the emergence of *Homo sapiens*. Current evidence from both mtDNA (Ingman et al. 2000) and Y-chromosome (Ke et al. 2001; Semino et al. 2000; Underhill et al. 2000) analyses suggests that non-African peoples share a common ancestry with Africans somewhere between 35,000 and 89,000 years ago, with a best estimate of around 52,000 years ago. The origins of *Homo sapiens* within Africa lie deeper at around 170,000 years ago (Underhill et al. 2000). Although migrations of hominids from Africa began nearly two million years ago (Tattersall 1997), it may have been those who migrated from a mere 50,000 years ago who replaced all previous migrants, including not only *Homo neanderthalensis* in Europe and *Homo erectus* in Asia, but also those colonies of *Homo sapiens* who had migrated earlier.

It may have been the emergence of autonomous speech in Africa, occurring gradually over the period from 170,000 to 50,000 years ago, that underlay the success of these late migrants. Autonomous speech would have freed the hands from involvement in language, and facilitated the development of manufacture. It would also have allowed people to explain techniques verbally while demonstrating manually, leading to a sophisticated pedagogy. One possibility is that African emigrants of 50,000 years ago had developed a sophisticated weaponry that allowed them to overcome indigenous populations elsewhere; a more benign interpretation is simply that they were better adapted through language and manufacture to deal with environmental contingencies. Whatever the case, the arrival of *Homo sapiens* in Europe some 40,000 years ago appears to have coincided with an explosion of manufacture and art, and led to the ultimate demise of the Neanderthals within about 10,000 years. There is also growing evidence for a slower development of manufacture within Africa over the period from

about 100,000 to 50,000 years ago (Mellars 1989; Yellen et al. 1995), which would have laid the foundation for their subsequent dominance of Europe and ultimately the rest of the world.

The point to be derived from this scenario is that language has long involved the combination of manual, facial, and vocal gestures, and it may be only recently that vocal speech has come to dominate. I want to argue now that it was through the association of the manual with the vocal aspect that right-handedness was born.

#### 4. The emergence of right-handedness

##### 4.1. How vocalization created handedness

According to the scenario sketched in section 3.6, there would have been selection for the addition of vocalization to the gestural repertoire. In the great apes, however, vocalization is probably still largely under the control of the anterior cingulate cortex and subcortical structures, so the inclusion of vocal elements in intentional communicative acts would have required a shift in the mechanisms of control. The new controlling structures no doubt involved Broca's area, which had long been responsible for the mapping between the perception and execution of manual actions. It may have been the incorporation of vocal control that caused Broca's area to become lateralized.

The homologue of Broca's area in the monkey is F5, which is the locus of the "mirror neurons." As described earlier, these have to do with the perception and production of manual reaching and grasping. In monkeys, the mirror-neuron system appears to be bilateral. In humans, however, the system is largely left-hemispheric (Nishitani & Hari 2000; Rizzolatti et al. 1996b; Sekiyama et al. 2000), and in humans Broca's area is of course involved in vocalization as well as manual activity. There is evidence, moreover, that Broca's area in the left cerebral hemisphere in humans is larger than the homologous area in the right hemisphere (Foundas et al. 1995a; 1996). Broca's area includes Brodmann's areas 44 and 45, and there is also evidence that the asymmetry may be restricted to area 44 (Amunts et al. 1999). But regardless of whether the anatomical asymmetries reflect functional asymmetries, there is little doubt that Broca's area in the great majority of humans is strikingly asymmetrical, with only the left side playing a role in speech, and perhaps in syntax. The homologous region on the right side may be involved in what has been termed musical syntax (Maess et al. 2001).

Broca's area might then have been the locus of the interaction between manual and vocal programming that allowed the vocal asymmetry to create a manual one. As a rough analogy, the cortical mirror-neuron system may be likened to a piano player; and the cingulate/subcortical vocal system, to a piano. The problem is to convert the manual actions of the piano player into sound by striking the keys of the piano. But there is an intrinsic bias among the keys themselves, such that the higher notes are to the right, and it is the higher notes that dominate the melody. This would eventually create a bias in favor of the right hand. Of course, in real piano playing the causality probably runs the other way, with the notes arranged as they are precisely because of the population bias toward right-handedness. In any event, to revert to the matter at hand, as it were, right-handedness may well have evolved from the synchroniza-

tion of manual and facial gestures with a lateralized system of vocal production.

