

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-

cal gestures in Broca's area of the prefrontal cerebral cortex. Both types of gesture probably have something to do with mirror neurones. This is almost certainly true, but is it useful or reasonable to try to determine whether asymmetries of vocal control, or of hand control, evolved first?

Evolutionary scenarios can be fascinating, but so can the myths of first cause told in all human societies. The argument that vocalisation came first and right-handedness was secondary depends on evaluating evidence of these asymmetries in other species. The upshot of Corballis's appraisal is that there is better evidence for early asymmetries in the control of vocalisation in nonhumans than for asymmetrical control of the limbs. Undoubtedly there are asymmetries of vocal control in some song-birds, but there is also footedness in parrots (Bradshaw & Rogers 1993). Questions about the origins of human handedness and speech require evidence for non-human primates. All primates vocalise and all have handedness, but in none other than humans is there unequivocal evidence of species asymmetry. It is the *divergence* of humans from apes in these respects that is most impressive. Asymmetrical control of vocalisation in humans, birds, and marine mammals is more likely to depend on convergent evolution than descent. The similarities suggest the importance of unilateral control for complex vocal output. They suggest why nature came up with a similar strategy for human speech. But the mechanisms involved are not likely to have been preserved through intervening species that do not have these adaptations.

The nature and quality of the evidence cited here for asymmetries in nonhuman species is debatable. Independent replication must be the criterion. In the published literature, negative evidence tends to be neglected in favour of positive findings. Similarities with humans are likely to be stressed in applications for funding. To be fair to Corballis, it must be acknowledged that almost every sentence in the target article includes a "may be" or a "perhaps," but I still find speculations woven from doubtful evidence. This is not to deny that there must be an important role for "mirror neurones" in the story of primate and human evolution. Beyond their role in manual gestures, they are likely to be involved in the production and interpretation of other nonverbal behaviours in primate social interactions. Both frontal and temporoparietal areas were aroused in a study of theory of mind awareness (Gallagher et al. 2000). Much more than vocalisation and hand use may be involved. To assert a link between handedness and vocalisation is not the same as specifying what it might be. The jump from vocalisation to speech is barely touched upon.

The target article lacks a clear account of human individual differences for brain asymmetry or handedness. Pathology remains the implicit default explanation, in the absence of a theory of natural variation. Corballis's estimates of the prevalence of right brain speech (sect. 5.2) neglect evidence from a population representative series of dysphasics (Annett 1975; Annett & Alexander 1996). Estimates from these sources were confirmed by a community survey (Pederson et al. 1995), with an incidence of just over 9% in the general population. The incidence tends to be underestimated by arguments from Wada tests on epileptic patients classified as right- or left-handed. If cerebral asymmetries for human vocalisation truly have the ancient lineage argued here, why should any modern humans be right-brained or left-handed? Was there a period when everyone was left-brained and right-handed? Was a new genetic mutation required to re-introduce variability? Where was this supposed universally right-handed species? Corballis seems ambivalent about these ideas.

The right shift (RS) theory (see Annett 2002 for a review) agrees with the thesis that the human bias toward right-handedness depends on the bias toward left-hemisphere speech, but it is as fruitless to ask which came first here, as it is with the chicken and the egg. The theory suggests that a single gene promotes left-cerebral dominance for speech by weakening speech related cortex in the right hemisphere. An incidental weakening of the left hand displaces a chance distribution of hand skill asymmetry in favour of the right. The chance distribution depends on nongenetic accidental variation in the growth of every individual. The right shift

gene (RS +) evolved in early humans to facilitate the amazing process by which human infants acquire the speech sounds of their native tongue. However, the gene did not become universal or fixed in humans, because it is associated with risks to other functions, and possibly with mental illness (Crow 1997). Whether RS + is present or absent, the universal and natural determinant of asymmetries of hand and brain is a chance variation. There is no need for a gene for chance, or complicated rules about when it is expressed. Corballis is mistaken in suggesting that other theories are equivalent. Annett (2002) argued that supposed alternative theories are variations on a similar theme, but quite out of tune with the facts.

Protosign and protospeech: An expanding spiral

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Abstract: The intriguing observation that left-cerebral dominance for vocalization is ancient, occurring in frogs, birds, and mammals, grounds Corballis's argument that the predominance of right-handedness may result from an association between manual gestures and vocalization in the evolution of language. This commentary supports the general thesis that language evolved "From hand to mouth" (Corballis 2002), while offering alternatives for some of Corballis's supporting arguments.

The numbered passages in *italic* below are based on the corresponding sections of the target article; unnumbered paragraphs convey my comments.

1. *Human language emerged from gestural communication. Vocalizations were gradually incorporated into the gestural system.*

I agree with this statement but note the problem that it might be taken to suggest that a complete human language in gestural mode existed prior to the incorporation of vocalization. I offer instead "The Doctrine of the Expanding Spiral": that is, that our ancestors had a form of "protosign" (a manual precursor of language) that provided essential scaffolding for the emergence of "protospeech," but that the hominid line saw advances in both protosign and protospeech, feeding off each other in an expanding spiral.

2.3. *True syntactic language probably did not evolve until after the emergence of the genus Homo around two million years ago.*

I would speculate, to the contrary, that the protosign and protospeech of early *Homo*, and even of *Homo sapiens* until perhaps 50,000 years ago, had little or no syntax. However, contrary to Bickerton (1995) and in agreement with Wray (1998), I would argue that such protolanguage did not consist primarily of words akin to today's words, only lacking syntax, but rather was *holophrastic* – that is, consisting primarily of utterances without internal syntax but whose translation into English, say, would require several words and the syntax to combine them. I speculate that the transition from protolanguage to modern human language with syntax and a compositional semantics was the result of cultural innovation across many millennia of the history of *Homo sapiens* (Arbib 2002). Protosign had the great advantage over protospeech in that it could convey many meanings by pantomime, with far greater richness than protospeech could gain from expressive grunts or onomatopoeia.

[A] third person sees you and a companion together, leaves for a moment, returns, and shows surprise at seeing you alone. You immediately . . . make a gesture [that means], "She went that way." But your gesture [also] shows which way she went . . . [Y]our hand pointed out the direction of your companion's departure, but your hand also stands for her, the one who departed. (Stokoe 2001, pp. xii–xiii)

2.4. *Given the intricate nature of syntax, it is likely that language itself evolved gradually through natural selection.*

Against this, I offer the hypothesis that syntax is more a cultural than a biological phenomenon – and therefore speak of a *language-ready brain* as one that can acquire language in a modern human society, while denying that human brains have syntax “biologically precoded.”

2.5. *Sign languages invented by the deaf have all the essential properties of spoken language, including a sophisticated syntax.*

Indeed. But it may be asked whether full sign language was a necessary precursor to spoken language or whether an Expanding Spiral of protosign and protospeech provided early *Homo sapiens* with a language-readiness that fell short of full language, signed or spoken. In many cases, “full” sign languages reflect, in part, the attempt of deaf people to import the richness of spoken or written language back into sign.

2.5. *Syntax could have emerged from the structure of individual gestures themselves.*

In similar vein, Stokoe (2001; continuing the quote from Stokoe above) asserts that: “The gesture also has . . . syntax because the hand for the person and its movement telling what she did are subject and predicate (or noun phrase [NP] + verb phrase [VP]).”

I think this is a mistake. It is true that a linguist can *sometimes* dub the hand shape of a sign as denoting an object and the movement of the hand as denoting an action, but these are not necessarily separable. And if they are not separated, they do not need syntax to put them together again. It is only the *translation* to, for example, English that has this syntax. Moreover, *airplane* is signed in ASL with tiny repeated movements of a specific handshape, while *fly* is signed by moving the same handshape along a trajectory (Supalla & Newport 1978). Here, both verb and noun combine handshape and motion. For me, the import of the airplane/fly distinction is that, while a “natural” gesture is unitary, extending the range of discourse requires distinctions that cannot be mimed directly. Thus, early humans might have developed a natural pantomime which stood equally for “a bird is flying,” “the flying bird,” “flying,” or “bird” – relying on the “listener” to interpret the sign correctly in context. As it became useful to distinguish these meanings, a community had to develop conventions to mark them, initiating the transition from pantomime to a conventionalized system of signed communication (Arbib 2003b).

3.1. *Facial gestures generally convey syntax, whereas manual gestures supply content, suggesting a progression from manual to facial gesture in the emergence of language.*

The first statement is false, thus invalidating the second. Emmorey et al. (2002, Fig. 1) show how a sequence of hand movements may employ classifier constructions to express spatial syntax. But note, too, that signers make fuller use of the facial musculature than speakers do. Is this because protosign evolved the appropriate muscle control, or because signers can exploit a more generic human capacity for fractionation of motor skills? Recent modeling of the development of manual skills seems to suggest the latter (Oztop et al. 2003). And consider learning to play the piano (surely not part of the experience of early *Homo*!) – with its cumulative mastery of finger exercises and the hierarchical progression from note to chord to phrase and on to syncopation.

3.1. *The next step may have been to add voicing.*

Since other primates have vocalization, we can expect that some voicing was always present. I suggest that the development of conventionalized gestures in protosign, rather than any syntactic structure in sign, provided the “evolutionary drive” for the development of a rich protospeech and the concomitant neural apparatus to control the articulators. The Expanding Spiral then allowed the expressiveness of protosign and protospeech to feed off each other to yield the evolution of the language-ready brain. By contrast, I find the frame/content theory of MacNeilage (1998) unconvincing because it grounds the syllable in mastication with no indication of how evolving modes of communication could provide the selection pressure for relevant changes in the articulators and their neural control.

3.3. *In view of the longstanding involvement of Broca’s area in manual activity, its enlargement in Homo habilis, nearly two mil-*

lion years ago, may reflect the incorporation of syntax into gestural communication.

Again, why posit syntax this early? The switch from a closed repertoire to the ability to create, learn, and use an open set of holophrastic utterances would possibly have been enough for this. The stasis of tool use in *Homo habilis* argues for a long period of stasis in protolanguage (cf. Noble & Davidson 1996), which might be more consistent with a limited stock of holophrastic utterances than with a flexible syntax. This would seem to accord better with Corballis’s later statement (sect. 3.6) that autonomous speech may have emerged gradually in Africa over the period from 170,000 to 50,000 years ago. I would suggest that language (as distinct from protolanguage) and rich systems of syntax also emerged, postbiologically, during this period.

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Is gestural communication more sophisticated than vocal communication in wild chimpanzees?

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Abstract: The communicative behavior of chimpanzees has been cited in support of the hypothesis that language evolved from gesture. In this commentary, I compare gestural and vocal communication in wild chimpanzees. Because the use of gesture in wild chimpanzees is limited, whereas their vocal behavior is relatively complex, I argue that wild chimpanzee behavior fails to support the gestural origins hypothesis.

Corballis argues that manual gesturing was the mediating factor in the evolution of handedness in humans. As he points out in the conclusion of his article, the key issue in his argument, therefore, is whether language evolved from gesture. To support the gestural origins hypothesis, Corballis uses the communicative behavior of wild chimpanzees to speculate about the communicative repertoire of a human/chimp common ancestor. He concludes that wild chimpanzee gestural communication provides a more plausible hypothetical substrate for the evolution of an intentional communication system than chimpanzee vocal communication does. In this commentary, I will compare what is known about gestural and vocal communication in wild chimpanzees. Leaving aside the significant problems associated with using modern apes to model the behavior of human ancestors (Marks 2002), I will argue that Corballis has overestimated the role of gestural communication in wild chimpanzee interactions while simultaneously underestimating the complexity of their vocal behavior. I suggest that wild chimpanzees offer little support for the idea that language evolved from a structured system of gesture, or, by extension, that manual gesture led to handedness.

Is it true, as asserted in section 2.1, that “chimpanzees and other apes make extensive use of gestures in the wild”? In an effort to support this claim, Corballis reviews three different studies of *captive* apes: de Waal (1982) and Tomasello et al. (1997) on chimpanzees, and Tanner and Byrne (1996) on gorillas. However, the behavior of captives, who are influenced by human caretakers and artificial environments, is irrelevant here. Moreover, published reports of wild chimpanzee behavior do not support Corballis’s representation of wild chimpanzee gestural communication. In Table 1, I have listed the gestures so far documented for wild chimpanzee communicative interactions. The evidence to date shows clearly that wild chimpanzees rarely use manual gestures, and that the vast majority of gestures they do use are employed in the context of

Table 1 (Arcadi). *Gestures documented in wild chimpanzee communicative interactions*¹

Name	Type	Context
Compressed-lips face	Facial	Aggression
Sneer	Facial	Fear/threat
Full open grin	Facial	Fear/excitement
Low closed grin	Facial	Fear/excitement
Full closed grin	Facial	Fear/excitement
Horizontal pout	Facial	Distress
Pout	Facial	Distress
Head tip	Postural	Aggression
Sitting hunch	Postural	Aggression
Quadrupedal hunch	Postural	Aggression
Swaying branches	Object manipulation	Aggression
Throwing	Object manipulation	Aggression
Flailing (stick)	Object manipulation	Aggression
Drag branch	Object manipulation	Aggression
Bipedal swagger	Locomotion	Aggression
Running upright	Locomotion	Aggression
Charging	Locomotion	Aggression
Arm raise	Manual	Aggression
Hitting toward, flapping	Manual	Aggression
Presenting	Postural	Submission
Crouching, bowing	Postural	Submission
Bobbing	Postural	Submission
Bending away	Postural	Submission
Kissing	Body contact	Submission
Embracing	Body contact	Submission
Mounting	Body contact	Submission
Reaching toward with palm up	Manual	Submission
Offering back of wrist	Manual	Submission
Branching	Object manipulation	Attention-getting – sex
Leaf clipping	Object manipulation	Attention-getting – sex
Leaf grooming	Object manipulation	Attention-getting – grooming
Arm high	Manual	Attention-getting – grooming
Arm high	Manual	Appeasement
Play start	Object manipulation	Attention-getting – play
Pointing	Manual	Draw attention to

¹The majority of these behaviors were first described by Goodall (1968; 1986). Nishida (1980) described leaf clipping; Plooij (1978) described arm high; Vèa and Sabater-Pi (1998) observed a single young adult male bonobo point three times; Inoue-Nakamura and Matsuzawa (1997) observed an infant chimpanzee point once.

dominance interactions. Indeed, the repertoire of gestures chimpanzees use to mediate aggressive conflicts appears unexceptional when compared with those of similarly social species with frequent status interactions (e.g., canids: Harrington & Mech 1978; Lehner 1978). Beyond the mostly facial and postural gestures used in agonistic contexts, wild chimpanzees occasionally use a small number of attention-getting gestures that solicit physical approach, but do not elicit communicative responses, in receivers. The most interesting gesture from the point of view of the gestural origins hypothesis – pointing – has been observed just once, and that in an infant, in tens of thousands of hours of wild chimpanzee observational research at many field sites across the species range.

While overstating the complexity of gestural communication among wild chimpanzees, Corballis also downplays the complexity of wild chimpanzee vocal behavior by emphasizing its dependence on emotional state. However, although it seems clear that chimpanzee vocalizations are tightly linked to emotional state, this is apparently also true of many of their gestures, as revealed by reports of attempts to conceal uncontrollable facial expressions (de Waal 1982; Goodall 1986). In addition, chimpanzees do have some control over vocal production; they can suppress calls in some contexts (e.g., during territorial patrols: Goodall 1986; when raiding village crops: personal observation), and they can modify call structure to a greater degree than has been observed in other primate species (Arcadi 1996; Arcadi et al. 1998; Mitani & Brandt 1994; Mitani et al. 1992; 1999). And finally, it is clearly not the case, as asserted in section 2.1, that chimpanzee vocalizations “are typically not directed to specific others.” Of the 15 chimpanzee vocalizations defined acoustically by Marler and Tenaza (1977), at least eight of them (cough, scream, squeak, whimper or hoo series, hoo, pant, pant grunt, and pant hoot) are directed at specific individuals with whom the vocalizers are interacting (Goodall 1986; Hayaki 1990), and one of these (pant hoot) is frequently used in long-distance calling exchanges, probably with known individuals (Arcadi 2000; Mitani & Nishida 1993).

In part based on his interpretation of wild chimpanzee behavior, Corballis concludes that gestures came under voluntary control before vocalizations in a population of human ancestors. But current research on wild chimpanzees offers no obvious justification for this hypothetical order of events. In the absence of human influence, nothing chimpanzees do vocally or manually bears much resemblance to language or to modern human gestural communication (Arcadi 2000). Consequently, the evidence from chimpanzees does not make a compelling case to eliminate the alternative and simpler evolutionary hypothesis, that is, that vocalizations came under voluntary control through selective pressures on an already variable and possibly socially influenced vocal repertoire (Arcadi 1996; Marshall et al. 1999; Mitani & Brandt 1994; Mitani et al. 1992; 1999), and that the integration of manual gestures into linguistic interactions evolved during or after this process.

Creative solution to an old problem

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Abstract: Corballis presents a plausible evolutionary mechanism to explain the tight linkage between cerebral lateralization for language and for handedness in humans. This argument may be bolstered by invoking Stokoe’s notion of *semantic phonology* to explain the role of Broca’s area in grammatical functions.

Corballis seems to have hit on something here. There has been no lack of speculation about the ontogeny and phylogeny of human cerebral lateralization. However, the arguments for why both handedness and lateralization for speech production and perception should be associated with the left cerebral hemisphere have

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

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

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

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

Perhaps harder to support is Corballis's notion that a shift from gestural (or signed) to spoken language was the key to the rapid ex-

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

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

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

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

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

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

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

regarded as a fundamental prerequisite for attaining spoken language. The implication is that the presence of mirror-neurons in humans may be irrelevant to our faculty of language, despite being associated with Broca's area.

Corballis is impressed by the suggestion (Holloway 1983) that there was an anatomical asymmetry in Broca's area in *Homo habilis* (see also Falk 1983). I am less convinced. Given the individual variability of gyral morphology in extant brains, any inferences (e.g., Falk 1983) made from patterns on endocasts of fossil skulls to underlying cortex must be regarded with caution, if not downright scepticism, and are, according to Oakley (1972), "no more reliable than any other form of phrenology" (p. 48).

Even if we accept the evidence concerning Broca's area, there remains the possibility that an asymmetry in this region, as with the planum temporale (Annett 1992; Beaton 1997), relates to handedness (see Foundas et al. 1998) rather than to speech. Toth's suggestion, based on examination of ancient stone tools and modern tool-making experiments, that *Homo habilis* was largely right-handed as long ago as 1.9 to 1.4 million years ago, is well known, although not without its critics (see Marzke & Shackley 1986; Noble & Davidson 1996). It is conceivable that some even earlier ancestor of modern humans was right-handed – perhaps for such actions as throwing sticks or stones (Calvin 1983a).

The claims that *Australopithecus (Ardipithecus) ramidus* (White et al. 1994) and *Australopithecus anamensis* (Leakey et al. 1995), not to mention *Orrorin tugenensis* (Senut et al. 2001) and *Sahelanthropus tchadensis* (Brunet et al. 2002), were bipedal raise the possibility (see, for example, Previc 1991) that handedness emerged more than four million, and possibly more than six million, years ago. The available fossils do not provide relevant evidence, but it may be appropriate to note that the *Homo erectus* (or *H. ergaster*) specimen referred to as Nariokotome boy shows certain features, such as a longer right than left ulna bone (Walker & Leakey 1993), which are found on the skeletons of modern, and therefore predominantly right-handed, humans (Steele 2000). If this was also the case for any of the other putative hominid species, it might indicate that a right-hand superiority for most actions, not just gestures, was present much earlier than Corballis proposes.

Regardless of when language or handedness evolved, it is a mistake, in my view, to think of handedness purely in categorical terms. Most discussions of laterality tend to ignore its variability (see Beaton 2003). With regard to preference, there is no clear dividing line between right- and left-preferent individuals when a range of manual activities, rather than a single task such as writing, is considered (Annett 1970). Thus, mixed- and left-handedness have to be explained as well as right-handedness. Those genetic theories which introduce an element of chance or randomness into their postulates (Annett 2002; Laland et al. 1995; McManus 1985a) can cope with this, but theories such as the one under scrutiny here have difficulty in accounting for the discrepancy that sometimes occurs between laterality of speech and the side of the preferred hand.

Corballis refers to the possibility that "one allele of a handedness gene codes for some underlying gradient to be expressed whereas the other essentially leaves handedness to chance" (sect. 5.3, last para.). It is thus not clear that his theory differs in principle from theories such as those of Annett and McManus. The only issue that distinguishes his evolutionary theory from the genetic theories concerns whether handedness should be considered a byproduct of speech lateralization or of an earlier lateralization for vocalization and gestures.

In speculating on the origins of laterality, it may be misleading to concentrate on handedness, albeit this is the most conspicuous behavioural asymmetry exhibited by humans. There are many other kinds of lateral preference – of which the preference for one or other foot is perhaps the strongest. There is no obvious connection between meaningful gestures and footedness, eyedness, or various other forms of side preference. If only these aspects of laterality, rather than handedness, were to be under consideration, it is unlikely that any causal link with vocalization or language would be postulated by Corballis or by anyone else.

Gesture in language evolution: Could I but raise my hand to it!

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Abstract: An intervening gestural stage in language evolution, though seductive, is ultimately redundant, and is not necessarily supported by modern human or chimp behaviour. The findings and arguments offered from mirror neurons, anatomy, and lateralization are capable of other interpretations, and the manipulative dexterity of chimps is under-recognized. While language certainly possesses certain unique properties, its roots are ancient.

A strong, if intuitively somewhat implausible, form of Corballis's admittedly seductive hypothesis appears as: "the precursors of *Homo sapiens* had evolved a form of signed language similar in principle, if not in detail, to the signed languages that are today used by the deaf" (Corballis 2002, p. 125). Were there really troupes of silent, rapidly signing prehomnids? Indeed, given how speech came to supersede gesture, and given left hemisphere (LH) mediation of communication in so many "lower" animals, as Corballis explains and reviews in his 2002 book, the insertion of an extra, gestural stage seems gratuitous and redundant. Our capacity to spontaneously develop signs, if deaf, no more supports an evolutionary primacy of sign in language development, than does the fact that we can read much faster than we can speak suggest that speech may have originated from some early analog of reading. An example maybe of evolutionary over-engineering, it is reminiscent of the discredited thesis that phylogeny necessarily recapitulates ontogeny. Nor is there evidence, in any case, that infants substantively gesture before speech unfolds; or that blind infants, or those born without forelimbs, have fewer problems in language acquisition than those born deaf. True, chimps exhibit many commonalities with our own gestures, but biomechanical and situational constraints may limit the range of options, with analogy rather than homology operating. The anatomical adjacency of cortical regions mediating speech and praxis (gesture) may merely reflect commonalities of seriality and generativity, whereby the two capacities may, admittedly, have interacted autocatalytically in their respective, or mutual, evolution.

Mirror neurons may certainly have played a key role in language evolution and may continue to do so in its acquisition, but they could be far more pervasive than just mediating, prefrontally, the sensorimotor correlates of gesture (Bradshaw & Mattingley 2001). Indeed, Hauser et al. (2002) claim that in macaques mirror neurons are *not* sufficient for imitation – a capacity which is necessary for a common, shared language, and which, while highly developed in parrots and dolphins, is, in fact, poorly developed in chimps and monkeys. At a more peripheral level, DeGusta et al. (1999) find that hypoglossal canal size is of little functional significance. Likewise, was a size increase in the thoracic region of the spinal cord – said by Corballis to occur late in our evolution – really necessary for better breathing during speech, given, for example, the articulatory capabilities of the African grey parrot?

The proposal that a left-hemisphere dominance for vocal communication emerged earlier than dexterity, with the latter a consequence of the former, does not necessarily follow; both may stem from another, prior, asymmetry (recursive seriality? – though I would opt also for a very early, initial, determining right-hemisphere preemption of emotional and/or spatial processing). Similarly, I feel that Corballis downplays recent findings of dexterity in chimps, which is especially prominent with the precision grip. Hopkins et al. (2002) make the important distinction (often overlooked) between hand *preference* and *performance*, and also conclude that language is *not* a necessary condition for the expression of hemispheric specialization. Indeed, they say it seems unlikely

that captivity, or any subtle effects of human handedness, would cause a systematic bias absent in the wild, though it may unmask or release latent effects.

Corballis claims that, unlike our speech, vocal control is relatively inflexible, involuntary, and emotional – though he also, separately, argues that manual gesture progressed to facial gesture, and thence to speech proper, by the addition of voicing, perhaps initially as *emotional* accompaniment; and that, therefore, chimps cannot be taught to speak. However, that bonobos do understand quite complex *spoken* commands, suggests that the problem for apes may be more in the realization of speech sounds than in their comprehension.

As Hauser et al. (2002) note, animal communication, though sharing many features with human language, lacks its rich expressiveness and open-ended recursive and re-combinatory power. We cannot yet conclude whether the evolution of the latter was gradual or saltatory; and if gradual, whether it extended pre-existing primate systems, or whether important features such as recursion were exapted away from other, previous, irrelevant but adapted functions like tool-making or social behaviour, and then made available for language. Thus, certain features of language may be spandrels, *by-products* of pre-existing constraints, rather than *end-products* of a history of natural selection.

In conclusion, I applaud Corballis's ingenious and seductive hypothesis, but I dispute whether "handedness would have emerged as vocalization was progressively incorporated into gestural language" (sect. 6, para. 3); the roots of both are surely far older than the latter.

Lateralisation may be a side issue for understanding language development

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Abstract: We add evidence in support of Corballis's gestural theory of language. Using transcranial magnetic stimulation, we found that productive and receptive linguistic tasks excite the motor cortices for both hands. This indicates that the language and the hand motor systems are still tightly linked in modern man. The bilaterality of the effect, however, implies that lateralisation is a secondary issue.

In attempting to construe a biological model for language, the issue of lateralisation cannot be ignored. The long-known correlation between manual dexterity and language lateralisation certainly was a starting point for the development of a gestural theory of language. Furthermore, language lateralisation is the single most critical factor for determining whether an ischemic stroke will lead to aphasia (Knecht et al. 2002). At this point, however, focusing on lateralisation issues may not be of additional help. It may simply distract from more important issues in enhancing language recovery. A comprehensive neurobiological understanding of the human language system will aid in the development of effective treatment options for language disorders, the most prevalent being stroke-related aphasia.

One methodological problem is that the evidence put forward with respect to language development is necessarily circumstantial, because of the retrospective character of the study designs. The gestural theory of language, as eloquently outlined by Corballis, has nevertheless substantially contributed to the construction of such a biological model of language. It relates language to

aspects of other complex motor behaviors. The theory predicts that the activation of "gestures" comprising spoken language is functionally linked to and should thus coactivate an extended network of manual actions. In concert with this view, treatment strategies adapted from motor rehabilitation have already been effectively applied in aphasia therapy (Pulvermüller et al. 2001; for a summary, see Breitenstein & Knecht 2003). Here we argue that the effectiveness of the motor-theory approach may be independent of lateralisation.

Recent data from our laboratory demonstrate that the hand motor cortex, as assessed by transcranial magnetic stimulation, is activated by a variety of linguistic tasks (Floel et al. 2001; 2002; 2003) – that is, during speaking, covert reading, and listening to sentences. The degree of motor system activation was comparable in both hemispheres, and the effects were independent of the side of language dominance or of handedness. Listening to nonspeech auditory stimuli (white noise, tones), viewing nonlinguistic visual materials, or listening to meaningless phonemes (Sundara et al. 2001) did not coactivate the hand motor cortices. In a just-completed follow-up study, we examined whether presentation of the prosodic component of sentences in isolation, without semantic and grammatical information, suffices to activate the bodily action system. The results replicated and extended our previous findings: Both listening to sentences and to variable prosodic contours (matched in duration and pitch variation with the sentences) bilaterally activated the hand motor cortex (Rogalewski et al. 2003).