It has been observed that right-handers tend to gesture with their right hands while they speak (Kimura 1973a), whereas left-handers show a more mixed pattern and a more pronounced tendency to gesture with both hands (Kimura 1973b). There is also evidence that voluntary control over facial movements, and especially the movements of the lower face muscles, is largely left-hemispheric (Gazzaniga & Smylie 1990), and nearly 90% of the human population have shown greater movement of the right side of the mouth when speaking (Graves & Goodglass 1982; Graves & Potter 1988). These observations are consistent with an asymmetry of manual and facial gestures induced by a prior asymmetry in the control of vocalization.

As we have seen, there is evidence that the left-sided dominance of Broca's area may have been present in *Homo habilis* but not in earlier hominids (Holloway 1983). Further, Toth (1985) examined flakes formed from the manufacture of stone tools, dating from 1.4 to 1.9 million years ago, and recorded an asymmetry apparently favoring right-handers over left-handers by a ratio of 57:43. The same ratio was produced by present-day right-handers given the task of sharpening stone tools, leading Toth to infer that these early hominids were right-handed. Indeed, as McManus (1999) put it, one should conclude that *all* of the population were right-handed, and he argues that the subsequent emergence of left-handers required a further genetic mutation. However, population estimates based on a sample ratio of 57:43 cannot be made with confidence, and it is perhaps about as likely that the ratio approximated the 2:1 ratio claimed for modern chimpanzees (Hopkins 1996). Either way, right-handedness in early *Homo* could mean that vocal elements had already been incorporated into language by two million years ago, although it does not necessarily mean that speech was the dominant mode. As we have seen, the adjustments to the vocal tract necessary for articulate speech appear not to have been complete until much later, and possibly not until the emergence of *Homo sapiens* 170,000 years ago.

##### 4.2. Cortical lateralization for perception of vocal calls

The lateralizing influence of vocalization on handedness may not have been entirely due to vocal production. Lateralized perception may also have played a role. The cortical component in primate vocalization may be more pronounced with respect to perception than with respect to production (Hauser 1996). Animal calls often have to do with emotional situations, such as danger to the group, and the lack of intentional control over them may be adaptive because it makes them impossible to fake (Knight 1998). For much the same reason, a fire alarm should be automatic, and not subject to whim, although one's reaction to a fire alarm should be purposeful. Similarly, an animal hearing a call from another animal may need to register it consciously in order to take appropriate action, whether to avoid danger or deal with territorial threat. Humans may have little control over such emotional signals as laughing or crying, but recipients need to register these signals consciously if they are to respond appropriately.

It is also clear that great apes are much better able to comprehend human speech than to produce it. For example, Kanzi, the bonobo studied by Savage-Rumbaugh and

her colleagues, shows quite sophisticated understanding of spoken sentences. In one experiment he was given a list of 660 unusual spoken commands, some of them as many as eight words long, and carried out 72% of them correctly. Kanzi was nine years old at the time, and scored a little better than the 66% achieved by a two-and-a-half year old girl (Savage-Rumbaugh et al. 1998). This need not imply that Kanzi has acquired the syntax of spoken English, but it demonstrates that he is at least able to segment spoken words and extract their meaning.

The cortical systems for the perception of species-specific calls in nonhuman primates also appear to be lateralized. For example, Heffner and Heffner (1984; 1990) found that discrimination of species-specific “coos” by Japanese macaques was significantly more impaired by lesions of the left auditory cortex than by lesions of the right auditory cortex, although there was substantial recovery over time following the left-sided lesions. In the majority of humans, the temporal planum, which is associated with language comprehension in humans, is larger on the left than on the right (Foundas et al. 1995a; Geschwind & Levitsky 1968; Jäncke & Steinmetz 1993), consistent with other evidence that the left hemisphere is dominant for language comprehension as well as for language production (see Corballis 1991 for a review). This asymmetry does not appear to be present in rhesus monkeys or baboons (Wada et al. 1975), but is clearly evident in chimpanzees (Gannon et al. 1998; Hopkins et al. 1998). It may well have been driven by lateralization of vocal production at the subcortical level and the need for cortical elaboration of perceived vocalizations. It is likely that this asymmetry was also present in the common ancestor of humans and chimpanzees, and it may reflect the evolutionary origins of an association between right-handedness and vocal communication.

#### 4.3. From gesture to skill: Handedness goes global

Of course, right-handedness does not apply only to gesture. Most people are right-handed for a host of other skilled activities, including writing and eating, and using tools, weapons, and sporting implements. Nevertheless, it may have been the gestural component that provided the initial nudge, as it were, toward a general dominance of the right hand. There has been some dispute as to whether handedness is fundamentally a matter of differential skill (e.g., Annett 1995) or differential preference. One reason for supposing that differences in skill are secondary to a more fundamental preference for one or other hand is that children with childhood autism (McManus et al. 1992) or fragile-X syndrome (Cornish et al. 1997) mostly show a preference for the right hand, but are equally divided with respect to which hand is the more skilled (see also McManus 1999). Hand preference in early childhood may be driven by the emergence of speech, but later influences the hand the child uses for other activities.

### 5. Individual differences

As mentioned earlier, genetic theories of handedness carry the often explicit assumption that handedness and cerebral dominance for language were dependent on a genetic mutation that uniquely defined the human condition (e.g., Annett 1995; Crow 1998; McManus 1999). This runs some-

what counter to the present approach, in which it is assumed that the seed for these asymmetries was sown much earlier in the left cerebral dominance for vocalization. It is nevertheless possible that the hypothetical genetic mutation did not create asymmetry as such, but served to establish the link between handedness and vocalization. There is some evidence, too, that human right-handedness and speech dominance may have been superimposed on a pre-existing asymmetry favoring the left cerebral hemisphere in about two-thirds of the population (Corballis 1997). This could perhaps explain why a number of other human asymmetries also approximate this proportion rather than the 90% incidence of right-handedness (Previc 1991). It is perhaps also worth recalling here the evidence of Hopkins (1996) that around two-thirds of captive chimpanzees are right-handed for some activities, although, as we saw earlier, this asymmetry has not been corroborated among chimpanzees in the wild (McGrew & Marchant 1997; 2001) and remains controversial.

#### 5.1. Lateralization of the temporal planum in chimpanzees

Curiously, though, the leftward bias in the size of the temporal planum appears to be more pronounced in the chimpanzee than in humans, where the proportion of individuals showing the bias is again only about two-thirds. In a post-mortem anatomical study, Gannon et al. (1998) showed a leftward bias in 17 out of 18 chimpanzees, a proportion that is significantly ( $p < .01$ ) above the expected 12 out of 18 according to a binomial test. Hopkins et al. (1998) report a similar degree of bias in an MRI study of the temporal planum in great apes. Among 12 chimpanzees, only one showed a bias favoring the right side, although in two others the authors considered the leftward bias too small to be meaningful. Wada et al. (1975) also found no asymmetry of the temporal planum in rhesus monkeys or baboons, although Hopkins et al. (1998) claim that they were unable even to locate a temporal planum in samples of lesser apes, Old World monkeys, and New World monkeys.

Left-right differences in size may of course be of little functional significance, and some of the data are contradictory. For example, Buxhoeven and Casanova (2000) showed the columns of cells in the temporal planum to be more widely spaced on the left than on the right in humans, but not in chimpanzees, and it was weakly reversed in rhesus monkeys. It has recently been claimed that the right temporal planum in humans may be specialized for spatial attention (Karnath et al. 2001) – perhaps humans have a more highly developed spatial sense than chimpanzees do, leading to compensatory development of the right temporal planum in humans. But, whatever the reason for the apparent discrepancy between humans and chimpanzees, the asymmetry of the temporal planum in chimpanzees seems clearly more pronounced than the asymmetry of hand preference. If it is of any functional significance at all, it may reflect a leftward bias in the processing of species-specific vocal calls.

#### 5.2. Handedness and cerebral dominance in humans

There is also some indication that the incidence of left-cerebral dominance for language in humans may be higher than that of right-handedness, supporting the idea that



right-handedness may be secondary to left-cerebral dominance. A number of studies have shown that even the majority of left-handers, some 70%, are left-cerebrally dominant for language (Milner 1975; Pujol et al. 1999; Rossi & Rosadini 1967; Warrington & Pratt 1973). If we accept the evidence of Milner (1975), based on results of the sodium amytal test, that 96% of right-handers are left-cerebrally dominant, and if we further assume that some 90% of the population are right-handed, then we can estimate that the overall incidence of left-cerebral language dominance is 93.4% – which is higher than the assumed 90% incidence of right-handedness. If we assume that the incidence of left-cerebral dominance in right-handers is as high as 99%, as estimated by Rossi and Rosadini (1967) and by Pratt and Warrington (1972), then the figure jumps to about 96%, well in excess of 90%.