The specificity of the effect for language perception underlines that it is not an unspecific effect of covert rehearsal. Furthermore, speech perception activates not only the hand motor system, but also the cortical motor representations of the orofacial "gesture" systems (Fadiga et al. 2002). This indicates a direct link between the language and the manual/ facial action systems, which is far more extensive than previously assumed and which might still be functionally relevant in modern man. For example, motor cortex activation, as part of a widely distributed cortical network, might contribute to the implementation of word meanings (Pulvermüller 1999). Our findings provide support for Corballis's view that today's language has developed from a gestural system of communication. Although yet to be developed, the close bilateral association between the language and manual motor systems could inform aphasia therapy, in that, for example, preactivation of the (manual) motor system of the undamaged side could facilitate language processing. The rationale is supported by preliminary evidence that (a) patients with aphasia improve on naming objects when pointing to objects (Hanlon et al. 1990) and (b) stutterers benefit from hand gestures (Mayberry et al. 1998). Additionally, a recent magnetoencephalographic study demonstrated that a wide-spread bilateral cortical network, including Broca's area and its homologue, were activated by the observation and imitation of orofacial gestures (Nishitani & Hari 2002).

In summary, the empirical database establishes a close link between the language and the motor systems. Within this framework, it may be possible to develop more systematic therapeutic strategies for language disorders. Future studies are required to examine the outcome of concomitant motor activation in language therapy in a larger group of aphasic patients in a more systematic manner.

Last but not least, future research should be directed toward both the relation of language faculties to other cognitive domains, as well as to the relation of language associated brain activity to brain activity related to other brain functions. Corballis's theory and data from different laboratories working on the link between the language and the motor systems imply that at least some aspects of language are part of a domain-general system (Hauser et al. 2002). This domain-general system is most likely represented bilaterally.

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A shrug is not a sentence

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Abstract: Corballis's claim that the origin of syntax lies in solely gesture is contested. His scenario does not explain why constraints on syntactic "movement" are apparently part of the human biological endowment for language. It also does not pay enough attention to the internal structure of sentences, and how they contrast with other linguistic units such as noun phrases.

Michael Corballis's scenario raises fascinating questions for physiologists and neurologists. I will concentrate here on three linguistic points, the last being the most important.

Corballis's use of the term *voicing* is odd. It is true, as he says in section 3.2, that [p], [t], and [k] are in many languages distinguished from another series of plosives, [b], [d], and [g], by voicing, in that the vocal folds vibrate during the production of the latter but not the former. But that is not the main way in which the so-called *voiceless* and *voiced* stops are distinguished in English, as it happens (more important factors are voice onset time in following vowels and the length of preceding ones). Besides, there are many languages in which contrastive voicing plays no role at all; that is, vibration of the vocal folds is entirely predictable (vowels, liquids, and nasals being voiced and plosives being usually voiceless). But that does not mean that in those languages the vocal folds are redundant. Consonantal place of articulation is signalled acoustically by formant characteristics of neighbouring vowels, even when the consonant itself is voiceless. So adding vocal fold vibration to facial gesture (if that is what happened) would have served mainly not to increase the repertoire of consonant sounds, but rather to increase their audibility at a distance and in particular to render them auditorily more distinct.

In section 2.5, Corballis argues that the origin of syntax can be traced to iconic gesturing. Different aspects of syntax almost certainly originated at different times and in different ways; but at least some of those aspects that belong to our biological endowment (rather than our cultural environment) more probably originated at a time when language was primarily spoken rather than signed, I think. Consider the sentences *When did the boy say he hurt himself?* and *When did the boy say how he hurt himself?* The first is ambiguous (it may relate to the time of the boy's injury or the time of his statement), whereas the latter is not (it can relate only to the time of the boy's statement). This is apparently not a cultural fact, relating to the English language in particular, because it is not something that children learning English natively make mistakes about (like saying *bringed* or *brung* for *brought*, for example). Yet, there is nothing semantically odd about interpreting the second sentence as relating to the time of the injury. Indeed, that interpretation is available to the variant of it, without "WH-movement," that conveys incredulity ("Surely my ears deceived me!"): *The boy said how he hurt himself WHEN?!* Why this discrepancy between the two sentences? It seems to have to do with constraints on the sort of "movement" that transports question-words such as *when* and *how* to the beginning of the clause in English. This relates to the gestural origin theory as follows. It is not clear whether syntactic movement plays such a large part in sign languages as in spoken languages. Indeed, it is understandable why it should not: some manual signs can be superimposed on one another, or made simultaneously, whereas spoken words cannot be superimposed in an utterance. The role of linear order is thus somewhat different in the two kinds of language. So, because that part of the human endowment for syntax which rules out one conceivable interpretation of the *When . . . how . . .* sentence seems crucially to do with constraints on reordering, it seems unlikely to have originated at a stage when language was mainly gestural (even if such a stage existed).

Corballis bases his belief in a gestural origin for syntax on suggestions by Armstrong et al. (1995). He says (sect. 2.5): "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.'" But what makes a sentence a sentence, (e.g., *Columbus discovered America*) rather than, say, a noun phrase (e.g., *Columbus's discovery of America*) is not its meaning but its internal structure. It is true that some sentences in some languages consist of a single word, and in that sense lack structure. But that is the exception rather than the norm. The gesture of grasping the left forefinger with the right hand does indeed have a structure that can be interpreted as sentence-like, but many other gestures do not – including the shrug. That is the flaw in Armstrong et al.'s scenario for the origin of syntax (Carstairs-McCarthy 1996). Indeed, it is precisely the lack of structure in the Neapolitan equivalent of the shrug that, according to one famous anecdote (Malcolm 1958, p. 69), persuaded the philosopher Wittgenstein that the analysis of "propositions" proposed in his *Tractatus Logico-Philosophicus* was on the wrong track.

What research on language evolution urgently needs is input from experts on the grammar of sign language. It is they who can comment most expertly on whether or not any biologically fixed characteristics of syntax-as-it-is, spoken as well as signed, can plausibly be seen as the residue of a predominantly gestural stage. Sign language experts may be reluctant to become involved in this area because it hints at the possibility that sign languages are different from spoken ones in a fundamental fashion that is not purely attributable to the medium – which in turn hints at the discredited notion that sign languages are inferior. However, difference does not imply inferiority. It may be that some of the poor design features of spoken language grammar (and poor design features certainly exist!) are attributable to an origin in something other than gesture (namely, the structure of the syllable in the phonology of spoken languages), and it may even be that contemporary sign languages lack some of these poor design features simply because deaf children are not exposed to spoken syllables (Carstairs-McCarthy 1999).

Vocalisation and the development of hand preference

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Abstract: What do the relationships observed in the occurrence of various limb, facial, and speech apraxias following left hemisphere damage mean for Corballis's theory? What does the right hemisphere's role in non-propositional and automatic speech production tell us about the coevolution of right hand preference and speech; how could the possibility that the right hemisphere may be "dominant" for some aspects of speech be accommodated by his theory?

We have supposed an evolutionary relationship between speech and handedness for a long time, as Corballis points out, but for many theorists the causality went the other way – from early gestural communication to the development of speech. Surprisingly, perhaps, Corballis does not discuss the relevance of apraxias to his interesting theory. One hundred and fifty years of lesion data suggests that both action- and gesture-processing and speech production are predominantly left hemisphere responsibilities. Impairments to the action system, causing a range of apraxias, are a common consequence of prefrontal and parietal left hemisphere damage, and different types of apraxia – limb, speech, buccofacial – commonly co-occur (but also dissociate), further supporting a close phylogenetic relationship. Since the time of Liepmann, apraxia of speech has been seen as a variant of limb-kinetic apraxia. Liep-

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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).

As before, the strongest implication may be that convergence among perceptual and motor systems is a critical underlying component of language. As Kendon (1991) points out, multimodal information is continually brought forth as an essential part of human cognition. That gesture can effectively stand in for signaling in the auditory-vocal modality highlights that integration is important, but not that the manual component per se has played a special role. On the contrary, speech is the normal means of linguistic communication across the entire human species, with gesturing always being ancillary. Gesture takes on language properties only by dire necessity, which is surely not the sort of evidence that compels a view that language evolved sequentially from gesture to speech. It instead suggests primacy for the latter, but with both modalities being more fundamentally rooted in the integration of sensory and motor channels in underlying neural organization.

While ultimately about right-handedness, Corballis's argument relies most heavily on the gestural-origins hypothesis and the various bits of evidence that can be marshaled in its support. In our view, he has not produced a straightforward progression of inexorable inferences and necessary implications. Instead, he presents a series of intuition pumps and primes the reader to think along the lines desired. Making the case requires rather more than intuitively pumping for it, and a critical and balanced evaluation of the data would be a better way to proceed.

Possible phylogenies: The role of hypotheses, weak inferences, and falsification

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Abstract: This commentary takes issue with Corballis's claim to have presented a falsifiable hypothesis. It argues that Corballis has instead presented a framework of weak inferences that, although unfalsifiable, might help to constrain future theory-building.

Corballis ends his article with the claim "my hypothesis is not simply a just-so story" (sect. 6, last para.) and that it could be falsified. In making this statement Corballis is displaying a sensitivity to past criticisms of the evolutionary endeavour, and he is laudably trying to expose his speculations to due scrutiny. Prior to this, Corballis lays out the structure of his argument and indicates possible points of weakness, but despite this openness, I am not convinced that the overall hypothesis in this paper is falsifiable, and I shall present my concerns in this commentary.

Falsificationism was proposed by Popper (1959) both as a response to the problem of induction and also as a principle of demarcation, a method of distinguishing the natural sciences from all other epistemological effort. Falsificationism is not a loose position, but it is one that places strict constraints on the structure of scientific hypotheses. Hypotheses must contain a lot of information enabling detailed and precise predictions to be drawn, and it is this detail that increases the probability of the falsity of the hypothesis, as well as making it clear how to falsify it. Nonetheless, when falsification does not occur, the utility of the statement is enhanced by this precision. There are many problems with falsification as a philosophy of science – not least, issues surrounding the theory-dependence of methods – but as a guiding principle of scientific clarity, it is much sought after.

Corballis's article consists of a number of hypotheses, rather than a single one, and as such the overall collection might best be viewed as a story, which does not make the work less scientific, simply synthetic. The story is a long conditional argument of approximately the following form:

1. *If* spoken language gradually evolved from a system of manual gestures (hypothesis 1) *and*:
2. *If* mirror neurons (in area F5) are important for establishing and maintaining a system of manual gestures (hypothesis 2) *then*:
3. The point in time at which area F5 became left-lateralized might mark the point at which vocal language took over from gestural communication (hypothesis 3), *and*:
4. This lateralization might explain the drive to predominant right-handedness in humans (hypothesis 4).

Each of these hypotheses is fleshed out with a variety of comparative, empirical, and archaeological arguments from the literature, and, as such, they are grounded in substantial amounts of theory. However, Corballis sees the whole story as critically dependent on the veracity of hypothesis 1. If this can be falsified, the rest of the story dies with it, although he cautions that this would not mean that left-lateralized vocal control did not precede handedness. But how might one attempt to falsify the hypothesis that vocal language evolved from manual gestures? A hypothesis of this sort, about a possible phylogenetic event, is very low in detail and precision. For example, there is no comment about how this might have happened and what characteristics it would lend spoken language. Instead, as with all gestural theories of language, it is predicated upon a set of tantalising "facts" – the existence of full, "natural" sign-languages, home-signing, infant use of deictic cues and the common act of gesturing whilst speaking (see Dickins 2002 for a discussion of gestural theories) – and Corballis has reproduced some of these "facts." None of these behaviours carry signatures of an ancient, prelinguistic, or even prevocal heritage and role. All could equally be interpreted as evidence of gesture supporting speech at any given moment in the long history of language. This hypothesis does not meet Popper's standard and is perhaps best regarded as a weak inference.

Over recent years, there has been much discussion about the role of mirror neurons in the evolution of language. Such neurons are in area F5 in monkeys, a homologue of Broca's area, and this fact has raised much excitement. Researchers have wondered whether the imitative possibilities permitted by mirror neurons are a precursor to a communication system with intentional properties (Rizzolatti & Arbib 1998). Corballis has incorporated this as hypothesis 2, suggesting that such neurons might be used in establishing a gestural system of communication, and the novelty of this system, combined with the comparative evidence, might be taken to indicate an ancient, prelinguistic provenance for gesture.

Hurford (2003) has recently argued that although mirror neurons indeed afford imitation, and this imitation might be a function of the later emerging (and lateralized) Broca's area to some extent, the critical aspect of language – that of attaching an arbitrary sound to a representation of a concept in a symmetrical relation – cannot be a part of this system. If the system imitates, it has to have something to imitate – see a gesture, perform the same gesture – and this alone will not afford symbolic representation. Mirror neurons may simply have been of use when the critical innovations for language emerged. This hypothesis fails to make claims precise enough to open it to falsification, because it significantly fails to account for the core aspects of the phenomenon to which it is addressed. However, we can salvage something of Corballis's story. The existence of mirror neurons does not necessarily support a gestural theory, but it is the case that Broca's area is left-lateralized in most humans. It might be that this aspect of the evolution of vocal control did drive handedness, whether or not there is a relationship between gesture and speech. So, in effect, we can divorce hypothesis 4 from the preceding three. Nonetheless, hypothesis 4 is not sufficiently fleshed out to make the order of predictions that Popper would demand of it, and Corballis presents only correlation data to support it, which he admits might be illusory, and this is again a form of weak inference.

Corballis's story is not falsifiable, but this does not mean we need dismiss it as a "just-so" story. Instead, such speculative arguments should be seen as an important precursor to constructing tight hypotheses. Corballis's weak inferences provide a form of

possible world argument in which prescientific hypotheses can be explored. This is not a process amenable to falsification, even though it borrows data from the natural sciences, but it is a process that helps us to think hard about hypotheses we might like to construct. It was this kind of thinking that Darwin put to great effect when constructing his natural history.

Handedness: Neutral or adaptive?

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Abstract: Corballis seems to have not considered two points: (1) the importance of direct selection pressures for the evolution of handedness; and (2) the evolutionary significance of the polymorphism of handedness. We provide arguments for the need to explain handedness in terms of adaptation and natural selection.

According to Michael C. Corballis, the brain lateralization for vocalization might precede the lateralized control of the hands. This certainly has to be taken seriously. However, we would like to comment on two points that he has apparently not considered: (1) the importance of natural selection for the evolution of handedness; and (2) the significance of the polymorphism of handedness.

In the theory presented by Corballis, handedness is described as a neutral character. Right-handedness is regarded as a direct consequence of the left-hemisphere dominance for vocalization. It is, however, difficult to consider handedness as a neutral character. For most manual tasks, especially those tasks involved in competitive activities, increasing performance by the specialization of one hand is certainly adaptive. For example, lateralized cats are faster at catching a virtual prey on a screen with one paw, compared to cats that have not specialized one of their paws (Fabre-Thorpe et al. 1991). In humans, hand or arm lateralization, whatever the side, is probably an adaptation for many activities, such as tool making and tool use (MacNeilage et al. 1987) or stone throwing (Calvin 1982; 1983a; 1987; 1993).

In fights, being lateralized certainly is an advantage. For example, many weapons are held with only one hand. Increasing the power, speed, and maneuverability of a particular arm or hand, that is, specializing it, is certainly pivotal. Aggressive interactions are responsible for fundamental selection pressures acting during primate and human evolution (e.g., Archer 1994; Bridges 1996; Daly & Wilson 1989; Furlow et al. 1998; Guilaine & Zammit 2001; Haas 1990; Wrangham & Peterson 1996; Zollikofer et al. 2002). The higher prevalence of right-handedness might well be due to a previously existing cerebral bias. But the specialization of one forelimb leading to right- or left-handedness is better viewed as the result of natural selection. The constitutive cerebral bias might well have driven the adaptive lateralization towards right-handedness. Nevertheless, it is unclear how the left-brain lateralization for vocalization alone, without natural selection for hand or arm specialization, would lead to the actual right-handedness.

An important problem is not tackled by Corballis's theory. The existence of a polymorphism of handedness remains unexplained. Yet, it is observed in all known human populations (Raymond & Pontier, in press) and described since the Palaeolithic (e.g., Bermúdez de Castro et al. 1988; Groënen 1997a; 1997b; Lalueza & Frayer 1997). Left handedness is associated with several fitness costs (e.g., Aggleton et al. 1993; Annett 1987a; Coren & Halpern 1991; Daniel & Yeo 1994; Gangestad & Yeo 1997; Geschwind & Galaburda 1985a; 1985b; 1985c; Grouios et al. 1999; McManus & Bryden 1991). The persistence of an apparently stable proportion of left-handers implies the balancing of these costs by some advantages.

One of the observed costs is the smaller size and weight of left-

handlers (Coren 1989; O'Callaghan et al. 1987; Olivier 1978). Size is a component of the reproductive value, at least in males (Mueller & Mazur 2001; Pawlowski et al. 2000). However, smaller size and weight is probably not a disadvantage in weapon fights. This is indicated by the fact that weapon fighting sports, such as fencing, do not have weight categories for competitions, as opposed to hand fighting sports, such as boxing. Generally, all sports using an object mediating an interaction between two opponents – racket, sword, ball – do not have weight categories, as opposed to all other interactive sports without such objects. This suggests that when weapons were prevalent in hominids, the weight (and probably height) disadvantage of left-handers in fights was considerably reduced. In addition, a frequency-dependent advantage favours left-handers in interactive sports (Goldstein & Young 1996; Grouios et al. 2000; Raymond et al. 1996). The persistence of the polymorphism of handedness might well be partly explained by an advantage of left-handers in weapon manipulation and fights. This polymorphism, as well as handedness itself, needs to be understood in the view of adaptation and natural selection.

Are human gestures in the present time a mere vestige of a former sign language? Probably not

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Abstract: Right-hand preference for conversational gestures does not imply close connections between the neural systems controlling manual and vocal communication. Use of speech and gestures may dissociate in some cases of focal brain damages. Furthermore, there are limits in the ability to combine spoken words and concurrent hand movements. These findings suggest that discourse production depends on multiple components which probably have different evolutionary origins.

Numerous theories have been advanced in an attempt to explain the manual asymmetry observed in many human activities. Corballis argues for a new evolutionary scenario on the basis of evidence from palaeontology, comparative psychology, and behavioural neuroscience. According to his account, right-handedness in genus *Homo* derives from an association of gestures and vocal signals in the communicative behaviour of our direct ancestors, whereby the dominant mode of communication progressively shifted from a manual to vocal modality. The hypothesis is intended to be falsifiable and indeed, several aspects of the theory deserve discussion. This commentary aims to examine the relevance of the specific argument concerning present-day human gestural activity. There is no doubt that people gesture as they talk and that in right-handers, these gestures are predominantly performed by the right hand. It does not follow, however, that the primitive language of humankind used the gestural modality and that present-day gestures are merely the remainder of that earlier stage. The alternative view favoured by other investigators is that spoken language derives from vocal communication or, more exactly, that gestures and speech coevolved in parallel from the beginning and that there are only limited connections between the two production systems.

Why do speakers gesture while talking? There is no simple answer to this question because different kinds of gestures probably depend on different mechanisms involved in discourse production. Some hand movements are called *iconic* or *representational* gestures because, like a drawing in the air, they depict the concept they express. Other gestures, sometimes called *beat* or *batonic* gestures, have simpler forms, no meaning, and relate to phrasal stress to emphasise some parts of speech. *Deictic* or *pointing* gestures constitute a third category in which reference is achieved

through spatial contiguity. That classification is not complete and it is possible to further subdivide conversational gestures according to a range of discourse functions. As far as representational gestures are concerned, recent observations indicate that the performance of this kind of movement relates to the mental activation of motor images (Beattie & Shovelton 2002; Feyereisen & Havard 1999). In that sense, these conversational gestures derive from action and the right hand is probably preferred because it is the dominant hand during interactions with objects, not the other way around.

Gesture laterality varies with gesture form and meaning. The right hand is preferred for performing representational gestures, but no asymmetry is found as far as beat gestures are concerned (Hostetter & Hopkins 2002; unpublished study of Debra Stephens quoted by McNeill 1982, p. 332). Thus, the claim that vocalisation created right-handedness is not true for all types of gestures: The beat gestures are simple, nonfigurative movements that are closely related to speech but are performed by the two hands in the same proportions.

Unilateral brain damages affect gestures and speech in different ways, and in agreement with Corballis's view, left-hemisphere dominance is stronger for language than for manual activity. Left hemispheric stroke patients were found to perform the same amount of conversational gestures as control subjects: fewer right-hand gestures but more left-hand and bilateral gestures (Foundas et al. 1995b). It was concluded that the right hemisphere contributes to the production of speech-related gestures (see also the complex pattern of lateralization described in a split-brain patient by Lausberg et al. 2000). In a picture description task, the rate of representational gesture production was higher in aphasic patients suffering from naming or repetition impairments than in control subjects, or in aphasics suffering from conceptual impairments (Hadar et al. 1998a). This rate of representational gesture production was lower in right-hemisphere patients suffering from visuo-spatial impairments (Hadar et al. 1998b). Therefore, some aspects of speech production (lexical access, phonological encoding) depend on different brain structures from those controlling the production of representational gestures, which entail visuo-spatial processing. Motor and verbal representations may be combined on another, preverbal level, during the conceptualisation of the message.

Combining words and gestures in discourse has a cost, however, and it constitutes a particular instance of dual-task performance. Vocal responses were delayed in a choice reaction time task when a representational or deictic gesture was to be performed concurrently (Feyereisen 1997; Levelt et al. 1985). Similarly, temporal characteristics of speech were altered when manual signs and spoken words were combined in simultaneous communication, a procedure aimed at augmenting the input available to deaf listeners (e.g., Whitehead et al. 1997). Thus, we see that there is competition between the two production systems and there are constraints in the development of an integrated bimodal system. In natural conversations, representational gestures are often performed during silent pauses to reduce such interference.

There are also limits to the combination of words and gestures on a morpho-syntactic level. Unlike manual signs, conversational hand gestures do not display the dual patterning found in spoken language. They are not built from elementary, meaningless units (kinemes) and they do not combine to form larger phrasal units. Nonetheless, in some circumstances, when speakers are prevented from using language to communicate, more complex manual signs can be invented (Goldin-Meadow et al. 1996). Similarly, during language acquisition, there is a transition phase during which hearing children combine a word and a gesture but provide no instances of gesture sequences (e.g., pointing to a bottle of milk and miming the act of drinking; Capirci et al. 1996). The development of vocal communication prevents manual gestures from developing into a full-fledged sign language, as happens in deaf communities. As a result, conversational gestures lack syntactic properties, and it is somewhat difficult to imagine that during evolu-

tion, syntax first appeared in a proto-sign language and then disappeared in the manual modality when vocal communication became dominant.

Analyses of conversational gestures in normal and brain-damaged individuals are consistent with the hypothesis of piecemeal evolution of separate components of language and action (Feyereisen 1999). In its broad sense, language use, be it vocal or manual, involves several specialised subsystems, some of which operate on distinct parameters and depend in part on specific brain regions.

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Unbalanced human apes and syntax

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Abstract: We propose that the fine discrete movements of the tongue as used in speech are what account for the extreme lateralization in humans, and that handedness is a mere byproduct of tongue use. With regard to syntax, we support the Armstrong et al. (1995) proposition that syntax derives directly from gestural motor movements as opposed to facial expressions.

We will discuss two areas in which we disagree with Corballis with regard to his hypothesis concerning the gestural origin of language. They are: (1) the importance of the tongue in lateralization, and (2) the importance of gesture as the prime mechanism for the evolution of syntax.

With regard to lateralization, Corballis places too much emphasis on handedness. He advances a gestural theory for the origin of language, yet he focuses on vocalization as a driving force for lateralization. It is this focus that perhaps led him astray on two accounts. First, it is possible that the trend toward lateralization for vocalization that Corballis suggests, is merely a side-effect of a general trend toward a lateralization for communication. For example, Hook-Costigan and Rogers (1998) found similar individual tendencies toward lateralization as those reported for group level handedness in primates in the hemi-mouth comparisons of marmosets when making communicative versus emotional vocalization and facial gestures.

Second, when nonhuman apes vocalize they do not move their tongues. However, we humans move our tongues extensively when we speak. The problem is to explain how we evolved from not moving our tongues during vocalizations to doing it all the time. As Corballis suggests, the neurological association between the motor movements of the tongue and hand are close; but even Darwin (1889/1998) saw the critical connection between the fine discrete movements of the hand and sympathetic movements of the tongue. For Hewes (1973b), via Darwin, the solution was that the fine discrete movements of the hand facilitated similar movements, with the tongue, of the type we use during speech. Waters and Fouts (2002) found that such sympathetic movements of the tongue and lips accompany the fine motor manipulations performed by chimpanzees to a greater degree than with gross motor movements. Such research, when coupled with theories regarding basic syllabic frames consisting of lip and tongue movements (MacNeilage 1998), provides a better proposal for basic human phonation. Also, it provides a mechanism for the association and transfer of more complex information across modalities.

Once the tongue started moving during speech, it presented a whole new situation with regard to motor control. The tongue is a single medial organ, and we have two competing hemispheres.

The hemispherical competition for the control of the tongue eventually is resolved by one hemisphere taking over its sole control. When unresolved, the hemispherical competition can result in stuttering (Jones 1966). The lateralized control of the tongue is what causes humans as a species and as individuals to become hemispherically unbalanced. The tongue is used extensively in speech and is controlled by one cerebral hemisphere. As a result, the controlling hemisphere receives more blood and nutrients, and, like a well-used muscle, becomes larger with regard to dendritic branching and sheer weight of gray matter (Gur et al. 1980). This in turn helps establish that hemisphere as the dominant one, which in turn produces the byproducts of handedness, footedness, and so on. The dominance and accompanying relative increase in gray matter in a particular hemisphere influences the type of cognitive processing at which that hemisphere can excel.

The second major issue concerns Corballis's thesis on syntax, and may actually be more damaging to his proposed timing for the evolution of language and the relationship between the lateralization of handedness. This issue arises with the lateralization of Broca's and Wernicke's areas in extant apes (Cantalupo & Hopkins 2001; Gannon et al. 1998). It is our position that, rather than posing a hindrance to gestural theories of the evolution of language, such evidence would be predicted by a functional analysis of these areas. This would support the hypothesis that the basis of syntax is inherent in holistic gestures.

Corballis suggests that the transfer of modality from manual to vocal gestures is related to the enhancement of holistic gestures by facial gestures in the development of syntax. To the contrary, Armstrong et al. (1995) point out that the development of syntax is inherent in the holistic gestures. This is not to suggest that accompanying facial gestures and vocalizations were not important enhancements to holistic gestures. However, while facial gestures may provide a basis for inflections, much of the basis for syntax is found in the gestures themselves. For example, the assignment of syntactic roles such as object and agent by verbs is more parsimoniously related to the semantic assignment of actor and object by the movement of hands in space. This is further supported by the observations that great ape gestures more often represent actions rather than objects (Plooij 1978; Tanner & Byrne 1996), and by the use of movement by signing chimpanzees to assign who is to give or receive the action (Rimpau et al. 1989).

With regard to the transfer of modality and the role of gesture for the evolution of syntax, the differential grips represented by mirror neurons in the homologue to Broca's area in rhesus monkeys take on more significance (Rizzolatti & Arbib 1998). These grips serve both as a mechanism for shaping vocalizations that accompany gestures, and as a neurological representation of the component parts of a holistic gesture. Furthermore, lateralization of Wernicke's area in the nonhuman apes, which functions in the prediction of visual sequences (Bischoff-Grethe et al. 2000), provides a mechanism for parsing the components of a holistic gesture (Fouts & Waters 2001). The result is a gestural origin of language that includes neurological continuity and functional relevance to data from extant apes. (For a more detailed explanation, see Fouts 1987; Fouts & Mills 1997; Fouts & Waters 2001; and Waters & Fouts 2002.)

A functional account of the neurological structures involved in language use, which takes into account behaviors of extant apes, suggests that the lateralization of these structures should not be treated as information to be explained away but rather central to a gestural theory of the evolution of language. If these structures are integral to the foundation of syntax, then handedness may be the effect of the push toward the use of a medial organ for a function that originated with the movement of objects (hands) in space, or a general push toward a left lateralization for communication. In either situation, Corballis has reiterated that the variability and genetic effects of handedness are available for selection; however, we believe that to raise the evolution of handedness and language above the rank of an interesting coincidence re-

quires greater attention to comparative behavioral research and linguistic theory than is presented in the target article.

Work and talk – handedness and the stuff of life

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Abstract: Wittgenstein shifted from a picture theory of meaning to a use-based theory of meaning in his philosophical work on language. The latter picture is deeply congenial to the view that language and the use of our hands in practical activity are closely related. Wittgenstein's theory therefore offers philosophical support for Corballis's suggestion that the development of spoken language is the basis of dominance phenomena.

Wittgenstein, one of the most significant philosophers of language of the twentieth century, underwent a metamorphosis in his understanding of language and thought which was apparently triggered by a conversation with Piero Sraffa, a Marxist economist. Sraffa made a Neapolitan gesture of brushing his chin with his fingertips, asking: "What is the logical form of that?" (Monk 1990, p. 261). Understanding the momentous nature of this exchange takes us to the heart of issues in the philosophy of language that are directly relevant to Corballis's proposal.

The early Wittgenstein championed an idea that has been dominant in contemporary Anglo-American philosophy of language: that language (and thought) incorporate a structured picture of the world made of elements that represent the things around us. This implies that an analysis of the logical structure of a sentence (or corresponding proposition) in combination with a lexicon relating its semantic units to features of the world reveals the meaning of that sentence (or the content of the proposition). The theory derives largely from Gottlob Frege, who argued that the propositional content of any utterance can be obtained by analysing it in the light of its semantic relationship to conditions in the environment ("truth conditions") and the way that they are combined grammatically (e.g., Frege 1977). The implication for cognitive psychology is that a complex computational mechanism working with semantic units and a quasi-mathematical syntactic structure can yield a meaning (or a small set of candidate meanings to be disambiguated on pragmatic grounds) for any utterance. On this account, language has a compositional semantics and a formal or computational grammar. Chomsky, Fodor, Pinker, and all the classical representational theorists work with some derivative of this theory.

The early Wittgenstein, preoccupied with the connection between language and reality, worked out this picture theory of meaning on the basis of Frege's work and its fundamental realist orientation. His own work was taken to imply that all meaningful propositions were either pictures of states of affairs in the world or had some other function quite apart from representation (such as expressing a feeling). Truth and falsity could be assigned to genuine propositions (or pictures of the world) only on the basis of their correspondence, or otherwise, with reality. Language, or at least its representational core, on this account was independent of the world, and sentences could be mapped onto states of affairs in the world by a set of ordered pairs of semantic units and their referents (or, for Tarski, well-formed sentences and sets of truth conditions). Understanding language involved a kind of cognitive calculus deployed in relation to utterances, written or spoken.

Sraffa's gesture had a different pedigree. Marxist theory stressed the link between language and praxis (Marx & Engels 1939). Language was not an abstract picture of the world composed by those with the leisure for intellectual contemplation of their surroundings; rather, it was practical and sprang from work, actual physical involvement with the stuff of life. Language was for

using and it bore the marks of that use much as the dirty hands of human workers bore the marks gained by actually dealing with the stuff of everyday reality.

Wittgenstein's later philosophy was deeply informed by the naturalism that pervaded early twentieth century thought. He was interested in the nature of the link between concepts and natural history (1953, p. 230). He could see that we used words for different purposes and compared our lexicon to a tool box, indicating that the simplistic picture of a one-to-one correspondence between words and canonical conditions in the world was deeply mistaken (1953, p. 6). He argued that our concepts are shaped by our interests and that the language that expresses them is like a set of instruments for enunciating the results of our investigations and directing our activity (1953, p. 151). Therefore, for the later Wittgenstein, language is deeply linked to and shaped by our doing things to each other and the world around us. Language has its primary affinity with the work of the hands rather than the data delivered by the eyes (which itself should be regarded as purpose-driven and organically connected to the rest of our activity). His remarks about the natural history of human beings let us examine Corballis's argument armed with philosophical thought that is directly relevant to its plausibility.

If Wittgenstein is right, language is intricately interwoven with our practical activity in the world such that it not only informs, but also elaborates, and extends our capacities to do things, collectively and individually, to the environment (Gillett 1992). On this view, that part of the brain uniquely suited to the rapid temporal sequencing of acoustic stimuli, as seems to be the case with the left temporal and associated inferior parietal areas (Altmann 1997), would have interesting relations to language. First, it would be closely involved in the complex patterns comprising gesture, utterance, and conventional use. Second, it would be poised to mediate the complex interconnections between the growing use of signs to facilitate our activity and the development of structured patterns of movement informed by neural connections associated with signs. Therefore, the dual facts that the left hemisphere is, in most higher animals, the side of the brain that is primed to serve as the substrate for rapid acoustic processing and that the left side of the brain controls the right hand, makes it plausible that the left side of the brain would be used to create the neuronal assemblies which allow the extension of gesture into speech as an adaptive tool. This would also imply that language is an intensely practical or world-involving activity and that the hand controlled by the left hemisphere would become the one entrusted with acting in concert with the discourse that has such a formative effect on much of our human activity.

Our great adaptation is language use and the advantages it provides, and language, according to the variety of philosophical naturalism I have sketched, is dependent for its soul on engagement with our practical activity. Therefore, it is not at all surprising that the hand linked to the area of the brain most fit for the cerebral realisation of language use should become dominant for most human beings.

Was a manual gesturing stage really necessary?

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Abstract: Given the primate propensity to make noise, it is unclear why a manual gestural stage would have been necessary in the development of either language or right-handedness. Cortical asymmetries are present in australopithecines but become clearly human-like with the appearance of *Homo* about two million years ago, including Broca's cap regions. Stone tool-making is still our only empirical entry into past cognitive processes.

I think Corballis has done a fine job of putting together so much of the literature in this useful review and in offering a set of coherent speculations regarding the interrelationships between handedness, speech, and gesture. However, I find it difficult to accept the primary role of gesture as a driving force toward either handedness or speech that he seems to argue. I am very surprised that the cognitive aspects of tool-making are completely avoided in this review, except with regard to handedness. I don't know whether my own attempts at arguing that tool-making and language had a similar cognitive basis (Holloway 1967; 1969; 1981) are correct, but I would have thought them surely worthy of discussion. I have never understood the stress on gesture as first offered by Hewes (1973), and as developed in this review. Primates are anything but silent animals, and I find it an enormous imaginative stretch that they, or our hominid ancestors, first had to go through a manual gesturing phase (or facial gesturing stage: All hominoids have facial gestures, all highly nuanced) before they could emit meaningful sounds that could impart information prior to developing what one assumes became true language. I would have thought that a more fruitful hypothesis would be that gesture and language evolved together, with gesture as primarily a device to amplify (and sometimes contradict) verbal messages. That other primates' sounds appear to be based on mostly limbic processes doesn't require that a gestural approach intervened between emotionally driven limbic sounds and cortically driven sound production. I don't see the logic of insisting that there was a gestural phase in hominid language evolution, and I see no hope that it could ever be proven from the fossil record. That is one major reason I return again and again in my papers to the stone tool-making processes, because these are our only remnants of past cognitive processing for hominids, up to the point where we see parietal art (see also Holloway 1996).

I thank Corballis for mentioning my 1983 paper showing cortical asymmetry in Broca's region for the KNM-ER 1470 specimen. In that regard, he might want to examine our paper (Holloway & de LaCoste-Lareymondie 1982) that found asymmetry patterns in ape and human brain endocasts to be quite different: That is, the patterns of left-occipital and right-frontal petalials occurred only in the hominid casts. This study was based on more than 100 endocasts for apes alone.

It must be pointed out that the paper by Cantalupo and Hopkins (2001) claiming asymmetries in Broca's areas 44 and 45 was based purely on MRI images of the sulcal patterns in those regions, and not on cytoarchitectonic evidence, which would be the best test of the asymmetries. We find (Sherwood et al. 2003) that the cytoarchitectonic patterns do not match the sulcal configurations as claimed by Cantalupo and Hopkins. We are currently studying the asymmetry patterns in Broca's region on modern human endocasts and thus far believe that there are indeed asymmetries that appear on the endocasts and that these are larger than on ape brains. Tentatively, we would suggest that Broca's region is slightly larger on the left side for right-handers than the left, but this is not an invariant pattern, and neither is there a sharp delineation between left and right Broca's activity in language processing depending on handedness in modern humans, at least as seen in PET scanning. This was one of our reasons for speculatively suggesting that the larger left Broca's cap region on the Indonesian Sambungmacan 3 *Homo erectus* indicated a possibility of speech long before the appearance of modern *Homo sapiens*, perhaps some one to two million years ago (MYA) (Broadfield et al. 2001). What the actual fossil record shows then, are hominids making stone tools about 2.6 MYA, right-handedness at about 2 MYA (see Toth, this article), asymmetries in Broca's area favoring the left side at about 1.8 MYA, as well as petalial patterns strongly indicating right-handedness. It's hard to escape the conclusion that some cerebral hemispheric specialization is in place. The earlier hominids, as represented by *Australopithecus*, cannot help with the chronology of these processes, as they seldom have both sides of the brain casts available, although some do show left occipital petalials (e.g., SK 1585). Their frontal lobe morphology does not

appear to have human-like Broca's regions, with or without asymmetry.

A number of minor issues require considerable skepticism. I would not take the MacLarnon and Hewitt (1999) argument regarding the spinal column diameter for the Nariokotome youth as evidence for lack of enough musculature to make speech sounds, given the wide range of variation in the spinal foramen aperture. The Kay et al. (1998) speculations regarding tongue movement abilities and the size of the hypoglossal canal have been thoroughly refuted (DeGusta et al. 1999; Junger & Pokempner 2002). Similarly, I find it difficult to believe that either the "elongated horizontally" or white sclera eyes really separate us in any meaningful way from our ape cousins (see target article, sect. 3.1). Gorilla, chimp, and orangutan eyes look very expressive to me. If repetitive movements involved in mastication are so important, wouldn't one expect bovids to have speech? I doubt that the proximity of manual and facial control help to give this hypothesis any real weight.

In sum, I still believe our best chance for putting together convincing scenarios regarding speech and language will rest with better analyses of stone tool making, and the interrelationships with neurological processes (e.g., Stout 2002). The brain endocasts of our ancestors will always be limited in proving this or that neurological/behavioral pattern, but the asymmetries are extremely important and should be considered more fully. I can only agree that it is our sociality that has most likely driven our behavioral and neurological evolution. The asymmetries are also important for considering the possibilities of cerebral hemispheric functional asymmetries, which we are just beginning to plumb with fMRI and PET scanning.

Brodmann's area 44, gestural communication, and the emergence of right handedness in chimpanzees

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www.emory.edu/LIVING_LINKS/i/people/hopkins.html

www.emory.edu/LIVING_LINKS/i/people/cantalupo.html

Abstract: The target article by Corballis presents an interesting and novel theoretical perspective on the evolution of language, speech, and handedness. There are two specific aspects of the article that will be addressed in this commentary: (a) the link between Broca's area and gestural communication in chimpanzees, and (b) the issue of population-level handedness in great apes, notably chimpanzees.

With respect to the functional correlates of Broca's area in great apes, in a recent paper from our laboratory, Cantalupo and Hopkins (2001) reported that Brodmann's area 44 (BA44) was larger in the left as compared with the right hemisphere in a sample of 27 apes comprising 20 chimpanzees, 5 bonobos, and 2 gorillas. Since the original publication of that paper, additional MRI scans have been obtained in chimpanzees and this now allows for a preliminary analysis of the association between BA44 and asymmetries in gestural communication as well as hand use for simple reaching in a sample of 20 chimpanzees. For the purposes of this analysis, a handedness index based on the number of right and left hand gestural responses was calculated following the formula [$HI = (R-L)/(R + L)$] using the combined data from two recent papers examining hand use and gestural communication in the Yerkes chimpanzees (Hopkins & Cantero, in press; Hopkins & Leavens 1998). HI values were derived for gestures that were (HI-YesVocal) or were not (HI-NoVocal) accompanied by a vocalization. We also correlated the BA44 data with a handedness index value for a measure of simple reaching (see Hopkins et al. 2002 for description). Asymmetries for BA44 were calculated for the entire region,

the lateral portion, and the medial portion following the formula [$AI = (R - L)/(R + L) \cdot 5$]. Shown in Table 1 are the correlation coefficients between BA44, and the HI values for gestural communication and simple reaching. We have also presented partial correlation coefficients for the association between the HI values for gestures and BA44 when adjusting for the association between simple reaching and BA44.

The correlations between the HI gesture values and BA44 are negative, indicating that increased right-hand use is associated with larger left-hemisphere BA44 values. Although in the initial analysis, the values do not reach conventional values of significance ($p < .05$), they are nonetheless close and may eventually be significant with a larger sample size. When the coefficients are adjusted for simple reaching, the HI values gestures are significantly associated with the medial portion of BA44 and borderline significant with the total BA44. Interestingly, the HI values for gestures do not correlate with the hand-motor region of the central sulcus, nor with the planum temporale (see Hopkins & Pilcher 2001; Hopkins et al. 1996 for description). If the association between BA44 and hand use for gestural communication association reaches statistical significance with a larger sample size, it would push back the time frame of the theory proposed by Corballis to at least five million years ago, when the ape-human-lineage split.

A second recurring theme of the target article is the presumed discrepancy between the findings in captive compared with wild chimpanzees. Some have suggested that the discrepancy in findings between captive and wild chimpanzees presumably reflects some type of acquisition of right-hand use by captive chimpanzees through observation of right-hand use by the humans who care for the animals. We wish to make several points in response to this argument. First, as has been argued elsewhere, there are many differences in types of measures used to evaluate handedness between captive and wild chimpanzees, and this might just as easily explain the discrepancy in findings as compared to inherent differences in the populations. Second, a recent study on handedness for coordinated bimanual actions reported population-level right-handedness in a second colony of chimpanzees, and the degree of asymmetry was nearly identical to those reported in the Yerkes chimpanzees (Hopkins et al., in press). In addition, a comparison of wild-caught, captive-born mother-reared, and captive-born human-reared chimpanzees in the combined sample of chimpanzees revealed a significant effect of rearing condition, with captive-born mother-reared chimpanzees being the most right-handed. The relevance of this finding is that the groups of chimpanzees that had been either directly exposed to human rearing (captive-born, nursery-reared), or been living in captivity and been exposed to humans the longest (wild-caught at ages less than two years), were the least right-handed. If either direct contact with humans or prolonged exposure to a right-handed human model of hand use was the sole means by which handedness was developed, then these individuals should have been the most right-handed, not the least. Third, recent meta-analyses of handedness in wild

Table 1 (Hopkins & Cantalupo). *Correlation coefficients between BA44 and HI values*

	HI-NoVoc	HI-YesVoc	Reaching
Overall correlation			
Total BA44	-.314	.031	.227
Lateral BA44	-.340	.096	.215
Medial BA44	-.237	-.032	.184
Partial correlations (adjusted for simple reaching)			
Total BA44	-.388+	-.005	
Lateral BA44	-.338	.079	
Medial BA44	-.470*	-.063	

chimpanzees do suggest population-level right-handedness (see Hopkins & Cantalupo, in press). For example, Boesch (1991) reported data on handedness for reaching, grooming, wade dipping (a form of tool-use), and nut-cracking (another form of tool-use).

A one-sample t-test on the percentage right-hand use data presented in this paper (Boesch 1991) revealed a significant right-hand bias for grooming $t(14) = 2.45, p < .03$ and the wade-dipping data approached statistical significance (mean % right-hand use = 65). Others have similarly reported population-level right-handedness in wild great apes for behaviors including bimanual feeding in mountain gorillas (Byrne & Byrne 1991) and simple reaching in bonobos (Ingmanson 1996). Perhaps more important, when the collective data are pooled in wild chimpanzees, the ratio of right- to left-handedness is about 2:1, a value approximating the distribution in captive chimpanzees. The primary difference is that our studies on handedness in captive chimpanzees have nearly four times as many subjects as some of the largest sample sizes in wild chimpanzees. A 2:1 ratio in right- to left-handedness, if truly the biological representation of handedness in chimpanzees, is a relatively small effect; therefore, large samples of subjects are and will be needed to detect the effect – a point often lost or overlooked in the comparison of findings between wild and captive chimpanzees. We believe that under the right conditions and the appropriate sampling, population-level right-handedness will be manifest in wild chimpanzees, and likely other great apes, with continued research in these magnificent animals.

We conclude by suggesting that the basic premise that lateralization for language and handedness are related in humans may be erroneous, and that perhaps it is better to consider them as separate abilities with distinct neural pathways rather than part of one modular system. The results from WADA tests and more recent blood-flow studies in humans are often cited as findings supporting the association between handedness and cerebral dominance for speech. However, it is important to emphasize that 70% of left-handed individuals are left-hemisphere dominant for speech – which, although statistically lower than the 96% of right-handed subjects who are left-hemisphere dominant for speech, still leaves the statistical majority of left-handed individuals left-hemisphere dominant for speech. The association between handedness and language dominance is relatively weak, and by no means are the two necessarily causally related (see Yeo et al. 2002 for review). From an evolutionary perspective, right-handedness may have evolved after the emergence of asymmetries associated with gestural communication, as Corballis has proposed, but handedness may not have been a direct consequence of selection for motor systems associated with language and speech in modern humans.

The hand leads the mouth in ontogenesis too

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Abstract: The evolutionary scenario described in this target article parallels developmental patterns observed in human infants. Early vocalizations are largely expressive, manual control develops more rapidly than intentional vocal articulation, and vocal and manual activity are linked. In ontogenetic development, language is strongly rooted in bodily action and gesture.

The notion that human language evolved from manual gestures can be traced at least as far back as Romanes (1888). What is new in this target article is the connection made between the emergence

of articulate speech from manual gestures and its implications for brain lateralization and the predominance of right-handedness among modern-day humans. Corballis makes an intriguing argument for the evolutionary emergence of right-handedness as a consequence of vocal-gestural associations formed through coproduction of bodily gestures and vocalization in communication. In our view, whatever the status of the evolutionary scenario outlined by Corballis may be, it is of considerable interest that it parallels developmental patterns observed in human infants. These parallels are evident in the nature and development of early vocalizations, the developmental precedence of manual control over intentional vocal articulation, and links between vocal and manual activity.

Corballis suggests that the first vocalizations produced by our evolutionary ancestors may have been emotional in nature and that these vocalizations evolved into the production of intentional speech. This is strikingly similar to the developmental pattern observed in infants. In newborn and very young infants, occurrence and quality of vocalizations are closely associated with arousal state. Early vocalizations, arising from the expiration of air through the vocal tract, consist of a natural, vowel-like resonance reflecting characteristics of the oral cavity. When an infant is relaxed, these vocalizations are interpreted as “comfort noises.” When an infant becomes distressed (e.g., because of hunger or discomfort), muscle tension and respiratory activity increase, resulting in crying. Over the course of the first year, these simple, relatively invariant vocalizations become the units out of which emerge the child’s first words and sentences (Thelen 1991).

With regard to intentional control, Corballis argues that the decided asymmetry in manual versus vocal control observed in primates may also have been evident in our common ancestor. This too is a characteristic of human infants. Intentional control of the hands and arms develops rapidly. By the age of two to three months, infants are able to grasp an object placed in the hands and bring it to the mouth for exploration (Lew & Butterworth 1997; Rochat 1989); and visually elicited reaching and grabbing emerge between the ages of three to four months and improve rapidly in subsequent months. By contrast, the development of infant intentional vocal control is a process that continues over a more extended period of time. Even after children have begun to produce language, vocal control is still somewhat imperfect, as indicated by the sound substitutions, reversals, and omissions that are common in young children’s language.

Another component of Corballis’s argument is that once gestures began to be used for communicative purposes, there was strong selective pressure to add vocalization. In his view, the inclusion of vocal behaviors in intentional communicative acts led to the forging of a link between vocal and manual activity and to a shift in the structural control of vocalization to Broca’s area, a structure long involved in the control of manual behavior. Although neurophysiological data indicating common underlying brain mechanisms linking vocal and manual behavior in adults (see Iverson & Thelen 1999 for a review) are not currently available for infants, behavioral evidence suggests that linkages between vocal and manual activity are in place during the newborn period. The Babkin reflex, for example, can be elicited in newborns by applying pressure to the palm; infants react to this manual stimulation by opening their mouths (Babkin 1960). Coordination between oral and manual actions is also common in young infants’ spontaneous movements. When newborns bring their hands to the facial area to introduce the fingers for sucking, they open their mouths as the hand is moving toward the facial area, in anticipation of its arrival (Butterworth & Hopkins 1988; Lew & Butterworth 1997). Moreover, certain types of hand actions (e.g., index finger extension) and vocal activity co-occur reliably in communicative settings in infants as young as 9 to 15 weeks of age (Fogel & Hannan 1985).

Elsewhere, we (Iverson & Thelen 1999) have argued that this initial coupling between hand and mouth, together with the relatively more rapid pace of the development of manual relative to vocal control, creates conditions under which manual activity may

play a role in the development of vocalization. In parallel to the evolutionary scenario outlined by Corballis, we believe that the co-occurrence of manual and vocal behaviors is a key factor in the development of vocal control. For example, the emergence of reduplicated babbling (strings of repeated syllables, e.g., /bababa/) at six to eight months may be at least partially driven by a sharp increase in rhythmic hand and arm activity that appears during this time (e.g., Thelen 1979). Several studies have reported strong, positive associations between the ages at which hand banging and canonical babbling emerge (e.g., Cobo-Lewis et al. 1996; Eilers et al. 1993). That the increase in rhythmic arm activity precedes babbling onset is suggested by the finding that frequency of such behaviors is significantly higher in prebabblers relative to babblers (Iverson 2003); babbling may therefore be a product of rhythmic manual activity “pulling in” activity in the vocal system, resulting in the rhythmic organization characteristic of reduplicated babbling. Indeed, acoustic analyses have revealed that relative to vocalizations produced alone, vocalizations co-occurring with rhythmic movement have significantly shorter syllable lengths and formant-frequency transitions. These are precisely the dimensions that distinguish the syllabic structure of reduplicated babble (and mature syllables in general) from prebabble vocalizations (Ejiri & Masataka 2001).

Finally, Corballis’s argument that right-handedness may have evolved from the synchronization of manual gestures with a later-developed system of vocal production has a possible counterpart in the relation between the onset of infant babbling and growing hemispheric specialization. Although the evidence is not unequivocal, it does suggest that at babble onset, there is a preference for unilateral hand reaching (Ramsay 1984; 1985), some indication of a right-hand bias in collaborative reaching (Bresson et al. 1977; but see Ramsay & Willis 1984), and significantly higher rates of rhythmic shaking with the right relative to the left arm in a laboratory rattle-shaking task (Locke 1995). However, hand preference is by no means fixed at this early age; correlations between handedness and language fluctuate over the course of the first two years, suggesting that, at least in development, relations between these two domains are complex and dynamic (Bates et al. 1986).

Although we do not wish to suggest that the course of phylogenetic change is recapitulated in ontogenesis, the evolutionary story outlined by Corballis is complemented by what is known about relations between vocalization and manual activity in human infants. In ontogenetic development, language is strongly rooted in bodily action and gesture; and it is at least possible that this might also have been the case in phylogenesis.

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Mirror neurons, Broca’s area and language: Reflecting on the evidence

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Abstract: A premise of Corballis’s theory is that speech arose when vocalization co-opted existing gestural functions in the left ventral premotor cortex. Yet, visuomotor functions in this region remain largely unchanged between humans and macaques and have no discernible connection to gestural communication. This functional continuity suggests that language production is not the result of modifying existing motor functions in this region.

Michael C. Corballis advances an intriguing claim: Right-hand dominance arose in our early hominid ancestors as a result of vocalization functions migrating into a region of the left ventral pre-

motor cortex already specialized for gestural communication. As processes involved in programming vocal and gestural actions became interwoven, manual behaviors became increasingly biased to the contralateral side. However, as I describe below, the addition of speech production to the repertoire of this cortical region appears to have occurred without substantially altering its long-standing visuomotor functions. In both macaques and humans, rostral ventral premotor cortex is involved in representing transitive (object-oriented) manual actions at various levels of abstraction. These functions have no known role in gestural communication in either species. Such continuity of function seems surprising if the advent of spoken language involved co-opting existing visuomotor functions used for gestural communication by ancestral hominids. Alternatively, this pattern may indicate that linguistic functions were added to the ventral premotor cortex independently of pre-existing visuomotor processes.

Neurons in the rostral portion of ventral premotor cortex in monkeys (area F5) represent transitive hand actions at several levels. Area F5 is subdivided into F5ab – in the posterior bank of the inferior arcuate sulcus – and area F5c – located in the dorsal convexity (Rizzolatti & Luppino 2001). Both subdivisions receive major inputs from somatosensory and visual areas in the parietal cortex. Many of the cells in area F5ab represent particular hand postures, and some F5ab units respond selectively to the observation of three-dimensional shapes even when no hand movements are executed. The shapes of effective visual stimuli are typically compatible with a given cell’s preferred hand configuration (Rizzolatti et al. 1996a), suggesting that they may code objects’ three-dimensional features for the selection of appropriate grasping and manipulation movements (Luppino et al. 1999).

The majority of cells within monkey area F5c code the goals of specific prehensile actions rather than the movements of which they are composed. On the basis of their response preferences, most of these units can be categorized as representing holding, grasping, or tearing actions (Rizzolatti & Luppino 2001). These responses are generally context-dependent: If the same hand movements are made as part of a different action, activity is weak or absent. This has led to the hypothesis that area F5c contains a vocabulary of hand actions in which the goals of hand-object interactions are represented explicitly (Rizzolatti et al. 1988).

Of greatest importance to Corballis’s theory are cells in F5c known as “mirror” neurons. These units discharge when macaques produce an action, and also when they perceive a comparable behavior performed by a conspecific or experimenter (di Pellegrino et al. 1992). Mirror cells are few in number relative to other F5c neurons. For example, of 532 cells studied, Gallese and colleagues observed mirroring responses in 92. Of these, 30 responded only when there was a precise correspondence between observed and executed actions (Gallese et al. 1996). Viewed in the context of other F5c cells, the response properties of mirror neurons may seem anomalous at first glance. However, mirror neurons’ responses also depend on the animal producing or observing an interaction between an effector (hand or mouth) and an object. Likewise, they do not respond to the observation of an action being pantomimed, or to the presentation of a desirable object (Gallese et al. 1996). In sum, mirror cells, like other F5c neurons, are coding transitive prehensile actions. They are distinguished by the fact that they code actions produced not only by the animal but also by other agents. A plausible hypothesis is that mirroring reflects an exaptation of processes that were initially involved in matching hand configuration to object shape (Oztop & Arbib 2002) and may now serve to compare one’s own prehensile actions to those of conspecifics for recognition (Gallese et al. 1996).

A growing body of evidence indicates that the above-mentioned visuomotor functions of area F5 are also carried out in homologous regions of the human ventral premotor cortex, BA44 and/or 45 (Petrides 1994; Rizzolatti & Arbib 1998). In the left hemisphere, BA44/45 is known as Broca’s area and is most commonly associated with language production. Yet, similar to monkey area F5, BA44 is involved in manual object prehension (Binkofski et al.