These calculations may be illusory, however, because they are critically dependent on the proportion of left-cerebral dominance among right-handers. If we take the lower figure of 92% estimated by Geffen et al. (1978), then the proportion reduces to about 90%, which is the same as the assumed proportion of right-handers.

### 5.3. Genetic considerations

McManus (1999) has proposed a single-gene, two-allele model that in fact predicts just such a reciprocal relation. One allele, dubbed D for dextral, codes for right-handedness and left cerebral dominance for speech, whereas the other, dubbed C for chance, leaves the direction of handedness and speech dominance to chance. All DD homozygotes will be right-handed and left-dominant for speech, whereas CC homozygotes will be equally divided among the four combinations of handedness and speech dominance. McManus further assumes that among DC heterozygotes, 75% will be right-handed and 75% left-cerebrally dominant for speech, but that these asymmetries will be determined independently. This model then predicts a reciprocal relation between the two asymmetries, with a majority of left-handers being left-dominant for speech and an equal majority of those right-dominant for speech being right-handed.

A possible difficulty with McManus's model is the assumption that handedness and speech dominance are determined independently in DC heterozygotes. Knecht et al. (2000) have shown that the incidence of right cerebral dominance, as measured by functional transcranial Doppler sonography, decreases linearly with the degree of right-handedness, ranging from 27% in extreme left-handers to 4% in extreme right-handers. This suggests a more continuous relation between handedness and cerebral dominance than implied by McManus's model – although the point is a fine one, because McManus's model does predict an overall correlation. Knecht et al.'s data do suggest a causal relation between handedness and cerebral dominance for language, but provide no information as to which way the causality runs.

There is also recent evidence for a genetic influence on hand preference in chimpanzees. Hopkins et al. (2001) have found that 86% of chimpanzee offspring born to right-handed mothers were right-handed, but only among those chimpanzees in the "non-risk" category, which excluded the "risk" category of first-borns and those born sixth or later in the sibling sequence. Among the risk category, the proportion of right-handed chimpanzees born to right-handed

mothers was only 46%. Moreover, the concordance of handedness between non-risk sibling pairs was as great among those cross-fostered as among those raised by their mothers, suggesting that the inheritance of handedness was genetic. The genetic influence implied by these findings seems so heavily qualified as to require replication, but even so the results do suggest that the laterality gene, if such exists, may not be uniquely human.

It is unlikely, though, that there are genes that code directly for handedness (Morgan & Corballis 1978). Rather, it is likely that genes influence whether or not some underlying, extragenetic asymmetry is expressed (see also Morgan 1991). For example, there is a mutant strain of mice in which the asymmetry of the heart was reversed (*situs inversus*) in precisely 50% of the population, and was normal in the remaining 50% (Brueckner et al. 1989), indicating that in the absence of the gene or genes determining normal *situs*, the direction of the asymmetry is random. The models for handedness proposed by McManus and Annett operate similarly, consistent with the view that one allele of a handedness gene codes for some underlying gradient to be expressed whereas the other essentially leaves handedness to chance. It is possible, then, that an underlying gradient is strongly expressed in the production and perception of vocalization. The influence on handedness, however, might be only weak in great apes but relatively strong in humans, because of the strong association between gesture and vocalization in the evolution of language.

## 6. Discussion

There is one sense in which it is understandable that the lateralized control of vocalization might precede the lateralized control of movements of the forelimbs. On a priori grounds, one might expect the limbs to be organized symmetrically. The limbs evolved in the first instance for locomotion, and linear movement is best ensured with a bilaterally symmetrical system. With a few exceptions, such as the sideways movement of the crab or the asymmetrical gallop of the horse, the limbs are both structurally and functionally symmetrical – whether legs for walking, fins for swimming, or wings for flying. Even with the evolution of other specialized roles for the forelimbs, such as picking fruits, holding onto branches, catching insects, or throwing missiles, there are general advantages to a symmetrical system, precisely because the objects of these actions are as likely to be directed to one side of the body as to the other.

Vocalization, in contrast, does not involve direct interaction with the spatial environment. Rather, it is programmed internally and results in output that is patterned in time, not space, and there is no apparent disadvantage to having that programming accomplished asymmetrically in the brain. Indeed, there may be advantages to asymmetrical organization in the absence of strong environmental pressures toward symmetry. Asymmetrical organization can make for more efficient packaging, which might explain why the internal organs of the body tend to be asymmetrically structured and located, and it is probably more efficient to have brain mechanisms programmed within a cerebral hemisphere than to have them spread between the hemispheres. This may also explain why vocalization was lateralized very early in our evolutionary history.