1999a; Ehrsson et al. 2001). Like F5ab, BA45 is selectively activated during perceptual processing of graspable visual objects (Chao & Martin 2000). BAs 44 and 45 exhibit properties similar to mirror neurons in area F5c. More precisely, PET studies report activation of BA45 during observation of grasping (Grafton et al. 1996; Rizzolatti et al. 1996b) and meaningful hand actions (Grezes et al. 1998). Investigations with functional magnetic resonance imaging (fMRI) reveal activation in BA44 during observation of finger movements (Iacoboni et al. 1999) and grasping actions (Buccino et al. 2001). A similar finding has been reported using magnetoencephalography (MEG) during the observation of grasping actions (Nishitani & Hari 2000). These neuroimaging studies report activations primarily within the left ventral premotor cortex during action observation. As Corballis points out, this may indicate that the human mirror system is intimately tied into language processes in Broca's area. By contrast, this asymmetry may be related to confounding effects of subvocalization during task performance (Heyes 2001). A recent fMRI study in my lab that controlled for this possibility detected bilateral BA44/45 activation during observation of transitive prehensile actions (Johnson, under review).

In conclusion, despite the emergence of language processes in Broca's area, visuomotor functions of the rostral ventral premotor cortex have remained relatively unchanged over the millennia separating humans and macaques. These processes were and continue to be involved in constructing representations of transitive prehensile actions, not gestural communication. This continuity across species suggests that language came to this region not by co-opting existing visuomotor functions but rather as a separate and entirely unrelated adaptation. Corballis may be correct in suggesting that handedness arose from a bias originating with the lateralization of vocal communication to the left hemisphere. But, like the left-hemisphere bias for language production, the handedness asymmetry did not take root in a pre-existing gestural communication system.

Dual asymmetries in handedness

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Abstract: The possibility that two forms of asymmetry underlie handedness is considered. Corballis has proposed that right-handedness developed when gesture encountered lateralized vocalization but may have been superimposed on a preexisting two-thirds dominance. Evidence is reviewed here which suggests that the baseline asymmetry is even more substantial than this, with possible implications for brain anatomy and genetic theories of handedness.

At first sight, Corballis appears to be proposing that the high incidence of right-handedness among humans is a consequence of a single factor, namely, an association between manual gestures and vocalization (dominant in the left hemisphere) in the evolution of language. It becomes clear, however, that a second source of asymmetry is also envisioned, and it is observed (sect. 6) that the association with vocalization may have been responsible only for a "shift from a two-thirds to a 90% right-hand dominance." What is the evidence for this two-to-one "preexisting asymmetry" (sect. 5) in favor of using the right hand rather than the left? Corballis refers to an earlier article (Corballis 1997) in which he proposed a modification of the single-gene, two-allele model developed by McManus (1985a; 1999). According to the model, a dextral allele, D, codes for right-handedness, whereas a chance allele, C, leaves handedness open to chance. McManus's assumption that the DD

genotype would be associated always with right-handedness has not been challenged, but his proposal that the other homozygous genotype, CC, would be associated with equal incidences of right-handedness and of left-handedness (i.e., probability of right-handedness = .50) is open to question. Corballis (1997) proposed that the ratio of right-handedness to left-handedness for the CC genotype is not 1 to 1 but instead 2 to 1 (i.e., probability of right-handedness = .67) and showed that this improved the accuracy of predicting a person's handedness on the basis of their parents' handednesses.

It has since been shown (Jones & Martin 2000) that to provide a satisfactory unified account of all the major distributional features of handedness – in particular, the parent, grandparent, twin, and sex influences upon handedness – more drastic modifications are necessary, including the introduction of a ratio of right-handedness to left-handedness in the absence of the D allele of approximately 3.8 to 1 (i.e., probability of right-handedness = .79). The use of the same value of this parameter in accounting quantitatively for distributions in all four areas (i.e., parent, grandparent, twin, and sex effects) provided converging evidence of its appropriateness. Subsequently, extensive new data of McKeever (2000) have also been shown to be in good agreement with the same model (Jones & Martin 2001). This time, the independent estimate of the ratio of right-handedness to left-handedness in the absence of the D allele was approximately 3.5 to 1 (i.e., probability of right-handedness = .78), closely replicating the value estimated previously.

There is evidence, therefore, that not only does the phenotypic baseline deviate from the position of symmetry with regard to the right and left hands, which has been assumed by McManus (1985a; 1999), but also that the deviation is even more extreme than Corballis's proposed 2 to 1 ratio of right-handedness to left-handedness, though of course still considerably less than the overall ratio in the population of approximately 9 to 1 (i.e., probability of right-handedness = .9). What are the consequences of the baseline asymmetry being in fact more extreme than the ratio of 2 to 1 which is assumed by Corballis? Two kinds of implication may be distinguished. First, there are relatively specific knock-on consequences if the same degree of asymmetry is assumed to be manifest in related structures. For example, Corballis notes that Gannon and colleagues (1998) reported a leftward bias in the size of the planum temporale in all but one member of a group of 18 chimpanzees, a result which he describes (sect. 5.1) as "curiously" greater than the 12 cases out of 18 expected on the basis of an asymmetry of two to one ($p < .01$ on a binomial test). However, the apparent anomaly is resolved if the present more extreme asymmetry is adopted, because this produces an acceptable prediction of at least 14 cases of leftward bias out of 18 ($p > .05$ on a binomial test).

A second and particularly interesting implication of the greater degree of baseline asymmetry is a corresponding diminution in the available range of variation in asymmetry that can be attributed to other factors. Within the context of genetic theories of handedness, the phylogenetic contrast between different alleles is thus blunted. This means, for example, that a satisfactory explanation can at last be provided for the relatively low levels of concordance in handedness observed among pairs of twins (see Jones & Martin 2000; 2001; McManus & Bryden 1992). Alternatively, in the context of Corballis's present hypothesis, a higher baseline of asymmetry for language gestures would serve to reduce the magnitude of the putative task of lateralized vocalization in driving up the incidence of right-handedness to its present 90% level, and this could perhaps be explored in the future in the shape of a quantitative model of the proposed shift. Comparing Corballis's present hypothesis more directly with recent genetic approaches to handedness, it would be interesting also to consider how it might accommodate converging theoretical indications of linkage to the X chromosome, irrespective of whether the phenotypic relation is assumed to be recessive (Jones & Martin 2000; 2001) or additive (Corballis 2001).

Finally, an attractive aspect of Corballis's present hypothesis is the central role within the gestural origin of language that is ascribed to mirror neurons (e.g., Nishitani & Hari 2000; Rizzolatti et al. 1996a) in Broca's area and its monkey homologue. Jeannerod (1994; 1997) has used the general term of motor imagery for those patterns of neural activation that occur in the absence of movement but that nevertheless resemble the patterns accompanying actual movements. Relatively small but consistent associations between handedness and level of cognitive performance have been observed for a number of tasks in the laboratory, appearing to provide evidence for the involvement of motor imagery in processes that include those of memory and perception (e.g., Martin & Jones 1998; 1999) and categorization (e.g., Viggiano & Vannucci 2002). The identification of motor imagery as mediating the interaction between characteristic patterns of motor behavior and relatively abstract cognitive processes would appear to fit well with Corballis's hypothesized nexus for gesture, language, and vocalization.

What functional imaging of the human brain can tell about handedness and language

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Abstract: Anatomic-functional studies in humans point out that handedness and language-related functional laterality are not correlated – except during language production; and that the convergence of language and hand control is located in the precentral gyrus, whereas executive functions required by movement imitation and phonological and semantic processing converge onto Broca's area. Multiple domains are likely to be actors in language evolution.

Corballis's hypothesis is based on the co-occurrence in humans of right-handedness and left-hemispheric specialization for language. We want to point out that this co-occurrence does not imply that handedness and language-related asymmetries are correlated, even in our species. The exact nature of this relation has yet to be understood. Functional imaging provides a unique opportunity to investigate hemispheric specialization for different language components in distinct brain areas and is beginning to shed some light on this issue. This approach has so far provided results confirming the heterogeneity of left-handers compared to right-handers (Szaflarski et al. 2002; Tzourio et al. 1998a), but the relation between handedness and hemispheric language specialization may not go beyond this group difference.

Functional imaging allows the direct testing of the correlation between handedness and brain activity during various tasks. This approach has led to evidence of a significant correlation between a handedness score and functional cerebral asymmetry of the motor cortex during a manual task. This result attests the strong proximity between handedness and the functional lateralization of the motor cortex (Dassonville et al. 1998). Such proximity does not exist between handedness and functional brain asymmetry for language. No correlation (in the statistical sense) was observed between handedness and speech listening (Josse et al. 2002; Tzourio et al. 1998b). Szaflarski reported a significant although weak correlation ($R^2 = 0.1$ at most) between the degree of handedness and the degree of lateralization associated with a semantic task (Szaflarski et al. 2002). However, most subjects pertaining to this study did not fit this linear relation (see Fig. 4 in that article). In our view such a correlation rather reflects the group difference described above. In other words, no results so far have really supported the assumption that the stronger the right-handedness is, the stronger is the leftward asymmetry of language areas during speech processing. Rather, the consensus seems to be limited to

the fact that a right-handed person is more likely to have a left hemisphere dominant for language, than is a left-handed person.

Actually, because handedness seems to rely on a functional asymmetry of the frontal motor region, it may well be that handedness is more closely related to frontal language regions and to motor aspects of language than to its perceptive components. Some recent results support this hypothesis. Indeed, although we could not find evidence of any handedness effect on speech-listening functional data, we did find in the same subjects such an effect on functional data related to verb generation (Josse et al. 2002). Interestingly, one of the differences between these two language tasks is that verb generation relies more on frontal motor regions than does speech listening. Note also that Szaflarski and collaborators observed that the effect of handedness on semantic-related data was more pronounced on frontal regions.

A stronger relationship emerges from the study of neuro-anatomical asymmetries and language hemispheric specialization evaluated with functional imaging. For example, subjects with a larger left planum temporale recruited more of some of the left hemisphere regions while listening to speech (Josse et al. 2002; Tzourio et al. 1998b), which partly supports Geschwind's hypothesis that anatomical asymmetries are markers of functional hemispheric specialization for language (Geschwind & Levitsky 1968). This can be linked to a theory by Zatorre stating that language hemispheric specialization emerged from constraints imposed by the processing of language sounds (cf. Zatorre et al. 2002), which proposes another scenario for language evolution focused on perceptive aspects.

Another part of the author's argument about the emergence of language left-hemisphere specialization in humans is founded on the close topographical relationship of mouth and hand sensorimotor cortices, which supposedly allowed interactions between vocalization and manual control during evolution. The author suggests that the seat of the convergence of manual and vocal control would be located within Broca's area (BROCA). This hypothesis needs to be qualified with respect to the anatomical location of BROCA. Recalling that BROCA includes the pars opercularis and the pars triangularis of the left inferior frontal gyrus, it must be underlined that functional imaging has challenged Broca's original observation (Broca 1861a) and demonstrated that BROCA is involved neither in simple motor control of manual activity nor in speech articulation. Rather, the convergence of these functions lies posterior to BROCA, in cortical motor and premotor areas within the precentral gyrus (with the anterior insula for speech articulation; Dronkers 1996). As a matter of fact, an attentive reading of language functional imaging studies reveals a robust and constant involvement of precentral areas not only during speech production but also during language comprehension and reading, consistent with the idea that speech production and manual control interacted during the evolution process.

BROCA is involved in the executive control of phonological processing (Paulesu et al. 1993) and semantic knowledge (Thompson-Schill et al. 1997). Its implication during movement imitation is in line with such an executive role, also evidenced during working memory and executive tasks. In order to document this statement, we conducted a short survey of several functional imaging studies dealing with movement imitation (Chaminade et al. 2002; Iacoboni et al. 1999), working memory (Braver & Bongiolatti 2002; Hautzel et al. 2002), and executive control, including inhibition (Dagher et al. 1999; Goel et al. 1997; 1998; 2000; Houdé et al. 2000; Jonides et al. 1998; Konishi et al. 1998a; 1998b; 1999; 2002). All studies reported an activation of BROCA (labeled ventral prefrontal in working memory studies), whether the material was verbal or not (see Fig. 1 here, and the review by D'Esposito et al. 2000). This convergence of language control, executive functions, and movement imitation in prefrontal areas, dedicated to higher-order cognition in monkeys, may also be part of the emergence of human syntax.

This evidence suggests that the emergence of language could

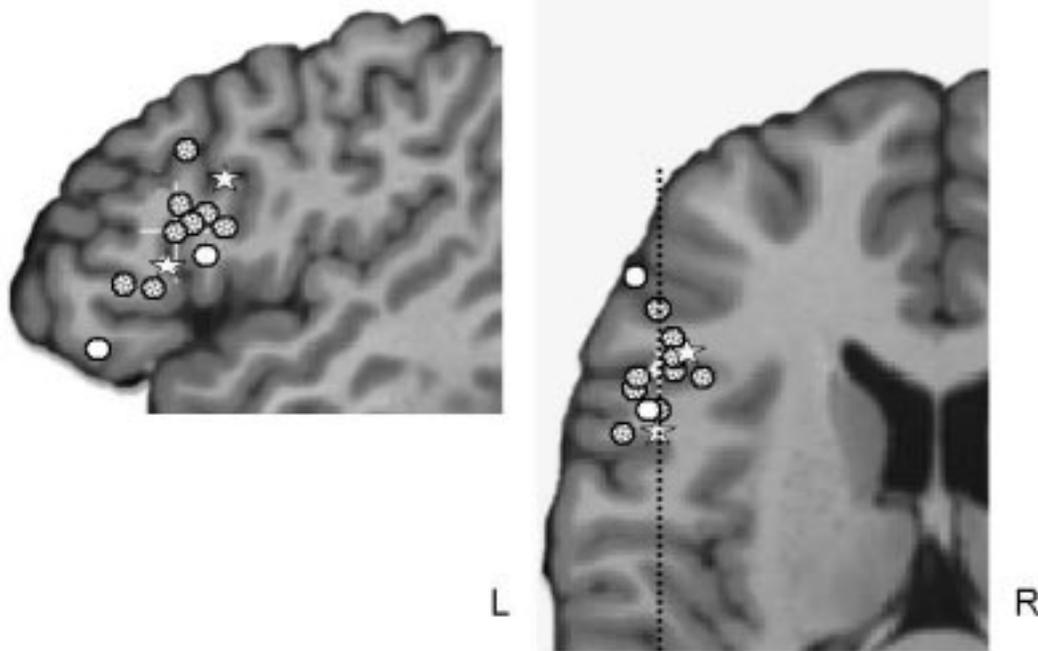


Figure 1 (Josse & Tzourio-Mazoyer). Plots of activity in BROCA during movement imitation (white dot: Chaminade; Iacoboni), working memory (stars: Hautzel; Braver) and executive control tasks (mainly inhibition, grey dots: Dagher; Goel; Houdé; Jonides; Konishi). The sagittal (left) and axial (right) slices pass through the mean dot coordinates in x and y, respectively, in the common stereotactic space (MNI single subject, SPM99; $x = -48 \pm 4$, $y = 19 \pm 8$, $z = 16 \pm 11$).

result from multiple domain interactions (motor, perceptive, executive, etc.) leading to multiple new competencies (Hauser et al. 2002).

NOTE

1. Nathalie Tzourio-Mazoyer is the corresponding author for this commentary.

**From mouth to mouth and hand to hand:
On language evolution**

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Abstract: This commentary points to the lack of sound data supporting Corballis's thesis that there is a general left-hemisphere dominance for nonverbal vocal production in mammals. I also point out that area F5 in the rhesus monkey, which Corballis considers as homologous to Broca's area, contains not only visual "mirror" neurons but also auditory "mirror" neurons. This weakens Corballis's thesis that language developed exclusively at the gestural level.

Corballis's thesis on the evolution of right-handedness and speech is based essentially on three assumptions, all of which invite a critical comment.

The first assumption is that before speech and right-handedness, there was a left-hemisphere dominance for nonverbal vocal production. Corballis cites six papers for support. Two of them (Ehert 1987; Fitch et al. 1993) deal with auditory perception, not vocal production. Another two (Bauer 1993; Nottebohm 1977) relate to animal groups (frogs, birds) with a forebrain anatomy and peripheral vocal system so different from that of mammals that it does not make much sense to use such species to explain phylo-

genetic developments that have taken place in higher primates. A fifth paper (Hollman & Hutchison 1994) relates to a brain region (preoptic-anterior hypothalamic area) in the gerbil that is involved in the control of male sexual behavior in general and, accordingly, shows a left-hemisphere dominance only in males, not females. Right-handedness and left-sided dominance for speech, however, are not sex-specific phenomena.

The sixth paper (Hook-Costigan & Rogers 1998), used by Corballis to support his thesis, in fact disproves his thesis. Hook-Costigan and Rogers do not report a left-sided dominance for marmoset vocalization in general, but rather, a left-sided dominance for contact trills and a right-sided dominance for mobbing calls. Finally, the paper that most directly addresses the question of vocal lateralization in nonhuman primates, Jürgens and Zwirner (2000) – has apparently escaped Corballis's attention. In this study, it has been shown that in 80% of squirrel monkeys, there is a lateralization of vocal fold control; of these, half show a left-hemisphere dominance, half a right-hemisphere dominance. In summary, there is no evidence of a general left-sided dominance for vocal control in mammals.

The second of Corballis's assumptions is that in the beginning language was gestural, not vocal. He further assumes that language at this stage was nonlateralized. The latter assumption is purely speculative and can neither be proved nor disproved at present. Corballis's main argument for the gestural origin of language is that area F5 in macaques, which he considers as homologous to Broca's area, contains neurons ("mirror neurons" according to Rizzolatti & Arbib 1998) which are active during execution as well as observation of specific hand movements. In the Abstract of his article, Corballis moreover claims that the macaque area F5 has nothing to do with vocal control. Figure 1 of this commentary shows that area F5 in the rhesus monkey overlaps extensively with the cortical larynx representation – that is, with that part of the motor cortex from which vocal fold movements can be elicited by electrical stimulation.

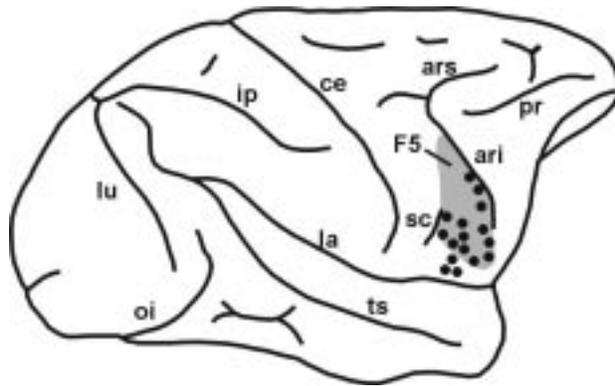


Figure 1 (Jürgens). Lateral view of the rhesus monkey brain with delineation of area F5 according to Matelli and colleagues (1985). Black circles indicate sites yielding vocal fold movements when electrically stimulated (Hast et al. 1974). Abbreviations: *ari*, sulcus arcuatus inferior; *ars*, sulcus arcuatus superior; *ce*, sulcus centralis; *ip*, sulcus intraparietalis; *la*, fissura lateralis; *lu*, sulcus lunatus; *oi*, sulcus occipitalis inferior; *pr*, sulcus principalis; *sc*, sulcus subcentralis; *ts*, sulcus temporalis superior.

Furthermore, Rizzolatti and colleagues report that there are numerous neurons in the inferior part of area F5, that is, below the hand representation, which fire during mouth movements and tactile stimulation of the mouth (Rizzolatti et al. 1981). In other words, there is no reason to assume that area F5 is exclusively devoted to manual tasks. There is also no reason to assume that F5 corresponds to Broca's area. There is general agreement that Broca's area corresponds to Brodmann's areas 44 and 45. According to the cytoarchitectonic studies by Galaburda and Pandya (1982), Petrides and Pandya (1999), and Paxinos and colleagues (Paxinos et al. 2000), area 44 lies in the posterior wall of the inferior arcuate sulcus and does not reach onto the lateral convexity. Area F5, according to Matelli and colleagues (1985), in contrast, extends across the lateral convexity between subcentral dimple and inferior arcuate sulcus. Only its most rostral part reaches into the inferior arcuate sulcus and thus overlaps with area 44. The macaque's area 45 lies in the anterior wall of the inferior arcuate sulcus and rostral to it; it thus does not show any overlap with area F5. In other words, cytoarchitectonically, the major part of area F5 corresponds to Brodmann's area 6; only its rostral-most part may be considered as homologous to Broca's area.

Corballis's third assumption is that after a nonlateralized gestural language had been established, there was a shift of language representation and preferred hand representation toward the left hemisphere, induced by the left-hemisphere dominance for nonverbal vocal behavior. Apart from the fact that there is no evidence for a left-hemisphere dominance for nonverbal vocal behavior, either in nonhuman primates (see above) or in humans (Ross & Mesulam 1979), the reader may ask himself: Why was that detour in speech evolution via a purely gestural language, if a lateralization of vocal behavior was already present from the very beginning of language evolution? In natural sciences, normally the simplest explanations are considered the best. Why not assume that language evolved from vocal and gestural behavior directly and in parallel? In a recent study, Kohler and colleagues (2002) reported that in area F5 of macaques there are not only visual "mirror neurons," but also auditory "mirror neurons," that is, neurons that discharge when the animal performs a specific action, as well as when it just hears the sounds produced by such actions. Furthermore, in the cortex bordering the inferior arcuate sulcus rostrally, that is area 45, Romanski and Goldman-Rakic (2002) found cells in the rhesus monkey that reacted specifically to monkey calls and, in some cases, even to single call types. These observations, together

with the fact that F5 contains a motor representation of the larynx, suggest that the cortex around the inferior arcuate sulcus is predisposed for audiovisual as well as visuogestural communication systems.

The above-mentioned arguments do not explain, of course, how right-handedness evolved. It should be kept in mind, however, that right-handedness at the individual level is not a recent, that is, hominid phenomenon, but is found in many nonhuman primates as well (McGrew & Marchant 1997). The question to which Corballis relates, accordingly, is not that of how right-handedness developed per se, but of which selection pressures were responsible for changing the ratio between right-handers and left-handers from about 1 to 1 to 9 to 1. I agree with Corballis that the factors responsible for the shift toward left-hemisphere dominance in both handedness and in language might have been the same. The high percentage of right-handed people with left-hemisphere dominance for language supports this assumption. On the other hand, the low percentage of left-handers with right-hemisphere dominance for language, and the finding of Foundas and colleagues (Foundas et al. 1998) that side of handedness correlates better with area 44 size than area 45 size, and side of language representation correlates better with area 45 size than area 44 size, make clear that handedness and language representation are not coupled as tightly as the high percentage of right-handers with left-sided language representation suggests.

From past to present: Speech, gesture, and brain in present-day human communication

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Abstract: This commentary presents indirect support for Corballis's claim that language evolved out of a gestural system in our evolutionary past. Specifically, it presents behavioral and neurological evidence that *present-day* speech and gesture continue to be tightly integrated in language production and comprehension.

Corballis's argument rests on the claim that modern-day spoken language evolved out of a gestural communication system in our evolutionary past. Although these sorts of arguments are difficult to substantiate – after all, geologists may never definitively support such a claim with evidence from mineral fossils – psychologists and neuroscientists can focus on present-day human communication to uncover *behavioral fossils* to support such a claim (Povinelli 1993). This commentary argues that by looking at the present-day link between speech and gesture, we can get a glimpse into how language emerged in our evolutionary past.

There is ample behavioral evidence that spontaneous hand gestures that naturally accompany speech play a powerful role in how humans process language. Corballis briefly touches upon this idea by referring to McNeill's theory of gesture-speech integration (McNeill 1985). To build on this, I will review recent empirical support for this theory. With regard to language production, Goldin-Meadow and colleagues demonstrated that gestures produced along with speech freed cognitive resources when children and adults explained their understanding of difficult mathematical problems (Goldin-Meadow et al. 2001). One of their interpretations of the findings was that because speech and gesture are packaged in different representational formats – linear and arbitrary versus global and imagistic, respectively – perhaps it is cognitively optimal to simultaneously distribute information across these modalities during communication.

In addition, there are several studies that demonstrate that gesture facilitates language comprehension in children and adults.

For example, Morford and Goldin-Meadow (1992) discovered that spontaneous hand gestures produced by an adult facilitated one- and two-year-olds' understanding of the adult's accompanying speech. Moreover, Kelly (2001) argued that hand gestures may interact synergistically with speech to help toddlers "break into" an understanding of complex pragmatic communication (e.g., saying "It's almost time for dinner" while pointing to a mess in front of a child). Finally, Kelly et al. (1999) demonstrated that speech and gesture mutually disambiguated one another during adult language comprehension – that is, gesture not only disambiguated the meaning of speech, but *speech itself* disambiguated the meaning of gesture.

Hence, there are solid behavioral data that suggest that speech and gesture are tightly integrated in present-day communication. But what is going under the surface of this behavior? The strongest evidence that speech and gestures are linked during communication comes from recent neuroscience studies investigating how the brain processes language. For example, Rizzolatti and Arbib (1998) theorized that traditional language areas in the human brain (e.g., Broca's area) may be involved in both the processing of language *and* the processing of hand motions. Further support that language and gesture may be linked in the brain comes from Pulvermüller and colleagues (Pulvermüller et al. 2001). They used a high-resolution EEG technique during a verb comprehension task and discovered that comprehension of action verbs activated parts of the primary motor cortex that were physically associated with those verbs (e.g., the verb "catch" activated arm regions, and the verb "kick" activated leg regions). These studies suggest that language and action regions in the brain have a close relationship during production and comprehension. However, no study to date has directly investigated how speech and gestural actions are integrated in the brain during real-time language processing.

Currently, this commentator is using a high-density event-related potential (ERP) technique to investigate this issue (Kelly 2003). This study measured ERPs to speech while adults viewed video segments of people speaking and gesturing about various objects. Preliminary analyses suggest that bilateral frontal sites differentiated speech that was not accompanied by gesture (e.g., saying the word "tall" without gesturing), from speech that was accompanied by matching gesture (e.g., saying the word "tall" while gesturing to a tall, thin object) and mismatching gesture (e.g., saying the word "tall" while gesturing to a short, wide object). Specifically, there was a greater negativity from 320 msec to 600 msec for the no-gesture stimuli compared to the matching and mismatching stimuli. This suggests that the brain processes speech that is accompanied by gesture differently from speech that is not.

The most interesting finding was that ERPs to the speech were different even within the different gesture conditions. Specifically, there was a classic N400 effect in the bilateral temporal regions for the mismatching but not matching stimuli.¹ It is important to note that the speech tokens in both conditions were *identical*, with the only difference between conditions being the different accompanying gestures. These results suggest that the brain integrates gestural information into its processing of speech fairly early in the comprehension process, and provides evidence that gesture and speech are tightly integrated in language processing. This type of research provides vestigial support for Corballis's general argument that speech and gesture were linked in our evolutionary past.

With specific regard to Corballis's lateralization argument, an interesting follow-up to the above study would be to investigate the influence that handedness plays in the brain's *production* of speech and gesture. For example, does the brain process right-handed gestures differently from left-handed gestures in language production? Perhaps by using neuroscience techniques that are relatively resistant to motion artifacts, one could investigate whether right-handed individuals demonstrate different neural patterns of language activation when they produce right-handed

versus left-handed gestures along with speech. If confirmed, this would provide further "present-day" support for Corballis's intriguing argument.

NOTE

1. The N400 effect reflects the unconscious neural integration of semantic information during language comprehension (Kutas & Hillyard 1980).

The secret of lateralisation is trust

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Abstract: Human right-handedness does not originate in vocalisation as such but in selection pressures for structuring complex sequences of digital signals internally, as if in a vacuum. Cautious receivers cannot automatically accept signals in this way. Biological displays are subjected to contextual scrutiny on a signal-by-signal basis – a task requiring coordination of both hemispheres. In order to explain left cerebral dominance in human manual and vocal signalling, we must therefore ask why it became adaptive for receivers to abandon caution, processing zero-cost signals rapidly and on trust.

My difficulty is with the core of Corballis's argument. Why should exempting the hands from their former communicational responsibilities have had the paradoxical effect of extending left-hemispheric control to these now-excluded hands? Primate-style vocalisations are controlled quite differently from modern speech. The "most critical adaptation necessary for the evolution of speech," as Corballis himself explains (sect 2.4), "was the change in brain organization that resulted in the intentional control of vocalization." Right-handedness is said to have emerged through the hands' involvement with vocal speech – but only as and when vocal signals themselves were becoming as easy to manipulate as manual ones, and only at a very late stage, when manual gesture was in fact being phased out. Presumably, then, during this critical period, specialised brain mechanisms for controlling manual, chewing, and other precisely calibrated sequential movements were extending their remit to previously irrepressible vocalisations. Insofar as these manipulative mechanisms imposed hierarchical order on formerly nonsyntactical vocal sequences, we might plausibly infer that they were already left-lateralised. Yet Corballis's explanation for right-handedness is the reverse of this – anciently left-lateralised centres of vocal control are said to have become extended to govern the hands. It may well be that the apparent contradiction can be resolved, but currently the direction of causality in this argument appears to me quite unclear.

A basic constraint in biological signalling is that if you can intentionally manipulate a signal, then you can fake it. Darwinian signal-evolution theory – not drawn upon by Corballis – sets out from the assumption that, without group-level public sanctions, generalised intentional honesty cannot be sustained. Except in the case of *Homo sapiens*, group-level moral codes are impossible – no biological population can afford to sustain the required system of sanctions. Intentional honesty is therefore an unrealistic assumption for receivers to make. This is why, throughout the entire history of life on earth, no biological species prior to *Homo sapiens* even so much as began to communicate on the basis of a conventional code. Conventional signalling is in this sense like "group selection" – theoretically conceivable but in practice of no Darwinian significance (Zahavi 1993). It does not happen because in a competitive world, no one can afford to remain faithful to the extremely costly contractual understandings and commitments which would have to be assumed.

By contrast, the secret of human left hemispheric specialisation – like the secret of language itself – is trust. Brain lateralisation is

driven by selection pressures to sequence, manipulate, and impose hierarchical order on low-cost digital alternations internally as if in a vacuum. But one side of the brain must be anchored in necessity if the other is to experiment with such freedom. One part of the brain must stay alert if the other is to become lost in its own signals. In just the same way, one foot must bear the weight of the dancer's body if the other is to trace fancy patterns in the air, or one hand must grip the slate if the other is to draw marks across its surface. Where the overall context is purely biological, the freely autonomous – normally left-lateralised – activity of imposing structure can certainly still take place. But the resulting movements will not qualify as socially trustworthy signals, being disqualified precisely for appearing so variable and unconstrained.

Even in nature, however, the songs of songbirds and cetaceans show that low-cost autonomous modulations can play a signalling role – on condition that they occur as variables within an otherwise costly, nonarbitrary, and therefore meaningful display. An example will illustrate this point. A weak or frightened animal is likely to be cautious, tentative, and exploratory. It must alternate between action and reaction, coordinating inputs from both hemispheres as it scans the environment for fresh information in advance of each new decision. Normally, for example, it would be risky for a songbird to shut its eyes or block off its ears. Paradoxically, however, for a babbler to “show off” that it can afford to do just that – to sing as if only the song mattered – can be an impressive display of self-confidence. Zahavi and Zahavi (1997) explain this as follows:

Why do babblers use precisely spaced syllables only when they are eager to fight? In order to emit rhythmic, regularly spaced, and clearly defined syllables, one has to concentrate on the act of calling. Any distraction – such as a glance sideways – distorts both the rhythm and the precision of sound; an individual cannot at one and the same time collect information and concentrate on performance. A call composed of precise, rhythmic syllables testifies that the caller is deliberately depriving itself of information, which means either that it is very sure of itself or that it is very motivated to attack, or both. (p. 21)

The Zahavis add that a human being who is in control of a situation likewise tends to issue threats in an ordered, rhythmic sequence, as if celebrating the fact that external reality can be ignored.

To disconnect from reality is to lose touch with the right brain. Less dominant figures cannot afford to do this, which may explain why they tend to rely more heavily on the right hemisphere while speaking (Armstrong & Katz 1983; Ten Houten 1976). Phonological processing is certainly less lateralised in human females than in males (Shaywitz et al. 1995). Lack of dominance makes it vital to stay sensitive to the total environment, drawing on the right hemisphere in order to do so. But autonomous left hemispheric control does not necessarily imply personal dominance. Its fundamental precondition is simply that low-cost signals – whether manual or vocal – need take no account of environmental feedback or resistance. The confident songbird shows off by “deliberately depriving itself of information,” ceding priority to the left hemisphere in the process. When signals need only connect up with one another, free of any requirement to engage with the external environment, it makes sense to encapsulate the computational circuits close together in one cerebral hemisphere while allowing the other to remain in touch with temporarily irrelevant reality.

Following Kobayashi and Kohshima (2001), Corballis notes that humans differ from primates in that human eyes are not inscrutable but enhance cognitive transparency. But this difference is more than an incidental curiosity. Ancestral social networks – even for sexually mature humans – must have been by primate standards anomalously supportive, making it safe to assume that anyone close enough to see the whites of the eyes was likely to be friend, not foe. Direction of gaze is an aspect of ordinary vision. But it may incidentally serve as a signal. A deliberate “wink” can speak volumes at virtually zero cost. Speech may be conceptu-

alised as an extension of the same principle. Where trust is sufficiently high, resistance on the part of listeners disappears, allowing the subtlest of signals to produce effects. Comprehension now involves inserting oneself imaginatively in the signaller's mind (Tomasello 1999). Speech signals do not need to generate their own trust – at the most basic processing level, an assumption of automatic trust is already built in. In fact, on this level it is legitimate to assume a conflict-free – in Chomsky's (1965, p. 3) terms, “completely homogenous” – speech community. So great is the trust, that language works almost as if one component of the brain – or one component of a computing machine – were simply transmitting digital instructions to another (Chomsky 1995; 2002). Quite regardless of whether signs are manual or vocal, it is this bizarre situation which liberates the potential of one hemisphere to arrange complexity independently of the other. We are left with a puzzling intellectual challenge: to elucidate how the necessary levels of trust could ever have been compatible with our selfish genes. Because I believe this to be the key theoretical issue, it will not surprise Corballis that I am critical of his thought-provoking but non-adaptive account, preferring my own more explicitly Darwinian alternative (Knight 1998; 1999; 2000; 2002).

ACKNOWLEDGMENT

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Integration of visual and vocal communication: Evidence for Miocene origins

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Abstract: Corballis suggests that apes lack voluntary control over their vocal production. However, recent evidence implicates voluntary control of vocalizations in apes, which suggests that intentional control of vocal communication predates the hominid-pongid split. Furthermore, the ease with which apes in captivity manipulate the visual attention of observers implies a common cognitive basis for joint attention in humans and apes.

Corballis suggests that intentionality in communication is exhibited in the visual domain by many primate species (sect. 2.1), but that voluntary control of vocalizations evolved uniquely within our lineage, sometime after the time when gestural language emerged, possibly as late as several hundred thousand years ago. Corballis states that “chimpanzee calls surely have little, if any, of the voluntary control and flexibility of human speech” (sect. 2.1).

Voluntary control over gestural communication by apes is well established (e.g., Leavens 2001; Leavens et al. 1996; Tomasello & Call 1997; Woodruff & Premack 1979), as Corballis notes (sect. 2.1). No researcher can speak to the state of mind of their ape (or human infant) subjects, but operational criteria for intentional communication are relatively standard and uncontroversial in both comparative psychology (e.g., Leavens & Hopkins 1998) and developmental psychology (Bard 1992). Among other criteria, intentional communication requires an audience and is sensitive to changes in the behavioral cues to attention in the audience. With some few exceptions (e.g., Povinelli & Eddy 1996), virtually all experimental and observational studies have confirmed these operational criteria of intentional communication in the gestural production of both free-ranging and captive apes (e.g., Bard 1992; Call & Tomasello 1994; Hostetter et al. 2001; Krause & Fouts 1997; Leavens et al. 1996; Tomasello et al. 1994).

Evidence is growing which is consistent with the interpretation that some voluntary control over vocal production is exhibited by

apes in some circumstances. This evidence derives from regional variations in vocal production, playback experiments in different populations of feral apes, and experimental observations of the co-deployment of gestures and vocalizations by apes in captivity. To briefly elaborate, van Schaik and colleagues (2003) reported regional variations in which wild orangutans (*Pongo pygmaeus*) from Sumatra and Borneo exhibit three vocalizations: kiss-squeak with leaves, kiss-squeak with hands, and "raspberries." Because these vocalizations were exhibited by representatives of only some groups and in fairly constrained contexts, this implies that these particular vocalizations have a learned component. Wilson et al. (2001) reported that the probability of calling by feral male chimpanzees (*Pan troglodytes*) in response to the playback of the pant-hoot calls of an unfamiliar male increased with the number of allied males present, suggesting that chimpanzees can suppress their vocal behavior when it is tactically wise to do so – such as when they may not have a superiority in numbers in the apparent presence of a stranger. Recent studies have also shown that captive chimpanzees deploy their vocalizations seemingly as an attention-getting tactic, vocalizing most when experimenters are less attentive or facing away from the signaler (Hostetter et al. 2001; Leavens et al. 1996; in press). Hence, the data are consistent with the idea that apes can exert voluntary control over their vocal production. Given Corballis's evolutionary assumptions about laterality of function, we might therefore expect to find evidence of functional linkages in the patterns of behavioral asymmetry exhibited by apes. Such evidence has been presented by Hopkins and his associates (cf. Hopkins & Cantero 2003; Hopkins & Leavens 1998; Hopkins & Wesley 2002): Chimpanzees who vocalize while gesturing are more likely to gesture with the right hand than are chimpanzees who do not vocalize while gesturing.

Corballis asserts that "captive chimpanzees can be readily taught by humans to point, and other animals pick up the habit evidently without further human intervention" (sect. 1). We have never consciously trained any of the more than 130 individual chimpanzees we have studied to point or otherwise gesture in the presence of unreachable food. This "spontaneous" development of pointing in captive apes has been noted by others (e.g., Call & Tomasello 1994). That pointing develops so easily in the absence of any explicit training and in populations of apes who have limited interaction with humans is significant insofar as human parents do not consciously train their children to point, yet children begin pointing, typically, by one year of age. We have suggested that in natural habitats, the "problem space," in which one ape is dependent upon another ape to acquire something distant to both interactants, is relatively rare (Leavens et al. 1996). This problem space is encountered on a daily basis not only by apes in captivity, who cannot directly obtain desirable but unreachable food, but also by human children who only slowly develop locomotor independence.

By virtue of the fact that key elements in infants' daily routines involve artifacts that are unreachable by them (e.g., toys, bottles), a problem space exists for year-old human infants in which adult humans must be manipulated to achieve the infants' goals. The relative locomotor autonomy and reduced artifactual dependence of similarly aged apes in the wild (cf. Tomasello 1999) means that they do not encounter, or only very rarely encounter, this problem space. When an object of desire is visible to the cage-bound ape or the relatively immobile human infant, and there is also present an adult human who has delivered similar such objects to the subject, then both ends and means are obviously available. The act of pointing implies that the signaler is aware of the need to draw the visual attention of an observer to the desired entity.

These observations – that some ape vocalizations seem to be either "cultural" (van Schaik et al. 2003) or tactically deployed (e.g., Leavens et al., in press; Wilson et al. 2001), and that apes in captivity spontaneously deploy pointing behavior (Leavens & Hopkins 1998; Leavens et al. 1996) – suggest an earlier evolutionary linkage between vocal and gestural production than that proposed by Corballis. The data are consistent with a claim for continuity

between humans and apes in their problem-solving capacities in these kinds of communicative contexts, which may be fundamental to later acquisition of language in our own lineage (e.g., Baldwin 1995; Butterworth 2001). Parsimony requires that these joint attentional capacities be attributed to the common ancestor of the living great apes and humans, which lived in the middle Miocene, about 12 to 15 million years ago. Because visual and vocal communication seem to be functionally linked in extant apes, language may have been multimodal from its inception.

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**Mouth to hand and back again?
Could language have made those journeys?**

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Abstract: Corballis argues that language underwent two modality switches – from vocal to manual, then back to vocal. Speech has evolved a frame/content mode of organization whereby consonants and vowels (content) are placed into a syllable structure of frames (MacNeilage 1998). No homologue to this mode is present in sign language, raising doubt as to whether the proposed modality switches could have occurred.

There is an old story about a driver in Maine who was trying to get from one place to another and asked a local for directions. The response was "You can't get there from here." If we reverse the origin and the destination, the Mainiac's problem is my problem with Corballis's assertion that there were two modality switches in the history of language: the first, from vocal to manual language, and the second, back again.

One reason to doubt that either of these transformations occurred at all is that by the time behavior had gone sufficiently up one garden path to be called language, additional selection pressures could not have been strong enough to make us abandon the enterprise in one modality and take it up in the other. We are seriously hampered here in being given virtually no conception of how far up the garden path language had actually gone before we sacrificed one modality for another on each occasion. But I want to take up a more accessible question, the question of *how* these transformations might have been made.

I speak here as one who takes seriously the question of how language transmission modalities actually work. In an earlier paper in this journal, I have argued that modality-specific constraints played a huge role in determining how the mental apparatus underlying modality use in speech (phonology) gets set up in the first place (MacNeilage 1998; see also MacNeilage & Davis 2000a). Corballis for the most part soars above the level of modality constraints. But if, as I suspect, bodily aspects of the transmission modality have a crucial formative role in language phonology, whether spoken or signed, this must have put severe constraints on the freedom to change modalities – in my opinion, *too* severe.

First, let us consider the basic properties of the two transmission modalities, using present-day sign languages as the best available model for the putative early hominid manual language. The manual system consists of two anatomically symmetrical but functionally asymmetrical multijoint limbs arrayed in a signing space centered on the torso and the face. Convention has it that there are four major parameters of sign (Klima & Bellugi 1979): hand shape, hand orientation, location (where in signing space a sign is made), and movement, with some auxiliary functions provided by the face. The vocal system has three subcomponents – respiratory, phonatory, and articulatory – with a directional layering whereby there is res-

piratory input to phonation and phonatory input to articulation. All three components contribute to prosodic features such as intonation, stress, and rhythm, counterparts of which seem less important in sign language. Tongue, lip, mandible, and soft palate positioning contribute to the segmental (consonant-vowel) level. Major parameters for consonants are place and manner of articulation and voicing. For vowels, it is tongue position and lip rounding.

As a frame of reference for considering how modality transformations might have occurred, let us consider the only comprehensive theory of evolution of the phonological component of language in any modality currently available, the frame/content theory of evolution of speech (MacNeilage 1998). According to this theory, the mouth close-open alternation underlying the syllable (closed for consonants, open for vowels) is the main functional property of speech. It is considered to have evolved from mandibular cyclicities associated with feeding in mammals (chewing, sucking, licking). This mandibular motor “frame component” eventually evolved a parallel cognitive frame component which now participates in the syllable structure constraint on segmental serial ordering errors whereby consonants and vowels (“content” elements) never get misplaced into each others’ positions in syllable structure. “No” never becomes “own.” The existence of this cognitive – or, more correctly, cognitive-motor – component in modern speech, probably mediated by the supplementary motor area, is indicated by the production of involuntary CVCV (consonant-vowel-consonant-vowel) . . . automatisms (e.g. “babababa”) in some different classes of neurological patient, including Broca’s original patient “Tan” (MacNeilage & Davis 2001). Ontogeny of speech is considered to recapitulate phylogeny, in that infants initially go through a frame stage of early speech characterized primarily by mandibular oscillation alone before entering a frame/content stage with independent control of the placement of consonantal and vocalic segments in a cognitive-motor syllable frame (MacNeilage & Davis 2000b).

Let us now use this conception to evaluate the phylogenetic problem of moving out of a vocal mode of language to a manual mode in *Homo habilis* and back into a vocal mode in *Homo sapiens*. For example, the first switch could have been from a frame stage of language to sign language, and the second could have been from sign language to the frame/content stage of spoken language. The putative first switch is a little remote for evaluation purposes, but as to the second switch, we know there is no homologue to frames, let alone a frame/content mode of organization in present-day sign language. It has no single biphasic rhythmic carrier, homologous to mandibular oscillation, on which the signaling complexities of the medium are superimposed. There is no equivalent to the syllable structure constraint on sign language errors. In fact there is little agreement as to how the term syllable should be applied to sign language, if it should be applied at all (Coulter 1993). I expect to find no repetitive sign language automatisms in signing patients homologous to the CVCV . . . automatisms of speech, because there is no functional component of sign language which has the required property. This, to me, takes away the most obvious basis for a systematic intermodality transformation process.

The picture does not seem to be any brighter at the grammatical level than it is at the phonological level. The way that the two modalities presently handle this level is very different. Spoken language makes primary use of the *time* domain, as it must, by employing word order, including free and bound grammatical morphemes, which have specified positions in the sentence and word, respectively. In sign languages, contrarily, syntax seems to be signaled primarily in *space*, by actions made simultaneously with those that signal the main semantic content (Klima & Bellugi 1979). The use of the face for grammatical purposes, which Corballis mentions, is a relatively minor factor. There is even evidence for grammatical universals in sign language that do not exist in spoken language (Sandler & Lillo-Martin 2000), implying that the most recent modality switch would have meant dropping language universals.

Another consideration that militates against there having been modality switches in the evolution of language is the well-known

lack of a systematic relation between American English and American Sign Language (ASL), even though ASL must have been formed in the presence of some knowledge of American English. It used to be thought that sign languages in general were derivative of available spoken languages, but the fact that they are not can be taken as further evidence of the problem of a conception of language evolution that requires a history of modality shifts.

My conclusion is that until we have some scenario as to how the two proposed modality switches occurred, that deals at least to some extent with the overall properties of spoken and sign languages (as we know them today), we should be very skeptical of the story Corballis gives us.

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Ontogenetic constraints on the evolution of right-handedness

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Abstract: Ontogenetic factors constrain the evolution of species-typical traits. Because human infants are born “prematurely” relative to other primates, the development of handedness during infancy can reveal important ontogenetic influences on handedness that may have contributed to the evolution of the human species-typical trait of a population-level right-hand dominance.

If left cerebral dominance for vocal communication evolved before right-handedness in humans and left-hemisphere dominance of speech (vocal communication) led to right dominance for hand use, then how can handedness become associated with vocalization? Corballis offers the very interesting solution that language evolved first as a manual and facial gesture system and vocalization was later incorporated into language gestures. Left-dominant vocal, manual, and facial gestures yielded right-handedness. However, when attempting to provide an evolutionary account for the occurrence of a species-typical trait, explanations of the development of the trait are often either ignored or simplified. Yet, how the trait develops constrains the optimality of the trait’s adaptive character and can reveal much about the sequence of the emergence and transformation of the trait during phylogeny (Michel & Moore 1995).

A peculiarity about handedness is that although there are only two hands, the trait is not categorical. Instead, the trait distributes continuously among individuals in a manner similar to height. However, because there are two hands, we can take the equivalent use or preference for each hand as a zero-point when examining the distribution of handedness. Unlike those species for whom there is a forelimb preference of use, the distribution for humans shows that there are significantly more individuals whose handedness scores exhibit a right preference than those who exhibit a left preference. Hence, the species-typical aspect of human handedness is the population bias in distribution that favors right-handedness (although chimps may show a population bias toward right-handedness that may reflect confounding in the research designs, as Corballis notes). Unfortunately, the exact proportion of right-handed individuals depends on the criteria used to define right- and left-hand use preferences. This dependency has plagued studies that have examined the relation of handedness to other functions, or neural anatomy (Bryden & Steenhuis 1991). The proportions of right-handers can vary from 95% to 65% (depending on criteria) and the remainder is usually defined as “non-right-handed,” reflecting the fact that they are a much more heterogeneous group.

In my own work on the development of handedness during infancy, I have chosen to use probability estimates to categorize the distribution into three groups: right-, left-, and undetermined-handedness (Michel 1998). With these categories, about 45% to 52% of infants during their first year had reliable ($p < .05$) right-hand use preferences (the variation depends on whether the preference is based on reaching or object manipulation), 13% to 18% had reliable left-hand use preferences, and 30% to 42% exhibited hand use that could not be reliably categorized (undetermined-handedness) (Michel et al. 2003). Latent class analysis revealed that there is a group of infants whose development seems to reflect the influence of a hidden variable that is biasing them toward a right preference (Michel et al. 2001). However, the proportion of such infants varies from 32% to 61% depending on the criteria used to define their hand-use preference. The results do confirm that even during infancy, there is a right bias in the distribution of handedness.

Previously, I had shown that the right bias in hand-use preference when reaching for objects during the first 18 months was predictable from the direction of the infant's preference for orienting his/her head to one side when supine or when inclined in a seated position. Approximately 63% of neonates exhibit a significant preference for orienting the head to the right during their first two months postpartum (Michel 1981). Infants with a distinct early preference for orienting the head to the left manifested a left-hand use preference when reaching for objects beginning at four to five months postpartum, and those with a distinct preference for orienting the head to the right manifested a right-hand use preference (Michel & Harkins 1986). Because tactile perception of texture and shape is not transferred between the hands (and presumably the cerebral hemispheres) until about 11 months postpartum (Michel 2003), the hand preference for acquiring objects will provide one hemisphere with sensorimotor experiences for about six to seven months that are not shared between hemispheres. This raises interesting questions about the consequences of such experience on the cerebral circuits underlying the manual-facial gestural system upon which Corballis wants to base language.

The evolution of an upright, two-limb, locomotion strategy had such profound effects on the female pelvic skeletal structure that humans seem to be born some two to three months earlier than would be estimated from the general characteristics affecting primate gestation lengths. Consequently, unlike the chimpanzee, the human mother must carry her infant for several months postpartum as she locomotes. And when the mother is not carrying the infant, it is frequently deposited in a supine position. This permits the opportunity for brain-stem asymmetries influencing head orientation (which occur prenatally in other primates) to contribute to the development of lateral asymmetries in infant cortical neural circuits either directly or via their influence on arm movements and self-induced events in the visual field (e.g., hand regard).

The infant manifests a handedness pattern that is very similar to that of the adult, and the infant handedness may be a consequence of a preferred head position. That preferred head position may reflect simple lateral asymmetries in brain-stem development that increase their influence on cortical development because the human infant is typically born "prematurely" for a primate of its type. Elucidating the relation between manual-facial gestures (and language/speech) and right-handedness will require much more sophisticated research on the development of handedness (especially during infancy) and the development of infant vocalizations, manual and facial gestures, and their relation to the neural circuits that contribute to their expression and ontogeny. Corballis's theory has set an important task for developmental psychobiological research.

Did they talk their way out of Africa?

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Abstract: Corballis suggests that fully vocal communication was invented by modern humans between 170,000 and 50,000 years ago. Because this new form of communication did not require hand gestures, he wondered whether this may have facilitated the development of lithic manufacture. I cast doubt on this interesting notion but offer an enhanced version that may have more potential.

I believe that Corballis's attempt to explain the origin of behavioural and cognitive modernity at 170,000 years may be a step too far in his argument. His idea (sect. 3.6) is that at this time speech became fully autonomous so that it no longer required gesture. He speculates that this may have allowed modern behaviour to develop and that it may have done so in two ways. I believe both of these to be weak. First, Corballis argues that because fully verbal communication would have freed the hands from communicative tasks, they could be more available for toolmaking, facilitating the development of manufacture. However, this alone is not sufficient to explain why toolmaking became more sophisticated; it is only to say that the hands would have had more time to make tools; and better tools do not necessarily take longer to make.

Second, Corballis argues that this freeing of hands would have made it possible to explain the manufacturing process to others verbally while demonstrating manually. This would have increased the transmission of knowledge and improved the quality of the tools. However, there is emerging evidence both from the ethnographic record and from experimental knapping studies that spoken communication is much less important in learning to make tools than one might think. In a number of hunting-and-gathering societies, such as the Ngatjatjara of Western Australia (Gould 1968) and the Northern Dene of the Canadian Subarctic (Christian 1977; Gardner 1976), knowledge of environment and subsistence is not transferred by means of verbal instruction but rather through watching and trying (Gardner 2002). The transmission of knowledge in these cultures occurs in a more implicit fashion than one might expect. Indeed, in the Paliyan of South India, issuing verbal descriptions of the manufacturing processes is considered to be offensive (Gardner 2000, pp. 89–93).

In an experimental knapping study (Ohnuma et al. 1997), two groups of students were taught how to manufacture a Levallois flake. Both groups had the opportunity of watching an experienced knapper make the product. In addition, members of the verbal group received verbal descriptions that accompanied the knapping; members of the nonverbal group had to communicate using gestures alone. Despite the fact that the teacher found that he could communicate complicated and precise details (e.g., how to smooth out the flaking surface; what angle to strike at) much more effectively using words than gestures, the increased communication did not lead to any improvement in performance. Those in the verbal group took just as long to learn the technique, and the flakes that they made were of only the same quality as the other group's.

It should be noted that this study was limited both in terms of just one tool type and of not having very many subjects. But it is a valid study nonetheless, and one that points the way forward towards a much-needed program of experimental knapping. In any case, I am not claiming that verbal communication is never helpful in the acquisition of skills, nor that such communication does not occur in any hunting and gathering society – it is helpful and it does occur. Nevertheless, these examples must temper the extent to which increases in verbal communication would have led to the widespread changes that Corballis seems to be proposing.

In any case, the real challenge is not to explain how humans taught each other existing manufacturing techniques, but rather to explain what caused the innovation of new types of tools and

new ways of living. It must be stressed (as always) that the behavioural changes that accompanied the evolution of anatomically modern humans were multifaceted and not merely to do with tool making. If Corballis wishes to make the case that the *mode* of language alone completed the process of human cognitive evolution, then he must explain why it led to the whole suite of changes – art, symbolism, the inclusion of grave goods in burial contexts, trade, use of new raw materials, and increasing transport of raw materials, to name just a few – that accompany the evolution of anatomically modern humans.

Having said all of this, Corballis's proposal is intriguing enough for me to want to have a go at enhancing it to lift it above these problems. I begin by seeing two interesting questions arising from what Corballis argued. First, it may be asked how the transmission of knowledge *does* take place in these societies, and second, it may be asked what people *do* talk about during manufacturing sessions if they are not talking about the manufacturing process itself. I believe that both these questions have the same answer: People tell stories. That is, in at least a number of hunter-gatherer societies, knowledge is transmitted indirectly through narrative descriptions of events. This occurs in the Yup'ik of the Western Alaskan coast (Morrow 1990), it occurs in the Northern Dene of the Canadian Subarctic (Christian 1977), and it occurs in the !Kung (Gardner 2002). The !Kung, for example, spend much of their time conversing – not instructing – while they make tools and gifts to serve their elaborate hxaro system of mutual reciprocity (Wiessner 1982). They make their tools slowly and talk quickly. Members of these groups may be unwilling to provide instruction but they are much more willing to produce narrative accounts of their experience, and these accounts provide a vehicle for the transmission of knowledge. These narrative descriptions are not produced *specifically* to transmit knowledge, they are produced because of a more general human tendency to think and talk in terms of narrative.

The question which then arises is this: Why did humans start telling stories? Well, here I can do no better than offer Corballis some of his previous work. In a 1997 paper (Suddendorf & Corballis 1997), Corballis introduced to scholars of evolution the concept of episodic memory. Episodic memory is autobiographical, containing records of our past experiences. It includes such things as the events, people, and things that we have personally encountered. They are crucially related to a particular place and time. They always have a subjective element and refer to the individual who holds them. This, surely, is the very essence of narrative, and it forms a significant portion of human conversation. Thus, the evolution of episodic memories may have allowed these hunter-gatherers (both past and present) to talk in the way that they do. Indeed, in that earlier paper Corballis himself suggested that, “a good deal of human conversation consists of mutual time travel down memory lane. Shared memories are the glue for the enlarged and complex social nets that characterise our species and go well beyond mere kinship” (Suddendorf & Corballis 1997, p. 139). But it may do more; I believe that recounting events in this way would have been a good vehicle for sharing knowledge of hunting, toolmaking, and any other area of subsistence.