According to the present account, handedness would

have emerged as vocalization was progressively incorporated into gestural language over the past two or three million years. Consequently, we would expect to find left-cerebral control of vocalization, but not right-handedness, in the earlier hominids or their primate forebears. Because it is unlikely that parallel developments would have occurred in the great apes, present-day apes may provide the best tests of the hypothesis developed here. We have already seen that there is controversy over whether the claimed bias toward right-handedness in captive chimpanzees (e.g., Hopkins 1996) is caused by subtly influenced by human handedness, as suggested by McGrew and Marchant (2001), or whether it is fundamentally biological in origin. Evidence from chimpanzees in the wild so far indicate equal distribution of left and right handedness.

Byrne and Byrne (1991) reported a population-level hand preference among gorillas in the wild preparing vegetable matter for consumption, favoring the right hand for the manipulative elements in about two-thirds of the animals. The asymmetry was statistically significant only on a directional test, however, and the authors remark that “We should . . . probably look elsewhere for the evolutionary origins of human right-handed manipulative dominance and brain asymmetry” (p. 541). Nevertheless the proportion of right-handers does conform roughly to that claimed by Hopkins (1996) in the chimpanzee. Further clarification of the extent and nature of handedness in the great apes will be critical to the hypothesis developed in this article. Even if the two-thirds figure is verified, however, it remains possible that the shift from a two-thirds to a 90% right-hand dominance was the result of the incorporation of a more strongly lateralized vocal system into language gestures.

Another critical area of inquiry has to do with the nature of Broca’s area and its homologues in the primate brain. Cantalupo and Hopkins (2001) have recently reported an MRI study showing that Brodmann’s area 44, which delineates part of Broca’s area in the human brain, is larger on the left than on the right in great apes (made up of 20 chimpanzees, five bonobos, and two gorillas). It is not clear whether this is associated with vocalization, or, as suggested by the authors, with manual gestures. Either way, the asymmetry may be considered evidence against the hypothesis developed in this article. If Broca’s area is involved in vocalization and is lateralized, it suggests cortical control of vocalization in the common ancestor of humans and chimpanzees, contrary to the notion that Broca’s area did not achieve vocal control until relatively late in hominid evolution. If it is involved in manual gesture and is lateralized, it runs contrary to the notion that handedness also emerged relatively late.

It is possible, though, that the asymmetry relates to the evidence on handedness in chimpanzees reported by Hopkins. Of the 20 chimpanzees examined by Cantalupo and Hopkins, 14 showed the right-sided enlargement – almost exactly the two-thirds bias shown in Hopkins’s work on handedness in the chimpanzee, although it is not stated whether the asymmetry was actually correlated with handedness in these animals. Again, the incorporation of vocalization into gesture may have been responsible for the shift from a two-thirds to a 90% asymmetry, rather than for the creation of the asymmetry *de novo*. It is again possible that the asymmetry of Brodmann’s area arises from the subtle effects of human handedness on these animals, rather than from any innate biological disposition. It also remains un-

clear whether these anatomical asymmetries have functional significance. In any event, further anatomical and, where possible, functional studies of Broca’s area should help unravel the sequence of events in the evolution of manual and cerebral asymmetry.

Finally, the hypothesis developed in this article rests on the truth or otherwise of the theory that language evolved from manual gestures, rather than from animal cries. It has not been my intention to elaborate the gestural theory in detail here; I have done that elsewhere (Corballis 2002). Nevertheless, if the gestural theory can be decisively ruled out, then the hypothesis developed here is also falsified. It need not follow, though, that the lateralization of vocal control was not the precursor to handedness; rather, it would simply indicate that gestural language was not the mediating factor.

The considerations of this final section suggest that my hypothesis is not simply a just-so story. It is potentially falsifiable from further evidence from our great-ape cousins, and perhaps from further fossil evidence on anatomical and inferred functional asymmetries in the early hominids. My hope is that the hypothesis might help focus future research on the evolution of language, lateralization, and manual activity. And, of course, be proven correct.

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### Myths of first cause and asymmetries in human evolution

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**Abstract:** The causes of asymmetries for handedness and cerebral speech are of scientific interest, but is it sensible to try to determine which of these came first? I argue that (1) first causes belong to mythology, not science; (2) much of the cited evidence is weak; and (3) the treatment of individual differences is inadequate in comparison with the right shift theory.

Corballis argues that the human species’ bias toward right-handedness originates from the location of control for manual and vo-