The feeling I have about Corballis's present argument about modern human behaviour (I am not addressing the other dimensions of his article) is that learning to speak with the mouth instead of with both the mouth and the hands seems to be a rather pragmatic change; and yet, the changes that modern humans bring seem much more profound than that. Indeed, to many scholars, the diversity and speed of the changes has suggested that some kind of fundamental cognitive transformation occurred that led to the radically new types of behaviour on display. The development of episodic memory is just such a transformation, and scholars of human cognitive evolution stand to benefit from including it in their discourse. If Corballis sees fit to incorporate this kind of notion into his own narrative, then I believe that what will emerge is an even more comprehensive account of language origins than he already has.

Laterality probabilities fluctuate during ontogenetic development

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Abstract: We argue that lateralities are not merely a result of phylogenetic processes but reflect probability functions that are influenced by task characteristics and extended practice. We support our argument by empirical findings on lateral biases in early infancy in general, and footedness in particular, and on hand preferences in nonhuman primates.

Corballis discusses handedness and lateralities in general as phylogenetically developed when he states that there is a “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” (sect. 1). We will argue that handedness is very much a function of the hands. Furthermore, he talks about handedness “whether defined in terms of preference or skill” (sect. 1). Others make clear distinctions between hand *preference* and hand *performance* or *skill*, and we will argue that this distinction is crucial. Even if initial hand preference might be phylogenetically determined, performance and eventual preference are determined in large part by ontogenetic development.

In this commentary, we discuss how lateralities develop ontogenetically, using the development of early handedness and footedness as illustration. We will further argue that lateral preferences are probability functions – not necessarily fifty-fifty – and that probabilities fluctuate during ontogenetic development. In the case of hand performance, we will argue that an initial lateral bias leads to excessive and prolonged use of the preferred hand over the nonpreferred hand. This causes increasing lateral differences between the two hands.

Lateral biases in early infancy. Early lateral biases have been found in various activities such as spontaneous head-turning (e.g., Rönnqvist et al. 1998), spontaneous hand closure (e.g., Cobb et al. 1966), and grasp reflex strength (e.g., Tan & Tan 1999). Furthermore, Corbetta and Thelen (1999) showed that biases in infants' arm movements are not stable characteristics but fluctuate during early development before they stabilize into clear lateral differences. Typically, hand skill develops towards greater asymmetry (Singh et al. 2001). However, most studies of hand skill tested performance on unimanual tasks that have a clear division of labor between the hands. This division often implies manipulation from one of the hands and a stabilizing function from the other. Such tasks would favor specialization of each hand, with prolonged practice leading to increased differences between the hands. This, again, would strengthen hand preference.

Changing lateral biases in foot performance. As with hand skill, foot skill is typically measured using unilateral tasks. In such tasks, one foot often stabilizes the body while the other acts on or manipulates an object (see Peters 1988). In such unilateral tasks, lateral differences in performance between the two feet typically increase with increasing age, although this pattern is less clear than for handedness. For bilateral tasks, such as, for example, walking, a more symmetrical use of the two legs would be favorable, which should lead to decreased lateralities over practice. This is exactly what we found in a recent study on the development of postural control in early walking.

At the onset of independent walking, infants walked in an asymmetrical pattern, indicating an early lateral bias (Pedersen et al. 2002). This bias was stronger when they carried extra loads. As they became more skilled walkers, lateral differences in this symmetrical task decreased. However, when we increased task demands by loading the infants, the lateral differences reappeared,

in that placement of one foot was systematically changed to create a larger base of support. Hence, whereas foot skill in unilateral tasks developed towards asymmetry, the opposite occurred in the symmetrical task of walking.

Hand preferences in primates. Corballis argues that the “strong predominance of right-handedness appears to be a uniquely human characteristic” (target article, Abstract). We argue that this may stem from the high incidence of manipulative actions in humans. As indicated above, manipulating objects favors specialization of the hands, thereby strengthening initial biases. Support for this position can be found in animal studies. Although a general bias towards one hand is not reported on a species level, non-human primates have been reported to show right-handedness under certain conditions. For example, gorillas, chimpanzees, and orangutans show a population-level right-hand preference in reaching from a bipedal posture but not so from a quadrupedal posture (Hopkins 1993; Olson et al. 1990). Only a bipedal posture frees both hands, allowing them to assume differential functions and thereby strengthen a lateral bias. Furthermore, Hopkins (1996) reports a weak right-handedness in chimpanzees, but only for some activities – for example bimanual feeding – and only in captivity. The latter may indeed have been “inadvertently shaped by the routine acts of the humans” (McGrew & Marchant 2001, p. 355).

Ontogenetic development of literalities. Empirical evidence indicates that lateral biases are present very early in development but fluctuate as a function of task characteristics and practice. From a dynamical systems perspective, development in general and movement behavior in particular are not deterministic but probabilistic (Thelen et al. 2001). Behavioral patterns are not prescribed but self-organize under the confluence of constraints resulting from the organism, the task, and the environment (Newell 1986). Within this framework, the expression of any lateral performance difference would be a function of initial asymmetries, subsequent environmental pressures towards further asymmetry or increased symmetry, and practice. The general dominance of the left hemisphere in vocalizations, handedness, footedness, and head-turning suggests that an initial asymmetry is indeed phylogenetically determined, in line with Corballis’s argument. An eventual lateral preference, however, is as much a result of ontogenetic development as it is of evolution.

In conclusion, we agree that initial lateral biases might exist. These initial biases lead to small performance differences that increase the probability of choosing one side over the other. With further practice and under the influence of task constraints, the strength of the lateral bias may change, creating either increased symmetric performance or stable lateral preferences.

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A zetetic’s perspective on gesture, speech, and the evolution of right-handedness

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Abstract: Charmed by Corballis’s presentation, we challenge the use of mirror neurons as a supporting platform for the gestural theory of language, the link between vocalization and cerebral specialization, and the relationship between gesture and language as two separate albeit coupled systems of communication. We revive an alternative explanation of lateralization of language and handedness.

The French philosopher Condillac proposed the gestural theory of language evolution in 1746; the anthropologist Hewes revived it in the 1970s (cf. de Condillac 1746/1947; Hewes 1973a; 1973b). Although this controversial theory has since had a number of advocates (Armstrong et al. 1995), Corballis has fleshed it out substantially, linking together ideas from a wide variety of fields including, most notably, the neurosciences (Corballis 1998a; 1998b). One of the major alternatives to a gestural theory of language – in which language can evolve gradually out of gesture – is a “Big-Bang” hypothesis, in which a number of the genetic specializations for humanlike language would evolve rapidly together (e.g., Crow 1998). Corballis’s eloquent discussion of how different stages in human evolution may have contributed to the transition from gesture to spoken language is certainly more appealing than a “step-function” spurt of evolution. However, as we argue below, its evidentiary bases are still meager.

The gestural theory has received more attention since Gallese and colleagues (Gallese et al. 1996) reported mirror neurons in monkey area F5. In addition to the target article, there have been a number of other related accounts that put mirror neurons at the heart of their gestural theory (e.g., Arbib 2002; Arbib & Rizzolatti 1997; Place 2000), and the author would have done well to clarify the differences between his approach and these accounts. One of the difficulties with basing a theory of language development around mirror neurons is that these neurons are not specialized for communicative gestures. Indeed, the opposite may be the case, as the reported data show neurons that respond during retrieval of food and other purposeful actions. Hence, mirror neurons are more typically considered in the context of “theory of mind” and not communication (cf. Williams et al. 2001). Recent data showing that mirror neurons respond to auditory as well as visual cues (Kohler et al. 2002) further undermine their characterization as protointerpreters of gestural communication. However, this may be only a minor issue that can be resolved by showing that mirror neurons (or, for that matter, Broca’s area) are equally or more strongly activated during gestural communication than during other actions. In any case, we believe this issue merits more attention.

To the best of our understanding, the major difference between this exposition of the gestural theory and other accounts is that here the left-hemispheric dominance for vocalization explains both right-handedness and left-hemispheric dominance for language. However, as the author himself notes, the evidentiary link between handedness and hemispheric dominance for language is still tenuous. Interpretation of the evidence that Corballis has considered is consistent with a genetic theory of handedness (Annett 1987b; McManus 1985b), in which right-handedness is coded genetically by an allele. However, Coren (1996) proposes an alternative to such theories. According to Coren, most scholars misconstrued the data demonstrating inheritance of handedness because left-handedness also correlates with early trauma (e.g., during birth). In the target article, Corballis does not adequately address Coren’s thesis, and even in his monograph (Corballis 2002), this account receives only minor attention.

About 13% of the current population is left-handed, and consistent data speak to the relationship between left-handedness and certain sensory disorders (e.g., Bonvillian et al. 1982; Lessell 1986), sleep disturbances (Coren & Searleman 1987), and other developmental disabilities (Temple 1990). Corballis (e.g., 2002) has admirably incorporated certain pathologies into his theory, touching on blindness, deafness, hemispatial neglect, and schizophrenia. However, we feel that the treatment of left-handedness, with its implications for his theory, has yet to be fully developed.

Using vocalization to explain handedness and language dominance has other weaknesses. This account rests largely on the lateralization of vocalization in birds. One species of frog is similarly lateralized in control of vocalization, but in other species data are available only regarding the perception of species-specific vocalizations, not their production. As pointed out in the target article, vocalization is not the only behavior with population-level asym-

metries. Hence, the happenstance of left-brain lateralization for vocalization in birds and one frog, and for language in humans, is by no means conclusive. It is, however, worth noting that lateralization in birds seems to be determined by the eye that is first opened, which is determined by the normal posture of the embryonic chick in the egg (Rogers & Bradshaw 1996). We suspect that this method of introducing lateralization is likely to be species-specific. Further, vocalization in birds is very different from language in humans. Specifically, the target article does not address nonlinguistic vocalizations in humans. Whether these mechanisms relate to Broca's area, or are lateralized, is of significance to the theory.

Corballis admits that he cannot explain how population-level lateralization for vocalization might develop or what sort of evolutionary advantage it might confer. Within this context, Skoyles (2000), in a commentary on the gestural theory proposed by Place (2000), provided an interesting alternative explanation of language lateralization. Skoyles claimed that "gestures . . . are more easily learnt and comprehended when those making and those perceiving them do so uniformly with one hand." This account seems feasible: It provides a strong evolutionary drive towards language lateralization and handedness and explains the interaction between them.

One final concern we wish to raise addresses the fundamental concept of a gestural theory of language. At the basis of such a theory is the claim that gesture and language, or gesture and vocalization, are tightly coupled. Two examples serve to illustrate the spectrum of views regarding this claim. On the one hand, Bates (Bates & Dick 2002; Elman et al. 1996) argues that language is a freeloading system superimposed on sensorimotor areas, causing language and gesture to be planned and orchestrated together because they share the same neural system. Bates views language as spilling into gesture, which is a by-product or an epiphenomenon. Consistent with this understanding, Broca's area is active not only during speech but also upon hand-waving, and motor and premotor areas are activated by language tasks even in the absence of motor activity such as silent reading (cf. Grafton et al. 1997; Toga & Thompson 2003). These findings suggest that gesture and speech are two outlets for the same thought processes (which some have argued are inextricably linked to a theory of mind, thus connecting these processes with the mirror neurons of the monkey). On the other hand, Donald (1991; 1999) maintains that language skates on the surface of gesticulations, and whether or not somewhere in our evolutionary history speech took over from gesture as the main conduit of language, mime survives as a separate channel of communication even in adulthood. Corballis does not view mime and speech as separate channels; he construes them as a progression of forms. However, his approach to this issue seems inconsistent: At times his view reminds us of Donald's, whereas at other times it is reminiscent of Bates's.

In conclusion, it seems to us that, despite a dearth of hard evidence, Corballis's arguments for a gradual development of language are very compelling. Initially, the target article left us skeptical, but reading Corballis's recent book (2002) significantly clarified his arguments. It seems reasonable that gesture played an important role in the development of language, and that part of this role may have related to the development and understanding of the actions of others. On the other hand, picking a particular component of the system (e.g., gestures) to be a precursor for a different isolated component of the system (e.g., vocalization and spoken language) seems arbitrary. We feel that the arguments for an explicit "gestural" theory of language, which requires a grammar-laden and symbolic gestural language to precede sign language, are less convincing, and that the connection to lateralization of vocalization in birds is overreaching.

Developmentally, the arm preference precedes handedness

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Abstract: I would like to stress that early development repeats the evolution of the species. Hence, to understand the origins of functional brain asymmetry and the underlying mechanisms involved in handedness, we have to seek information not only from what we know about human evolution, but also from how an early hand preference develops in our own species.

To understand the evolution and the development origins of hemispheric specialization is an important part of understanding what it is to be human. However, despite a number of different theories and models, this is still unclear (e.g., see Hopkins & Rönnqvist 1998). Hence Corballis's target article is a good attempt to bring this understanding further.

When evaluating the evolutionary depth of human handedness, we need to bear in mind the distinction between hand preference and manual specialization – something that is not always done in studies addressing the evolutionary origins of human handedness. To develop a hand preference, we obviously need to have hands. Hence, Corballis's comparison between a uniquely strong right-handedness in humans and a left cerebral dominance with regard to vocalization in animals (without hands) which are ontogenetically far from *Homo sapiens*, does not establish any convincing comparative norms with an animal model of human developmental processes. Indeed, asymmetries in both brain structures and behaviors have been found among many species much closer to our own. Lateralized brain functions have also been found in a lot of other species without hands and even in those who do not have a vocal tract (e.g., Bisazza et al. 1998; Bradshaw & Rogers 1993). Adult rhesus macaques also exhibit a pattern of hemisphere dominance for processing species-specific vocalizations analogous to that of adult humans (Kimura 1993).

Lateralization of movement patterns appears very early in human life. There is a considerable body of evidence of postural and other motor biases in both spontaneous movements and various responses (e.g., head-turning, Moro response), which, in most newborns, show a right-side bias (e.g., Hopkins et al. 1987; Michel 1981; Rönnqvist 1995; Rönnqvist & Hopkins 1998). Even in fetuses, a right-sided preference for both arm activity and thumb sucking is reported to occur already at 10 and 15 weeks gestational age (Hepper et al. 1991; 1998), as well as a postural bias to the right (de Vries et al. 2001). This is in line with the suggestion of a normal lateralized gradient of neuronal differentiation and maturation from right to left (Best 1988). Such evidence indicates that laterally differentiated cerebral systems are relatively invariant (at spinal, supraspinal, and cortical levels) relative to later-appearing functional asymmetries. Hence, the point to be made is that although gestures may be precursors to speech, the neural system controlling early movements is probably lateralized long before vocalization.

Contrary to the general view, recent findings from human infants suggest that the control of more refined right-arm movements controlled by ipsilateral motor pathways from the right hemisphere precede the left-hemisphere control of the right hand (Hopkins & Rönnqvist 2002). In a recent study comparing the three-dimensional kinematics of both arms during reaching in five- to six-month-old infants, we were able to bring to light a hitherto unreported expression of a lateral bias (Hopkins & Rönnqvist 2002). This consisted of fewer movement units in the right than in the left arm, both for unimanual and bimanual reaches. In conjunction with the fact that we did not find a hand preference for contacting the object, this relative precocity of the right arm raises an interesting point about the nature of the early development of

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 & Rönqvist 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 devel-

opmental processes of handedness may be attained only when it is theoretically dissociated from issues surrounding the origins and acquisition of language.

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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 nonexistent 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 Canalupo 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-

scanning tools became available; e.g., Tanaka et al. 1999). Although as Good et al. (2001) point out, there is a strong presumption throughout the neuroanatomical literature that all structural left-right asymmetries strongly indicate functional asymmetries, there are many inconsistencies in textbook accounts, including the larger frontal lobe of the nondominant hemisphere and the lack of gender differences in language performance to parallel the sex differences found in degree of structural asymmetry (Good et al. 2001; Walker 1980). The most reasonable conjecture based on the studies above would, I suggest, be the acceptance of the null hypothesis for the relationship between structural and functional left-right asymmetries in the human brain. This in itself would have little impact on Corballis's claim that functional asymmetries for spoken language lead the human population asymmetry in hand preference. Indeed, accepting that some of the volume asymmetries in human and great ape brains are unrelated in either case to functional language specializations would solve problems that Corballis otherwise has with Cantalupo and Hopkins (2001) and Pilcher et al. (2001). Kennedy et al. (1998) suggested that the major source of variance in human cortical volume is individual differences applying to individual gyri, which is relatively independent of larger-scale variation; and that, in particular, local variations in the frontal and temporal language specific regions do not correlate well with total cortical volume.

Much of the target article is speculation which may never be disconfirmed by evidence. But there are accumulating data on the (largely conserved) genetic factors that control structural asymmetries of the kind that are disturbed in *situs inversus* (Hamada et al. 2002; Hobert et al. 2002; Mercola & Levin 2001) and the faint beginnings of knowledge of the genetic factors responsible for uniquely human capacities, some of which often, but not always, display left-right asymmetry (Ennard et al. 2002; though see, e.g., Meaburn et al. 2002). A detailed molecular account of the extent to which speech entails handedness may therefore be eventually attainable, but it is unlikely to correspond very closely to Corballis's narrative.

Why homolaterality of language and hand dominance may not be the expression of a specific evolutionary link

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Abstract: Although gestures have surface similarities with language, there are significant organisational and neurolinguistic differences that argue against the evolutionary connection proposed by Corballis. Dominance for language and handedness may be related to a basic specialisation of the left cerebral hemisphere for target-directed behaviour and sequential processing, with the right side specialised for holistic-environmental monitoring and spatial processing.

Gesture and language are separated by fundamental differences in structure and in cortical representation. Language is constructed of subunits which are organised in phonological and grammatical structure. This is true for both words and signs, despite their very different surface appearance. Signs have a phonology in which elements such as hand shape and location contrast with each other in the same way as the phonemes of spoken language. Although very similar in appearance to signs, gestures are holistic, semantic expressions without comparable substructure. The absence of grammatical structure can be seen in the very example of instrumental gestures (Armstrong et al. 1995) referred to by Corballis, which cannot be differentiated into noun, verb, or sentence.

Gestures are much less strongly lateralised, and the cortical areas involved do not overlap closely with the areas involved in language, whether spoken or signed. Although gesture and sign language use the same modality, observation of communication abilities following brain injury exhibits a clear dissociation (Corina et al. 1992; Hickok et al. 2002; Marshall et al., in press). Left-hemisphere injury strongly impairs signing, regardless of the degree of sign iconicity, whereas gestures remain largely intact. In contrast, right-hemisphere injury leaves most features of sign language intact, even in the presence of substantial visuospatial impairment (Atkinson et al., in press; Corina et al. 1999; Loew et al. 1997). This dissociation also highlights the different processing capacities of the left and right hemispheres (in adults).

We suggest that this evidence speaks against the occurrence of a gestural protolanguage; although speech and language developed from vocalisations that accompanied gesture, gesture itself did not achieve linguistic structure. There are also several lines of evidence to suggest that sign language was not an intermediate step between gesture and speech, the most striking being that both signed and spoken language are processed in the same regions of the left auditory cortex (MacSweeney et al. 2001; 2002). The later-evolved communication was built on cortical areas used in earlier forms of communication. In analogy to the communicative twinning of gesture and speech, sign language may be accompanied by distinct syllabic vocal gestures (echo phonology) (Woll 2001).

We agree with Corballis that there must be an evolutionary reason why both language and hand dominance are predominantly located in the left hemisphere, but we caution against the comparison with anatomical lateralisation. Although there may be subtle differences in the volume of specific homotopic areas in the mature human brain, it is well known that the right hemisphere can assume the functions of the dominant left side following injury in early childhood. Both halves of the brain are pluripotential; the observed differences are not organic but functional-developmental, possibly related to different maturational rates of the hemispheres. Although left-hemisphere dominance for specific functions was established early in evolution, this has occurred without leaving any convincing anatomic trace.

We consider that hemispheric lateralisation is related to a fundamental neurobehavioural division that occurred early in evolution. The left hemisphere has become specialised for target-directed behaviour (including vocalisation), whereas the right hemisphere is specialised for monitoring of the environment (Sieratzki & Woll 2002).

As a result, the left hemisphere directs sequential processing, and the right hemisphere controls holistic spatial processing. It is therefore reasonable to hypothesise that target-directed vocalisations became localised in the left hemisphere and that later, the particular capacity of Broca's area to map perception onto execution, to which Corballis refers, led to its becoming the site of language. Handedness is less strongly determined by an overall neurobehavioural disposition, with a variety of independent determinants (genetic, ergonomic, social) coming into play.

In conclusion, we suggest that the contrasting functional specialisation of the hemispheres reflects the fundamental duality of behavioural challenges that a species faces in its interaction with the environment. The homolaterality of language and hand dominance is more an outcome of this specialisation rather than the expression of a specific evolutionary link.

Causal beliefs lead to toolmaking, which require handedness for motor control

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Abstract: Toolmaking requires motor skills that in turn require handedness, so that there is no competition between the two sides of the brain. Thus, handedness is not necessarily linked to vocalization but to the origin of causal beliefs required for making complex tools. Language may have evolved from these processes.

The key question raised by Corballis is whether left-hemispheric dominance for vocalization came before or after handed asymmetry. It is important to recognize that lateralization of brain function is widespread among vertebrates (Wiltschko et al. 2002), although Corballis does not give this sufficient attention. What is the evolutionary origin of such lateralizations? The answer most likely lies in the original symmetry of the brain and the later advantage of specializing its functions to one hemisphere or the other. As McManus (2002b) puts it, the two hemispheres connected only by the corpus callosum would work much better by cooperating and specializing their functions rather than working as a single system, for doing so could easily result in competition, serious delays, duplication, and confusion.

This argument is of particular relevance to motor control (Wolpert 2003). From an evolutionary viewpoint, the brain has but one function to control movement. Movement was present in the cells that gave rise to multicellular organisms some 3,000 million years ago. This movement was a great advantage in finding food, dispersing to new sites, and escaping from predators. Muscle-like cells are found in all animals, including primitive ones like hydra. The first evidence for brain-like precursors is the collection of nerves that are involved in controlling movement like the crawling of earthworms or flatworms. Getting the muscles to contract in the right order was a very major evolutionary advance and required the evolution of nerves themselves. Here we find the precursors of brains – circuits of nerves that excite muscles in the right order. Its role in homeostasis is secondary.

Humans, as distinct from other primates, have a belief in cause and effect. There are experiments showing that chimpanzees do not have such concepts, particularly with respect to simple manipulation of their environment (Povinelli 2000). Children, by contrast, have causal beliefs as a developmental primitive, and these can be demonstrated in infants. I have suggested that the evolution of causal thinking is related to tool use, as it is not possible to make a complex tool without understanding cause and effect (Wolpert 2003). Moreover, it was technology that drove early human evolution, both biological and cultural.

Manipulating the environment with one's hands involves complex motor control, and on the basis of the arguments just given, it seems that it would not have been possible to make even simple tools without brain lateralization of the motor control system. The relationship in evolution between tool use, causal thinking, and language is an interesting but difficult problem; each might have served to haul along the others. It is striking that tool use and language both appear in children at about 18 months. All three involve what Calvin (1993) has referred to as stringing things together.

Most theories see language as helping how tools are used, and toolmaking and tool use as learned. However, my emphasis is on tool use preceding the use of gestures, because of its great adaptive significance. There is no point in gesturing if one does not have a clear concept of cause and effect. One needs language only if one has something useful to say, and until cause and effect were understood, there was little to say. It was cause and effect that required language for further understanding.

But it is recognized that tools and language share some critical features – rule-governed behavior and common sequencing neu-

rology. Human technology involves the cooperation with others – individuals do not make tools alone. This is true today of the Aborigines. Calvin proposes an interesting possibility related to throwing. He examines the idea that throwing evolved to capture game. It provided action at a distance, and improved accuracy and distance would have been adaptive evolutionary steps. There could have been a transition from sticks to stones to a fast handaxe which might spin and inflict serious damage. Throwing required improved control of arm movements for accuracy, and throwing for hunting became linked to pointing, a key early gesture. Then pointing could have become associated with vocal grunts. Moreover, movements of the arm could distinguish predator from prey. Language most likely had its origins in the neural basis of motor control. Evolution cannot invent something quite new but can only tinker with what is already there. As has been argued, the neurological basis of motor control has very similar features to the syntax of language. Just consider how the same muscles – “words” – can be activated in an astonishing variety of movements – “sentences” (Lieberman 2000).

But what were the changes in the brain that enabled all this great advance to occur? Human manipulative skills are not much greater than apes', but the difference lies in how these are used. Apes can trace writing but they do not use motor skills in the same way as humans, and this is genetically determined because it is an intrinsic property of the brain. The key difference lies not just in the increase in brain size, but in the way the brain is organized in relation to motor control. There has to be both analysis and reflection as to what to do, and then the ability to do it; and this involves new cognitive processes. This is associated with the significant enlargement of the associative areas of the frontal neocortex.

Author's Response

Hand-to-hand combat, or mouth-to-mouth resuscitation?

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Abstract: Many commentators have raised issues concerning the idea that language evolved from manual gestures. I deal with these first, reiterating the points that speech is very different from animal vocal calls, and that cortical control over manual action provided the best platform for the evolution of intentional communication and language. I then deal with commentaries on the origins of handedness. The critical questions are whether there is indeed an evolutionary coupling between handedness and lateralized control of speech, and if there is, whether a prior lateralization of vocal control provided the nudge that gave most of us left-sided speech and right-handedness.

R1. Introduction

Perhaps not surprisingly, a number of commentators were concerned about my thesis that language originated in manual gestures, which was the main premise of my argument that handedness may have been driven by asymmetric control of vocalization. I therefore consider the gestural theory first, and then go on to issues about laterality.

R2. On gestural theory

R2.1. General points

Dale, Richardson & Owren (Dale et al.) think that the gestural argument is driven by a series of “intuition pumps,” and I agree that intuition is not always a good guide to truth. Nevertheless, I suspect that the gestural theory is actually profoundly counterintuitive, which is perhaps why it has never really caught on. I may be deluded, but the case was made for me by looking at the evidence, not by appealing to intuition. **Bradshaw** seems to agree that the gestural theory is intuitively implausible. Mindful of the theme of Wolpert’s (1993) book *The Unnatural Nature of Science*, I take heart from this.

Annett does not see the point in trying to determine the ordering of events in evolution, although to my mind that’s a large part of what evolutionary theory is about. She also accuses me of perpetrating the “myth of first cause.” My aim was not to suggest a first cause – I would need to go back to the origins of life, and the question of why living molecules are asymmetrical, to do that. I did once venture into this territory (Corballis & Beale 1976), and McManus (2002a) provides some more up-to-date speculation. I am still working on the Special Theory – the General Theory is yet to come.

R2.2. Do we need the gestural stage?

A number of commentators (**Bradshaw, Feyereisen, Holloway, Jürgens**) argue that gesture and speech evolved in parallel, and that it is gratuitous to insert an extra gestural stage when animal communication has long been vocal, as is speech. One of my arguments, though, was that animal vocalization is an unlikely platform for the development of speech. Speech is very different, involving the construction of new meanings according to complex combinatorial rules, whereas animal calls are holistic and unsegmented. Chomsky (1966) wrote: “Modern studies [of animal communication] so far offer no counterevidence to the Cartesian assumption that human language is based on an entirely different principle” (p. 77), and I know of no reason to revise this opinion. It suggests to me that language required a more sympathetic medium in which to find initial expression. Chimps cannot talk, but they can communicate in a language-like way using gestures. This suggests to me that if you wanted to build language in the common human-chimp ancestor, you would start with gestures. She just would not be ready for speech.

R2.3. Did gesture come first?

Other commentators accept a gestural component, but disagree as to its primacy. **Arcadi** usefully provides a list of primate communicative gestural interactions, and then suggests that I overemphasized gestures relative to vocalization, at least with respect to behavior in the wild. He suggests that manual gestures were integrated into spoken language *after* vocalizations were brought under voluntary control. Again, this seems to me to overlook the evidence from the signing apes. Perhaps it is wrong to draw conclusions from captive apes, as Arcadi suggests, but the issue here has more to do with competence than with performance – what apes *can* do, rather than what they *do* do. I think it is reasonable to conclude from studies with captive

apes that bodily actions provided a much better platform for the evolution of language than vocalizations.

Arbib accepts the idea that manual gestures and vocalizations were involved in the evolution of language, nicely characterizing the interaction between them as “an expanding spiral,” with each feeding off the other. However, he questions the idea that voicing was added in later, suggesting that voicing was “always present.” It is instructive to watch Kanzi vocalizing as he gestures, but these vocalizations seem to be emotional accompaniments rather than integral components of the gesture. My guess is that emotional cries may have had little to do with the evolution of speech, and even in modern humans they remain largely independent of speech, and may interfere with it. It is difficult to speak coherently while laughing or crying.

Feyereisen notes that unilateral brain lesions often result in dissociations between speaking and gesturing, and that gestures often interfere with speech, suggesting that they are controlled by different systems. There are, of course, different kinds of gestures accompanying speech, as he points out, and I should not have implied that all gestures made during speech are linguistic. This is discussed more fully in my book (Corballis 2002). Of course, gesturing is not always at odds with speaking, and can aid word finding (Rauscher et al. 1996) – and **Kelly’s** commentary provides further evidence that gesture can facilitate the processing of speech. McNeill’s (1985) evidence for precise synchrony between speech and accompanying gestures also seems at odds with Feyereisen’s claim that gestures during speech are often performed during silent pauses to reduce interference.

R2.4. Do apes have voluntary control over vocalization?

Part of my argument for gestural theory was based on the premise that apes have little or no voluntary control over vocalization. This is challenged by **Arcadi** and **Leavens**. Arcadi notes, contrary to the observations of Goodall that I cited, that chimps can sometimes suppress vocalization, and sometimes fail to suppress facial expressions – just like humans, in fact. Leavens cites evidence that both free-ranging and captive apes can modify calls in response to the audience, and can use calls to attract attention, implying intentionality. He also notes that there are regional variations that imply a learned component. As I noted in section 2.1 of the target article, it has been suggested that regional variations can sometimes be explained in terms of habitat variations (Mitani et al. 1999) rather than in terms of learning, but it is in any case not clear to me that evidence of learning is evidence of voluntary control – Pavlov’s experiments do not show that salivation in dogs is voluntary.

Nevertheless, I accept that there may be some degree of voluntary control, but I would still contend that the degree of voluntary control over vocalization falls far short of that over manual actions. Ploog (2002) asks the question, “Is the neural basis of vocalization different in non-human primates and *Homo sapiens*?” His answer, based on detailed analysis of cortical and subcortical systems of vocal control, is “yes.” And we are still waiting for a chimp to talk, even at the level of protolanguage.

R2.5. Mirror neurons and Broca’s area

Much of my argument was based on the changing role of Broca’s area, and the discovery of mirror neurons in the ho-

mologue of Broca's area in the monkey. As **Beaton** rightly observes, Broca's area, like nostalgia, no longer seems to be what it was. Beaton and **Bradshaw** both make the point that, although mirror neurons seem tailor-made for imitation, monkeys do not seem able to imitate, although it has been argued that mirror neurons must have been "key elements" in the subsequent evolution of imitation and theory of mind (Williams et al. 2001). It is also true, as **Raz & Donchin** point out, that mirror neurons seem to have little to do with communication in monkeys. My intention was really just to point out that they seem to provide an ideal platform on which to build an intentional communication system, and it is, of course, tantalizing that they should be located in the homologue of Broca's area. I really have nothing to add to what **Arbib** (2002) and **Arbib and Rizzolatti** (1997) have said as to how the mirror system might have been elaborated into a communication system, and eventually into syntactic language. **Armstrong** also comments usefully on this issue.

I agree with **Dale et al.** that the properties of mirror neurons do not prove that language originated in manual gestures (there ain't no *proof*), and that many aspects of cognition must depend on high-level mapping between perceptual and motor systems. But I think it is significant that one of the cortical areas involved in the programming of speech in humans should be involved in the programming of manual action in monkeys. **Jürgens** cites evidence that area F5 is involved with movements of the mouth as well as the face. I think this supports my scenario that the face (and mouth) was increasingly involved in communicative gestures. **Jürgens** also mentions the so-called auditory mirror neurons that respond when the animal either performs an action or hears the sound made by the action. This has to do with action, not speech, and so has little to do with the notion that manual gesture preceded speech. There seems little doubt that there is a strong cortical component in the perception of complex sounds by nonhuman primates – hence **Kanzi's** apparent ability to understand spoken speech at a level well beyond his ability to produce it.

What is perhaps more problematic for the gestural theory is **Jürgens's** claim that vocal fold movements can be elicited by electrical stimulation of F5 in the rhesus monkey (e.g., **Jürgens & Zwirner** 2000). This does not necessarily mean that cortical control of vocalization served as a useful platform for the evolution of language – whatever the nature of the cortical control over vocalization, I doubt that it has anything like the flexibility of control over the hands or face, and probably did not reach the level of fine control required for speech until well after the split from the chimpanzee line (again, see **Ploog** 2002). Despite a recent claim that **Kanzi** has shown some glimmerings of speech (**Ananthaswamy** 2003), I will wager that chimps or bonobos will never achieve anything like vocal speech; but decades of study have shown that they are capable of at least a form of protolanguage through manual gestures.

Johnson-Frey also elaborates on the properties of mirror neurons and argues that the functions of these neurons, and of other neurons in area F5, have remained essentially unchanged between macaques and humans. Yet this area (or its homologue) is involved in both speech and signed language in humans, but not in primates. Something changed. He nevertheless agrees that handedness may have originated in the lateralization of vocal communication, but "did not take root in a pre-existing gestural communication system." Quite so, I don't think it did.

There is recent evidence that both Broca's and Wernicke's areas are active even when people "read" speech from facial gestures, consistent with the view that "the core perceptual processes for speech are embodied" (**Calvert & Campbell** 2003, p. 67) – a view that I also tried to express, albeit less succinctly. We do need more precise characterizations of the role of Broca's area and Broca's area homologues in both humans and primates, and it is in any case clear that mirror neurons by themselves do not explain language (**Raz & Donchin**), but I will be surprised if the evolution of this area is not critical to our understanding of how language came about.

R2.6. Other anatomical considerations

Part of my argument for the late development of speech relative to gestural communication was based on fossil evidence on the enlargement of the hypoglossal canal and the thoracic spinal cord, involved in control of the tongue and of breathing, respectively. **Bradshaw** and **Holloway** provide counterevidence, and it may be that the evidence I cited on these structures does not survive scrutiny. Nevertheless, I may well have underestimated the changing role of the tongue in the transition from facial gesture to speech, as suggested by **Fouts & Waters**. Increased control over the tongue must surely have been critical in the evolution of speech – not for nothing are spoken languages called "tongues." As for **Bradshaw's** worry about the talkative African Grey Parrot, advanced vocal control in birds may well have been a consequence of adaptations associated with flying, as suggested by **Deacon** (1997). If we had flown, we might have arrived there earlier.

I like **Knight's** elaboration of the suggestion that the human eye is by nature more expressive than that of nonhuman primates, supporting my view that facial gestures were important in the transition between visible gestures and speech. **Holloway**, though, doesn't agree that the eyes have it.

R2.7. Developmental considerations

A number of commentators appealed to evidence from child development, some supportive of gestural theory, some not. Although we must be wary of **Haeckel's** adage that ontogeny recapitulates phylogeny, developmental evidence may provide useful leads as to the evolution of oral-manual coupling.

Iverson & Thelen note that intentional control of the hand precedes that of the vocal articulation in human development, as in phylogeny, and add useful observations on the early coupling of oral and manual actions. **Kelly** augments my discussion of the relations between speech and gesture in both children and adults, illustrating the role that gesture can play in the processing of speech. This supports my view that language is really just one gestural system, in which manual gestures, facial gestures, and vocal gestures all contribute in varying degrees, depending on what one wants to convey, and on how and to whom one wants to convey it. There is little doubt that vocal gestures now dominate, but they aren't everything, despite the unfortunate invention of the cellphone. Text-messaging may be redressing the balance.

As evidence against the role of gestures, **Bradshaw** asserts that blind infants have fewer problems in language ac-

quisition than those born deaf. That may be true, understandably, of speech acquisition, but the evidence suggests that deaf children learn sign language if anything more rapidly than hearing children learn to speak (Meier & Newport 1990). In any event, there is evidence that people born blind gesture manually during speech even when they know the receiver is blind as well (Iverson & Goldin-Meadow 1998). Evidence from both the blind and the deaf seem to me to support the gestural theory rather than refute it.

Feyereisen points out that the emergence of speech prevents manual gestures from developing into fully-fledged sign language, suggesting that it is unlikely that sign language evolved as a fully-fledged syntactic system before being supplanted by speech. This is an interesting argument, but I think it does illustrate the perils of recapitulationism. Suppose it is true that language evolved as a fully syntactic gestural system, as I contend, before being supplanted by speech. The very fact that speech took over at some point in evolution leads one to expect that children would *not* develop full syntactic sign language – although deaf children, deprived of the opportunity to learn to speak, do go on to full sign language. Indeed, *pace* Feyereisen, one might be surprised at just how far signing *does* develop in normal children before speech so rudely interrupts. There is evidence that infant gestures are symbolic, and that early symbolic gestures may even help explain the vocabulary spurt that occurs later in development (Acredolo et al. 1999). There is also evidence that encouraging normal babies to use symbolic gestures (“baby signers”) may have a long-term impact on language development (Goodwyn & Acredolo 1998; Goodwyn et al., in press).

In the target article, I mentioned the evolutionary scenario proposed by Diamond (1959), suggesting that vocal speech may well have evolved from effortful grunts rather than emotional cries. My attention has since been drawn to the work of McCune and her colleagues (e.g., McCune et al. 1996), who have shown that the earliest grunts that babies make accompany movement or effort. Grunts then accompany acts of focal attention, followed by grunts that are communicative, but not yet referential. Echoing Diamond, McCune et al. suggest that speech may have emerged in similar fashion in primate evolution. This scenario, if correct, depends on the prior emergence of communicative gestures.

One of the ideas I tried to convey was that, once introduced, voicing may have been later modulated to increase the vocabulary of facial gestures. **Carstairs-McCarthy** suggests that voicing does little to increase the repertoire of consonants, despite the common distinction between voiced and unvoiced consonants. He may be right, because whispering seems to include the full range of phonemes. Perhaps someone can explain this to me.

R2.8. Signing versus speech

Part of my argument for the gestural origins of language came from studies of signed languages themselves, especially those developed by deaf communities, and the claims that signed languages have all the essential linguistic properties of spoken languages. Several commentators nevertheless questioned whether speech could have emerged out of signing.

MacNeilage argues that speech and sign language differ in fundamental ways, making it unlikely that speech

simply took over from signing. One important difference, he suggests, is that rhythm is especially important to speech, but not to signing, and arises from mandibular cycles associated with feeding. **Arbib** raises doubts about this scenario, and in any case sign language is not devoid of rhythm. **Petito et al.** (2001) have shown that seven-month-old babies exposed only to manual sign, display hand movements with a frequency tuned to the rhythm of signing. Babies exposed to speech did not show this rhythm. Besides illustrating that signing is also bound by rhythm, this research shows that infants are malleable with respect to acquiring these rhythms.

Carstairs-McCarthy suggests that the linguistic structure of sign language might be fundamentally different from the structure of spoken language. There can be no doubt that there are modality constraints that inevitably create differences between signing and speaking, and the question is how deep these differences go. **Neidle et al.**'s (2000) sophisticated application of contemporary linguistic theory to the analysis of the syntax of American Sign Language (ASL) suggests to me that signing and speech do not differ fundamentally, although there may well be deep differences that have yet to be fully explored. In any event, if our predecessors did indeed sign, it need not necessarily be the case that their signing closely resembled modern sign languages like ASL, as I pointed out in section 3.1.

Fouts & Waters and **Armstrong** provide further elaboration of the idea, which I borrowed from **Armstrong et al.** (1995), that the origins of syntax are more likely to be found in gestural communication than in vocalization. This is questioned by **Arbib** and by **Carstairs-McCarthy**, although **Carstairs-McCarthy** (1999) has himself traced the origins of syntax to the structure of the syllable. It is not entirely clear to me that this approach is any different in principle from **Armstrong et al.**'s idea that syntax evolved from the structure of the gesture.

Woll & Sieratzki also note that nonlinguistic gestures are organized differently from linguistic ones, and suggest that sign language was therefore probably not an intermediate step between gesture and speech. But I did not claim that all gestures are linguistic, just as not all vocalizations are speech. What I did try to argue was that *all* language is gestural, and that there was a gradual shift from manual to facial gestures, including the incorporation of vocal elements.

R2.9. Tool-making and the “human revolution”

Holloway and **Wolpert** suggest that the cognitive basis for language is likely to have emerged from tool-making, which seems to me to strengthen the gestural argument rather than weaken it. Tool-making is basically gestural, at least in a broad sense, and has the required properties of intentionality, sequencing, and forward planning. Tool use is also readily translated into gesture, as I know from once successfully communicating my need for a corkscrew in Russia. Nevertheless, I am reluctant to pursue this theme too far, because tool development was actually very slow from the emergence of stone tools some 2.5 million years ago until the emergence of anatomically modern humans around 170,000 years ago. Indeed, it has been argued that tools did not really take off until the so-called “human revolution” around 40,000 years ago (e.g., **Mellars** 2002), although this is disputed (**McBrearty & Brooks** 2000). In **Bickerton's** (2002) colorful (but no doubt exaggerated) words,

in the first 1.95 million years [after the emergence of *Homo erectus*] almost nothing happened: The clunky stone tools became less clunky and slightly more diversified stone tools, and everything beyond that, from bone tools to supercomputers, happened in the last one-fortieth of the period in question. (p. 104)

Besides, the tool-making abilities of our hominid forebears appear to be rivaled by those of other primates, and even by bird-brained creatures (e.g., Hunt et al. 2001). I have therefore preferred the view that gestural language may have actually impeded the development of tools, until autonomous speech took over and freed the hands.

Armstrong and Pearce both take issue with this scenario. Armstrong rightly protests that signed languages are perfectly serviceable, and indeed ASL is the language of instruction at the university level at Gallaudet University. Yet signed language is undoubtedly available to all, so why don't hearing people use it as a matter of choice? This is a sensitive issue, but one that needs further exploration. Armstrong may well be right in suggesting that there was more to the human revolution than the emergence of autonomous speech, although I reiterate that seemingly small changes in communication systems can have profound influences on human culture, as illustrated by the impact of writing systems.

Pearce suggests that the freeing of the hands would merely have given the hands more time to make tools, and providing more time does not lead to better tools. (I wish, though, that I had more time to write this response, but agree that it probably wouldn't make it any better.) He also cites evidence that vocal language plays little role in the transmission of tool technology. I appreciate his attempt to develop an alternative scenario, reintroducing me to one of my earlier articles, and thereby demonstrating my own failure of episodic memory. But I do wonder why speech should have enhanced the sharing of episodic memories any more than manual signing did, and whether this could really have brought about the dramatic changes associated with the human revolution.

Arbib suggests that it was the invention of syntax, not of autonomous speech, that occurred 50,000 years ago, and that presumably led to the subsequent chain of events in human cultural development. Certainly, the human revolution was dramatic, and syntax would have dramatically enhanced communication. Yet the idea that syntax was a cultural invention flies in the face of the arguments of Chomsky, Pinker, and others that syntax is an instinct, a biological rather than a cultural disposition. Arbib nevertheless proposes, much as Bickerton (1995) did, that the brain was "language-ready," so perhaps there is a fine line here between the biological and the cultural, although it is difficult to understand how the brain could have evolved to be ready for something as powerful as syntax before it is actually manifest. I can see that ears might be ready to hold glasses before those helpful devices were invented, but syntax seems too profound a capacity to be merely a spandrel. Pinker and Bloom (1990) have compellingly made the case that language, including syntax, evolved as a product of natural selection.

Although I do not think syntax was an invention, I argued that autonomous speech may have been an invention, inviting the same kind of criticism – although the step from the mixture of gesture and vocalization to autonomous speech is not nearly so dramatic as the step from protolanguage to

syntax. Since writing the target article, however, I have had cause to believe that the step to autonomous speech may not have been an invention, but may have been due rather to a genetic mutation.

R2.10. The FOXP2 gene (an update)

That mutation may have occurred on the *FOXP2* gene, located on chromosome 7. A genetic disorder of speech and language suffered by members of a large family, known as the KE family, is transmitted as an autosomal-dominant monogenic trait, encoded by a mutation on *FOXP2* (Lai et al. 2001). Some have argued that this gene is a grammar gene (e.g., Pinker 1994), but although those affected have difficulties with both receptive and expressive grammar, the core deficit is more likely one of articulation (Watkins et al. 2002). There is now evidence that the *FOXP2* gene underwent changes in our predecessors at some point subsequent to the split from the chimpanzee lines and probably within the past 100,000 years (Enard et al. 2002). Enard et al. write that their discovery "is compatible with a model in which the expansion of modern humans was driven by the appearance of a more-proficient spoken language" (p. 871). Perhaps, then, the mutation of the *FOXP2* gene was the final adjustment that allowed speech to become autonomous, freeing the hands, and unleashing, by whatever means, the human revolution.

Of course, this need not preclude the idea that there was an element of invention. Autonomous speech and the selection of the mutated *FOXP2* gene may perhaps be an example of Baldwinian evolution, a result of a human culture itself dependent on language.

R3. Handedness and cerebral asymmetry

R3.1. On the nature of handedness and cerebral asymmetry

Pedersen & Vereijken raise the question of whether handedness is a matter of preference or of performance, which they regard as "crucial." **Annett** and **McManus**, whose leads I have followed, differ with respect to this issue: Annett (1995) has argued that handedness is fundamentally continuous and a matter of performance, whereas **McManus** (1999) has argued that it is fundamentally dichotomous and a matter of preference. **Pedersen & Vereijken** cite evidence showing that initial preference can be modified through chance events in later development, so that performance differences are continuous.

Beaton does not see that the genetic theory I discussed differs in principle from those of **Annett** and **McManus**. Nor do I – in fact, I based my discussion mostly on a slightly modified version of **McManus's** theory. I therefore agree with **Beaton** that there is not much difference among these theories, but try telling that to either **McManus** or **Annett**. Differences are in the eye of the holder. **Beaton** also suggests that I implied that handedness was a categorical variable, but if this is so it was unintentional. In following **Annett** and **McManus**, I, too, recognize the random element in the determination of handedness.

Annett strangely complains that my article lacked a clear account of human individual differences, despite a whole section (sect. 5) on them. Perhaps the problem was that I focused on **McManus's** (1999) genetic model rather than

Annett's own right-shift theory, which she insists is different. Her commentary should rectify this. She also raises the question of whether there was a period in which all people were left-brained and right-handed, and whether a further mutation reintroduced variability in the form of a minority of right-brainers and left-handers. McManus (1999) has proposed precisely this scenario, which I personally find unlikely.

The genetic models of Annett and McManus also provide the answer to **Faurie & Raymond's** complaint that I ignored the polymorphism of handedness, and that I implied that handedness is a neutral character. Although I did not mention it explicitly, the assumption behind these two-allele models is that there is a heterozygotic advantage; in Annett's (1995) version, it is suggested that those with a double dose of the laterality allele might suffer some impairment in spatial skills, whereas those with a double dose of the "chance" allele might be susceptible to verbal impediments (see also Corballis 1997). These models imply selection based on cerebral asymmetry rather than on handedness per se. **Walker** suggests that strong lateralization may increase "susceptibility to unilateral capacity deficits," which might be another reason for the heterozygotic advantage.

There are alternatives to the idea of a heterozygotic advantage. There is some appeal in **Faurie & Raymond's** simpler hypothesis that left-handedness may confer an advantage in fighting, but only so long as left-handers are in the minority. Nevertheless, it may even be true that right-handedness itself is an adaptive trait in humans, and it has been claimed that left-handers die younger than right-handers do (Coren & Halpern 1991) – but see Harris (1993) for a critique. One possibility, considered by Coren and Halpern, is that right-handers, being in the majority, have created environments somewhat hostile to left-handers. Given only a slight majority of right-handers (perhaps the 2:1 majority noted in chimpanzees by **Hopkins & Cantalupo**), this could have led to runaway selection of right-handers as a product of increasing cultural evolution and environmental control, leading to the present-day 9:1 majority. This could be another example of Baldwinian evolution, but does not explain the initial preponderance of right-handers. And left-handers, finding themselves in a minority, may have developed a compensatory feistiness that helped preserve them – but only so long as they were a minority.

Pedersen & Vereijken question my statement that "handedness is a function of the brain rather than of the hands themselves" (target article, sect. 1, first para.). I do not think there is anything in the shape of the hands, or in their musculature or sensory receptors, that would lead one to predict that one hand would be better than the other at throwing, or at writing, say, although I concede that wear and tear, or extensive unimanual practice, may lead to peripheral differences. What I meant was that we are not like lobsters, where the claws are actually shaped for different functions, one a big "crusher" claw and the other a little "cutter" claw (Govind 1989).

Raz & Donchin revive the notion that left-handedness results from pathology, an idea that has rather fallen from grace, partly for empirical reasons (e.g., Harris & Carlson 1988), and partly because genetic models seem reasonably successful in accounting for most of the variation in handedness. Nevertheless, there is probably a small proportion of people who are left-handed as a result of pathology, and

I agree that the precise role of pathology in the determination of handedness has yet to be fully understood.

R3.2. What about the right hemisphere?

Code rightly chides me for neglecting right-hemispheric contributions to language. I do not of course consider the right hemisphere or the left hand to be useless appendages, and it is not surprising that they should adopt functions that complement those of their mirror partners. The dominant facts, so to speak, remain: The left hemisphere in most people is dominant for speech as an expression of propositional language, and the right hand is dominant in most manual activities. But because there is evidence from other species that the right hemisphere may be dominant for emotional expression, there is indeed some question as to whether this is a secondary consequence of a prior left-hemispheric dominance, or whether left-hemispheric dominance arises by default from a prior right-hemispheric dominance, as also suggested by **Bradshaw**. I do not know the answer to this, but it need not affect the argument that it was vocalization that gave the nudge to the left in the case of speech and handedness. Perhaps frogs feel with the right brain, and croak with the left.

Sommer & Kahn suggest that, because vocalization is largely emotional in nonhuman primates, it is more likely to be controlled by the right than by the left hemisphere. This runs counter to the evidence I reviewed in the target article, suggesting that left-hemispheric control of vocalization goes back to our common ancestry with the frog (Bauer 1993).

R3.3. The development of laterality

A number of authors emphasized development as a clue to the evolutionary sequence, again risking the perils of recapitulationism. Both **Corbetta** and **Rönnqvist** provide evidence that motor asymmetries are manifest very early in development, and have been recorded even in fetal activity. They suggest that manual asymmetry develops before vocal asymmetry, with the implication that it may also have evolved earlier. Yet, orofacial movements favoring the right side of the mouth are present not only in adult speech (Graves & Potter 1988), but also in the babbling of five-month-old babies (Holowka & Petitto 2002), and fMRI recording has shown left-hemispheric activation, similar to that in adults, in response to both normal and backward speech in three-month-old infants (Dehaene-Lambertz et al. 2002). It has also long been known that the asymmetry of the temporal planum, a language-mediating area, is present in neonates (Witelson & Pallie 1973), and even as early as the 29th week of gestation (Wada et al. 1975).

Michel presents data suggesting that the incidence of right-handedness in infancy is less than that shown later in life – although, as he also points out, the incidence can vary widely depending on how handedness is defined. **Pedersen & Vereijken** point out further that lateral preferences fluctuate in infancy, only later stabilizing. They suggest that this is because practice tends to stabilize earlier probabilistic biases, although it is not clear how practice could lead to a higher incidence of lateral preference than that initially present. An alternative view is that the early trend to right-handedness is augmented later in childhood by the increasing dominance of vocal language over gestures.

Armstrong makes the very useful point that hand preference appears in signing before it does in object manipulation in young children. If this is paralleled in evolution, it supports my view that the origins of handedness are to be found in the evolution of language, rather than of tool use.

R3.4. Handedness and cerebral dominance: Are they correlated?

A theme common to several commentaries was that handedness and cerebral dominance for speech are not perfectly coupled (**Hopkins & Cantalupo, Jürgens, Raz & Donchin, Sommer & Kahn**). The strongest statement was that of **Josse & Tzourio-Mazoyer**, who claim that functional-imaging studies reveal no correlation. This claim appears to be based on right-handers only, because the authors concede that right-handers are more likely to be left-dominant for language than are left-handers. This might be taken as evidence that asymmetry operates as a kind of on-off switch, as proposed by McManus (1999), rather than as a gradient-like influence. It is well established that some 70% of left-handers are left-hemisphere dominant for speech, whereas the figure for right-handers is probably close to 99%, and variations in the degree of handedness and cerebral dominance within right-handers might well be because of a multitude of environmental influences, such as practice, pathology, culture, and so forth.

Yet, some studies do show a correlation suggestive of a more graded influence (e.g., **Knecht et al. 2000**), and it may well be that functional imaging does not provide reliable measures of degree of lateralization. But in any case it would be obviously wrong to assert that handedness is fully determined by speech dominance. Rather, the relation is likely to be probabilistic, a nudge rather than a push. I tried to deal with this in terms of the notion that the relation between handedness and cerebral dominance might depend on a genetic locus, such that one allele leads to right-handedness and left-cerebral dominance, essentially tying the two together, whereas the other leaves both asymmetries to chance. This notion has been elaborated in different ways by **Annett (1995)** and **McManus (1999)**. The additional suggestion of my own that the default condition, in the absence of the laterality allele, might be a 2:1 bias rather than 50–50 chance might explain why the proportion of left-handers with left-cerebral dominance is around 70%, and why this figure also characterizes a number of other human and animal asymmetries (**Corballis 1997**). We revert to the 2:1 bias when kissing (**Güntürkün 2003**). **Jones & Martin** suggest some interesting variants on the genetics of handedness, including the possibility of X-linkage, which I have discussed elsewhere (**Corballis 2001**).

R3.5. Is there a functional link between speech and the hand motor area?

Whatever the nature of the correlation between handedness and speech dominance, there is evidence for a functional link, at least in right-handers. I cited the evidence of **Kimura (1993a)** that hand gestures during speech are predominantly right-handed, at least in right-handers. There is also evidence that the left motor hand area is activated during reading aloud, but not during the production of non-speech sounds (**Seyal et al. 1999; Tokimura et al. 1996**), and the leg area of the motor cortex, unlike the hand area, is not

affected by reading aloud (**Meister et al. 2003**). Silent reading appears to have no influence on the hand motor area, suggesting that the link has to do with overt speech, and not with reading per se (**Tokimura et al. 1996**). **Meister et al. (2003)** suggest that these effects are because of “phylogenetically old links between motor hand and language areas” (p. 405), consistent with the gestural theory of language origins, although they do not explain why it was the left hemisphere that dominated. These studies seem to contradict the evidence summarized by **Breitenstein, Floel, Drager, & Knecht (Breitenstein et al.)** that linguistic tasks excite the motor cortices for both hands – although, as **Breitenstein et al.** point out, this evidence does at least support the gestural theory.

R3.6. When did consistent lateralization emerge in evolution?

The question of when species-level right-handedness emerged in primate or hominid evolution remains controversial, as I indicated. **Beaton** suggests that it may have arisen in the earliest hominids with bipedalism, and **Corbetta** and **Pedersen & Vereijken** cite evidence that the incidence of right-handedness increases in some species of primates, including capuchin monkeys and chimpanzees, when they operate from a bipedal posture than from a quadrupedal posture. Consistent handedness in nonhuman primates still seems largely restricted to laboratory studies, and appears to be seldom, if ever, recorded among primates in the wild. **Pedersen & Vereijken** reiterate the point that the right-handedness of captive chimps may have been inadvertently shaped by humans, but this is vigorously disputed by **Hopkins & Cantalupo**. In any event, the incidence of right-handedness is markedly higher among humans than among other primates, so that it is possible, as I suggested both in the target article and elsewhere (**Corballis 1997**), that what is unique to humans is not right-handedness per se, but the jump from around 67% to 90% right-handedness – and **Hopkins & Cantalupo** affirm that the asymmetry in chimpanzees is about 2:1, not about 9:1, as in humans. Despite remaining questions over species-level handedness in primates, **Annett** avows that it is the divergence of humans from apes, with respect to both handedness and speech, which stands out. I think this is probably right, despite the growing swirl of evidence about asymmetries in nonhuman species.

Corbetta also cites indirect evidence that human handedness may go back some 2.6 million years to the oldest prehistoric tools. This implies, she suggests, that handedness may have evolved before lateralized vocal control. However, this ignores that ole croaking frog (**Bauer 1993**), not to mention the evidence I cited on lateralization of vocal production and perception in birds, mice, rats, marmosets, and monkeys – although see **Jürgens** for his critical comments. Although I think that syntactic language probably did not begin to emerge until the appearance of the genus *Homo*, when brain size began its spectacular increase, this need not mean that vocalization had not already begun to be incorporated into the protolanguage that earlier hominids had begun to develop. Hence, the nudge to left-cerebral dominance, and right-handedness, might have begun earlier than two million years ago.

Hopkins & Cantalupo present intriguing evidence for correlation between handedness and the asymmetry of

BA44 (the Broca's area analog) in the chimpanzee, suggesting that the link may go back at least five million years. If true, this certainly stretches the argument that the asymmetry came from lateralized control of vocalization, although it perhaps does not rule it out. Hopkins & Cantalupo's data raise the possibility again that there was a pre-existing tendency to right-handedness in the great apes, perhaps related to limited vocal control, but that the critical jump that raised the incidence of right-handedness from 70% to about 90%, and that led to the eventual appearance of speech, occurred after the ape-hominid split.

In any event, **Holloway** questions the claim by Cantalupo & Hopkins (2001) that BA44 is larger on the left than on the right in a majority of great apes, stating that their MRI evidence is not supported by cytoarchitectonic evidence. Nevertheless, I remain bemused by the claim that the asymmetry of the planum temporale in apes is higher than it is in humans, and well above 90% (Gannon et al. 1998). I was surprised that this was not mentioned by Holloway, given that he was one of the authors, but his opinion that the asymmetry of Broca's area is less marked in apes than in humans comes as something of a relief. **Walker** argues quite persuasively that human functional lateralization has nothing to do with structural asymmetries, and suggests that this is probably true of structural asymmetries in the brains of great apes as well. If true, this nicely lets me off one or two hooks.

Sommer & Kahn suggest that left-hemispheric specialization could have come about through duplication of a gene, so that the redundant copy is free to mutate. The left hemisphere was the benefactor, at least if language is considered a blessing. They go on to suggest that the critical gene may have been the *FOXP2* gene, discussed earlier in this Response. If Enard et al. (2002) are correct in their estimate of when the critical mutation occurred, this would suggest that cerebral lateralization for language functions, and perhaps language itself, emerged within the last 100,000 years. I am doubtful, however, as to whether *FOXP2* is really the gene postulated by Annett (1995) or McManus (1985a) – or whether the mutation was really the “big bang” proposed by Bickerton (1995) or Crow (1998). Nevertheless, *FOXP2* seems certain to feature prominently in evolutionary theories about the evolution of language.

R3.7. Could handedness derive from lateralized vocal control?

Knight does not see why lateralized control over vocalization should influence handedness if the hands are no longer critical to communication. I tried to argue, though, that there must have been a considerable period of overlap, in which language consisted of both vocal and manual gestures. Indeed, it still does, although vocal gestures now dominate.

Jürgens questions the evidence that vocalization is left-hemispheric in other species. He also suggests that evidence from frogs and birds is irrelevant, because they differ markedly in anatomy from mammals. True, although if vocalization is largely subcortical in mammals (including primates), then evidence from species with whom we share an ancient common ancestor may not be altogether irrelevant. Subcortically, perhaps our so-called reptilian brain is not really so different from a frog brain (well, in some of us, anyway) – see MacLean (1980). Moreover, Ploog (2003)

traces the evolution of vocal signaling systems to the frog (or more accurately, the common ancestor of primates and frogs), but sadly does not accept the theory that language (as distinct from communication) originated in manual gestures.

Raz & Donchin also point out that lateralization in birds is determined by the eye that is first opened, although I am not sure that this applies to the lateralization of birdsong in passerine birds – and also, in response to Raz & Donchin, I am not sure that other manifestations of lateralization are relevant to my hypothesis. I do think that we need more evidence on the nature and lateralization of vocalization, and I thank **Jürgens** for referring me to his own work in which there is no evidence of overall left-sided control of the vocal folds in squirrel monkeys (Jürgens & Zwirner 2000). I shall be interested to know whether further research also fails to show consistent lateralization of vocal control in primates.

Cook suggests that I have the causal chain backwards, but actually I find myself mostly in agreement with his commentary. He suggests that the progression of lateralization was from animal vocalizations to speech asymmetry to handedness, but that my proposal runs from manual gestures to speech asymmetry to handedness. But in fact I also traced the origins of handedness to lateralized vocal control. Where we differ, I suspect, is in how lateralized motor control eventually spilled over into other asymmetries, such as handedness and footedness. His view, I think, is that this occurred with the executive control required for speech, whereas I proposed that the mediating factor was gestural language. But let's not go over that again.

R3.8. Alternative explanations for lateralization

A number of authors suggested alternative ideas as to why lateralization might have evolved. Perhaps the most esoteric was that of **Knight**, who avowed that the secret of lateralization is trust. This smacks a little too much of hemispheric personification for me to go along with it entirely, but I think it does again conform to the notion that human language is fundamentally different from other kinds of animal communication. Following Passingham (1981), **Cook** argues that hemispheric lateralization was necessary for the control of speech because the organs of speech are midline structures. **Fouts & Waters** suggest similarly but more specifically that the secret of lateralization lies in the tongue, and that because the tongue is a medial organ, lateralized control was necessary to eliminate the possibility of interhemispheric conflict. **Wolpert** thinks that asymmetry may have evolved in the context of complex motor skills such as toolmaking because it permits cooperation rather than competition between the hemispheres. **Gillett** seems to suggest that the left-hemispheric advantage for rapid acoustic processing may have led to left-hemispheric dominance for speech as well as right-handedness, and **Rönnqvist** and **Wolpert** (now on a different tack) note Calvin's theory that the left-hemispheric dominance for speech may have been built on circuits established by throwing – a predominantly right-handed activity – thereby reversing the direction of causality that I proposed. **Raz & Donchin** also note a suggestion by Skoyles (2000) that communicative gestures might be more easily learned and comprehended if performed with a single hand. I am doubtful about this last suggestion. Would a one-armed gesturer communicate

more adequately than a two-armed one? Would sign language work better if gesturers tied one arm behind their backs?

There may well be truth to some of these ideas, and in section 6 of the target article I wrote that “it is probably more efficient to have brain mechanisms programmed within a cerebral hemisphere than to have them spread between the hemispheres.” I have elaborated on this elsewhere in ways similar to those suggested by the commentaries; for example, I argued that lateralization might have evolved to overcome interhemispheric competition, and create an “executive” in the left hemisphere (Corballis 1991; see also Gazzaniga 2000). But these various accounts do not explain why the asymmetry is in the same direction in the great majority of humans. Perhaps the advantage of a consistent directional bias is simply that it serves to guarantee the asymmetry, rather than just leaving it to chance – although the genetic models discussed earlier include a chance component anyway, as I think they must. In any event, my aim was simply to suggest that it might have been a prior left-hemispheric control over vocalization that determined the direction of subsequent asymmetries, including that of language and handedness. The advantages of asymmetry itself may be multiple, but must always be weighed against the advantages of symmetry.

Of course, it may well be the case that handedness and the left-cerebral dominance for speech reflect “separate abilities” (Hopkins & Cantalupo) and that their shared dependence on the left hemisphere is just “an interesting coincidence” (Fouts & Waters), but I do not really think so. In any case, I think it is still worth trying to find a commonality, even if my specific hypothesis as to its origin is wrong.

R4. Conclusion

One way to disabuse oneself of a silly theory, I have been told, is to submit it to *BBS*. I am at least confident that the commentaries have added immeasurably to the original article, and given us all a lot more to think about. I remain reasonably secure about the gestural theory itself – but then I would, wouldn't I, given that I have invested quite a lot of effort into promulgating it. All I can really say to doubters is, try it on for a while. You may find it fits.

I also think it likely, despite the doubts of some commentators, that there is indeed a link between handedness and the left-cerebral control of speech, and the balance of evidence still seems to me to support the idea that it was an asymmetry in the control of the organs of speech that provided the nudge. Whether this asymmetry originated in the lateralized control of vocalization itself, and whether it has ancient roots, now seem more problematic. I think we need more evidence about the control of vocalization, from both evolutionary and neurological perspectives.

Finally, it was nice to have the posthumous support of Wittgenstein, as least as interpreted by Gillett, as well as Dickins's suggestion that my theorizing is reminiscent of Darwin. With this kind of backing I was tempted not to reply to the other commentaries at all. Dickins also suggested that my theory was unfalsifiable, but this view was evidently not shared. Indeed, I think all of the commentators for their elaborations and critical comments, and for generally entering into the spirit of the game.

References

Letters “a” and “r” appearing before authors' initials refer to target article and response, respectively.

- Aboitiz, F. & Garcia, R. (1997) The evolutionary origin of the language areas in the human brain. A neuroanatomical perspective. *Brain Research Reviews* 25:381–96. [GJ]
- Acredolo, L., Goodwyn, S., Horobin, K. & Emmons, Y. (1999) The signs and sounds of early language development. In: *Child psychology: A handbook of contemporary issues*, ed. L. Balter & C. Tamis-LeMonda. Psychology Press. [rMCC]
- Aggleton, J. P., Kentridge, R. W. & Neave, N. J. (1993) Evidence for longevity differences between left handed and right handed men: An archival study of cricketers. *Journal of Epidemiology and Community Health* 47:206–209. [CF]
- Altmann, G. (1997) *The ascent of Babel*. Oxford University Press. [GRG]
- Amunts, K., Schleiger, A., Bürgel, U., Mohlberg, H., Uylings, H. B. M. & Zilles, K. (1999) Broca's area revisited: Cytoarchitecture and intersubject variability. *Journal of Comparative Neurology* 412:319–41. [aMCC]
- Ananthaswamy, A. (2003) Has this chimpanzee taught himself to talk? *New Scientist* 177 (2376):12. [rMCC]
- Annett, M. (1970) A classification of hand preference by association analysis. *British Journal of Psychology* 61:303–21. [AAB]
- (1975) Hand preference and the laterality of cerebral speech. *Cortex* 11:305–28. [MA]
- (1987a) Handedness as chance or as species characteristic. *Behavioral and Brain Sciences* 10:263–64. [CF]
- (1987b) Implications of the right shift theory of handedness for individual differences in hemisphere specialisation. In: *Individual differences in hemispheric specialization*. NATO ASI Series A: Life sciences, vol. 130, ed. A. Glass. Plenum Press. [AR]
- (1992) Parallels between asymmetries of *planum temporale* and of hand skill. *Neuropsychologia* 30:951–62. [AAB]
- (1995) The right shift theory of a genetically balanced polymorphism for cerebral dominance and cognitive processing. *Current Psychology of Cognition* 14:427–80. [arMCC]
- (2002) *Handedness and brain asymmetry: The right shift theory*. Psychology Press. [MA]
- Annett, M. & Alexander, M. P. (1996) Atypical cerebral dominance: Predictions and tests of the right shift theory. *Neuropsychologia* 34:1215–27. [MA]
- Arbib, M. A. (2002) The mirror system, imitation, and the evolution of language. In: *Imitation in animals and artifacts*, ed. C. Nehaniv & K. Dautenhahn. MIT Press. [MAA, rMCC, AR]
- (2003a) Language evolution: The mirror system hypothesis. In: *The handbook of brain theory and neural networks*, ed. M. A. Arbib. MIT Press. [RD]
- (2003b) Review of Stokoe (2001), *Language in hand: Why sign came before speech*. *Journal of Linguistics* (in press). [MAA]
- (submitted) Beyond the mirror system: From monkey-like action recognition to human language. [CC]
- Arbib, M. A. & Rizzolatti, G. (1997) Neural expectations: A possible evolutionary path from manual skills to language. *Communication and Cognition* 29:393–424. [rMCC, AR]
- Arcadi, A. C. (1996) Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. *American Journal of Primatology* 39:159–78. [ACA, aMCC]
- (2000) Vocal responsiveness in male wild chimpanzees: Implications for the evolution of language. *Journal of Human Evolution* 39:205–23. [ACA]
- Arcadi, A. Clark, Robert, D. & Boesch, C. (1998) Buttress drumming by wild chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates* 39(4):503–16. [ACA]
- Archer, J., ed. (1994) *Male violence*. Routledge. [CF]
- Armstrong, D. F. (1999) *Original signs: Gesture, sign, and the source of language*. Gallaudet University Press. [DFA, aMCC]
- Armstrong, D. F. & Katz, S. H. (1983) Brain laterality in signed and spoken language: Neural factors in the evolution of linguistic behavior. In: *Glossogenesis. The origin and evolution of language*, ed. E. de Grolier. [CK]
- Armstrong, D. F., Stokoe, W. C. & Wilcox, S. E. (1995) *Gesture and the nature of language*. Cambridge University Press. [DFA, arMCC, AC-M, RSF, AR, BW]
- Atkinson, J. R., Campbell, R., Marshall, J., Thacker, A. & Woll, B. (in press) Understanding “not”: Neuropsychological dissociations between hand and head markers of negation in BSL. *Neuropsychologia*. [BW]
- Babkin, P. S. (1960) The establishment of reflex activity in postnatal life. In: *Central nervous system and behavior* [English trans. from *Fiziologii Zhurnal*, USSR, 1953, pp. 922–27]. Russian Scientific Translation Program, National Institutes of Health. [JMI]

- Baldwin, D. A. (1995) Understanding the link between joint attention and language. In: *Joint attention: Its origins and role in development*, ed. C. Moore & P. J. Dunham. Erlbaum. [DAL]
- Bard, K. A. (1992) Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development* 62:1186–97. [DAL]
- Barsalou, L. (1999) Perceptual symbol systems. *Behavioral and Brain Sciences* 22:577–660. [RD]
- Bates, E. & Dick, F. (2002) Language, gesture, and the developing brain. *Developmental Psychobiology* 40:293–310. [AR]
- Bates, E., O'Connell, B., Vaid, J., Sledge, Paul & Oakes, L. (1986) Language and hand preference in early development. *Developmental Neuropsychology* 2:1–15. [JMI]
- Bauer, R. H. (1993) Lateralization of neural control for vocalization by the frog (*Rana pipiens*). *Psychobiology* 21:243–48. [arMCC, UJ]
- Beaton, A. A. (1997) The relation of *planum temporale* asymmetry and morphology of the *corpus callosum* to handedness, gender, and dyslexia: A review of the evidence. *Brain and Language* 60:255–322. [AAB]
- (2003) The nature and determinants of handedness. In: *The asymmetrical brain*, ed. K. Hugdahl & R. J. Davidson. MIT Press. [AAB]
- Beattie, G. & Shovelton, H. (2002) What properties of talk are associated with the generation of spontaneous iconic hand gestures? *British Journal of Social Psychology* 41:403–17. [PF]
- Bermúdez de Castro, J. M., Bromage, T. G. & Fernández Jalvo, Y. (1988) Buccal striations on fossil human anterior teeth: Evidence of handedness in the middle and early Upper Pleistocene. *Journal of Human Evolution* 17:403–12. [CF]
- Best, C. T. (1988) The emergence of cerebral asymmetries in early human development: A literature review and a neuroembryological model. In: *Brain lateralization in children*, ed. D. L. Molfese & S. J. Segalowitz. Guilford Press. [LR]
- Bickerton, D. E. (1995) *Language and human behavior*. University of Washington Press. [MAA, arMCC]
- (2002) From protolanguage to language. In: *The speciation of modern Homo Sapiens*, ed. T. J. Crow. Oxford University Press. [rMCC]
- Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G. & Freund, H. (1999a) A fronto-parietal circuit for object manipulation in man: Evidence from an fMRI-study. *European Journal of Neuroscience* 11:3276–86. [SHJ-F]
- Binkofski, F., Classen, J. & Benecke, R. (1999b) Stimulation of peripheral nerves using a novel magnetic coil. *Muscle and Nerve* 22:751–57. [SHJ-F]
- Bisazza, A., Roger, L. J. & Vallortigara, G. (1998) The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, amphibians, and reptiles. *Neuroscience and Biobehavioral Reviews* 22:411–26. [LR]
- Bischoff-Grethe, A., Proper S. M., Mao H., Daniels K. A. & Berns G. S. (2000) Conscious and unconscious processing of nonverbal predictability in Wernicke's area. *Journal of Neuroscience* 20:1975–81. [RSF]
- Bodamer, M. D. & Gardner, R. A. (2002) How cross-fostered chimpanzees (*Pan troglodytes*) initiate and maintain conversations. *Journal of Comparative Psychology* 116:12–26. [SFW]
- Boesch, C. (1991) Handedness in wild chimpanzees. *International Journal of Primatology* 12:541–58. [WDH]
- Bonvillian, J. D., Orlansky, M. D. & Garland, J. B. (1982) Handedness patterns in deaf persons. *Brain and Cognition* 1:141–57. [AR]
- Bonvillian, J. D. & Richards H. C. (1993) The development of hand preference in children's early signing. *Sign Language Studies* 78:1–14. [DFA]
- Bookheimer, S. (2002) Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience* 25:151–88. [IECS]
- Bradshaw, J. L. & Mattingley, J. B. (2001) A sensory analogue of motor mirror neurones in a hyperaesthetic patient reporting instantaneous discomfort to another's perceived sudden minor injury? *Journal of Neurology, Neurosurgery and Psychiatry* 70:135–36. [JLB]
- Bradshaw, J. L. & Rogers, L. J. (1993) *The evolution of lateral asymmetries, language, tool use, and intellect*. Academic Press. [MA, aMCC, LR]
- Brain, R. (1945) Speech and handedness. *Lancet* 249:837–41. [aMCC, NDC]
- Braver, T. S. & Bongiolatti, S. R. (2002) The role of frontopolar cortex in subgoal processing during working memory. *Neuroimage* 15:523–36. [CJ]
- Breitenstein, C. & Knecht, S. (2003) Spracherwerb und statistisches Lernen (Language acquisition and statistical learning). *Nervenarzt* 74:133–43. [CB]
- Bresson, F., Maury, L., Pierot-Le Bonniec, G. & de Schonen, S. (1977) Organization and lateralization of reaching in infants: An instance of asymmetric functions in hands collaboration. *Neuropsychologia* 15:311–20. [JMI]
- Bridges, P. S. (1996) Skeletal biology and behavior in ancient humans. *Evolutionary Anthropology* 4:112–20. [CF]
- Broadfield, D. C., Holloway, R. L., Mowbray, K., Silvers, A., Yuan, M. S. & Marquez, S. (2001) Endocast of Sambungmacan 3 (Sm3): A new *Homo erectus* from Indonesia. *The Anatomical Record* 262:369–79. [RLH]
- Broca, P. (1861a) Perte de la parole, ramollissement chronique et destruction partielle du lobe antérieur gauche du cerveau. *Bulletin de la Société de Anthropologie, Paris* 2:235–38. [CJ]
- (1861b) Remarques sur la siège de la faculté du langage articulé, suivie d'une observation d'aphémie. *Bulletin de la Société Anatomique de Paris* 2:330–57. [AAB, aMCC]
- (1865) Sur la siège de la faculté du langage articulé. *Bulletins de la Société d'Anthropologie de Paris* 6:377–93. [AAB, aMCC]
- Browman, C. & Goldstein, L. (1991) Gestural structures: Distinctiveness, phonological processes, and historical change. In: *Modularity and the motor theory of speech perception*, ed. I. G. Mattingly & M. Studdert-Kennedy. Erlbaum. [aMCC]
- Bruckner, M., D'Eustachio, P. & Horwich, A. L. (1989) Linkage mapping of a mouse gene, IV, that controls left-right asymmetry of the heart and viscera. *Proceedings of the National Academy of Sciences USA* 86:5035–38. [aMCC]
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H. T., Likius, A., Ahountas, D., Beauvillain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., De Bonis, L., Coppens, Y., Dejax, J., Denys, C., Düringer, P., Eisenmann, V., Fonone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P. P., De Leon, M., Rasse, J.-C., Sapanet, M., Schuster, M., Sufre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A. & Zollikofer, C. (2002) A new hominid from the upper miocene of Chad, Central Africa. *Nature* 418:145–51. [AAB]
- Bryden, M. & Steenhuis, R. E. (1991) Issues in the assessment of handedness. In: *Cerebral laterality: Theory and research*, ed. F. L. Kitterle. Erlbaum. [GFM]
- Bub, D. N. (2000) Methodological issues confronting PET and fMRI studies of cognitive function. *Cognitive Neuropsychology* 17:467–84. [AAB]
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G. & Freund, H. J. (2001) Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience* 13:400–404. [SHJ-F]
- Butterworth, G. (2001) Joint visual attention in infancy. In: *Blackwell handbook of infancy research*, ed. J. G. Bremner & A. Fogel. Blackwell. [DAL]
- Butterworth, G. & Hopkins, B. (1988) Hand-mouth coordination in the new-born baby. *British Journal of Developmental Psychology* 6:303–13. [JMI]
- Buxhoeveden, D. & Casanova, M. (2000) Comparative lateralisation patterns in the language area of human, chimpanzee, and rhesus monkey brains. *Laterality* 4:315–30. [aMCC]
- Byrne, R. W. & Byrne, J. M. (1991) Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla-G-Berengei*). *Cortex* 27:521–46. [aMCC, WDH]
- Cain, D. P. & Wada, J. A. (1979) An anatomical asymmetry in the baboon brain. *Brain, Behavior and Evolution* 16:222–26. [SFW]
- Call, J. & Tomasello, M. (1994) Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology* 108:307–17. [DAL]
- Calvert, G. A. & Campbell, R. (2003) Reading speech from still and moving faces: The neural substrates of visible speech. *Journal of Cognitive Neuroscience* 15:57–70. [rMCC]
- Calvin, W. H. (1982) Did throwing stones shape hominid brain evolution? *Ethology and Sociobiology* 3:115–24. [CF]
- (1983a) A stone's throw and its launch window: Timing precision and its implications for language and hominid brains. *Journal of Theoretical Biology* 104:121–35. [AAB, CF]
- (1983b) *The throwing Madonna: Essays on the brain*. McGrawHill. [LR]
- (1987) On evolutionary expectations of symmetry and toolmaking. *Behavioral and Brain Sciences* 10(2):267. [CF]
- (1993) The unitary hypothesis: A common neural circuitry for novel manipulations, language, plan-ahead, and throwing? In: *Tools, language and cognition in human evolution*, ed. K. R. Gibson & T. Ingold. Cambridge University Press. [CF, LW]
- Cantalupo, C. & Hopkins, W. D. (2001) Asymmetric Broca's area in great apes. *Nature* 414:505. [arMCC, RSF, WDH, RLH]
- Capirci, O., Iverson, J., Pizzuto, E. & Volterra, V. (1996) Communicative gestures and the transition to two-word speech. *Journal of Child Language* 23:645–73. [PF]
- Carlson, D. F. & Harris, L. J. (1985) Development of the infant's hand preference for visually directed reaching: Preliminary report of a longitudinal study. *Infant Mental Health Journal* 6:158–72. [DC]
- Carstairs-McCarthy, A. (1996) Review of Armstrong et al. (1995). *Lingua* 99:135–38. [AC-M]
- (1999) *The origins of complex language*. Oxford University Press. [aMCC, AC-M]
- Chaminade, T., Meltzoff, A. N. & Decety, J. (2002) Does the end justify the

- means? A PET exploration of the mechanisms involved in human imitation. *Neuroimage* 15:318–28. [GJ]
- Chao, L. L. & Martin, A. (2000) Representation of manipulable man-made objects in the dorsal stream. *Neuroimage* 12:478–84. [SHJ-F]
- Chomsky, N. (1965) *Aspects of the theory of syntax*. MIT Press. [CK]
- (1966) *Cartesian linguistics: A chapter in the history of rational thought*. Harper and Row. [rMCC]
- (1988) *Language and the problem of knowledge: The Managua lectures*. MIT Press. [aMCC]
- (1995) *The minimalist programme*. MIT Press. [CK]
- (2000) Language as a natural object. In: *New horizons in the study of language and mind*, ed. N. Chomsky. Cambridge University Press. [aMCC]
- (2002) *On nature and language*. Cambridge University Press. [CK]
- Christian, J. M. (1977) Moosehide processing. In: *The individual in Northern Dene thought and communication: A study in sharing and diversity*, ed. J. M. Christian & P. M. Gardner. National Museums of Canada. [TMP]
- Christiansen, M. H., Dale, R., Ellefson, M. & Conway, C. M. (2001) The role of sequential learning in language evolution: Computational and experimental studies. In: *Simulating the evolution of language*, ed. A. Cangelosi & D. Parisi. Springer-Verlag. [RD]
- Cobb, K., Goodwin, R. & Saelens, E. (1966) Spontaneous hand positions of newborn infants. *Journal of Genetic Psychology* 108:225–37. [AVP]
- Cobo-Lewis, A. B., Oller, D. K., Lynch, M. P. & Levine, S. L. (1996) Relations of motor and vocal milestones in typically developing infants and infants with Down syndrome. *American Journal of Mental Retardation* 100:456–67. [JMI]
- Code, C. (1994) Speech automatism production in aphasia. *Journal of Neurolinguistics* 8:135–48. [CC]
- (1996) Speech from the right hemisphere? Left hemispherectomy cases E. C. and N. F. In: *Classic cases in neuropsychology*, ed. C. Code, C.-W. Wallesch, Y. Joannette & A.-R. Lecours. Psychology Press. [CC]
- (1997) Can the right hemisphere speak? *Brain and Language* 57:38–59. [CC]
- Conway, C. M. & Christiansen, M. H. (2001) Sequential learning in non-human primates. *Trends in Cognitive Sciences* 5:539–46. [RD]
- Cook, N. D. (2002) *Tone of voice and mind*. John Benjamins. [NDC]
- Cooper, D. N. (1999) Human gene evolution. In: *Evolution of the human genome*, ed. D. N. Cooper, S. E. Humphries & T. Strachan. BIOS Scientific. [IECS]
- Corballis, M. C. (1991) *The lopsided ape*. Oxford University Press. [arMCC]
- (1992) On the evolution of language and generativity. *Cognition* 44:197–226. [aMCC]
- (1997) The genetics and evolution of handedness. *Psychological Review* 104:714–27. [arMCC, GVJ]
- (1998a) Cerebral asymmetry: Motoring on. *Trends in Cognitive Sciences* 4:152–57. [AR]
- (1998b) Evolution of language and laterality: A gradual descent? *Cahiers de Psychologie Cognitive/Current Psychology of Cognition* 17:1148–55. [AR]
- (1999) The gestural origins of language. *American Scientist* 87(March–April):138–45. [aMCC]
- (2001) Is the handedness gene on the X chromosome? Comment on Jones and Martin (2000). *Psychological Review* 108:805–10. [rMCC, GVJ]
- (2002) *From hand to mouth: The origins of language*. Princeton University Press. [MAA, JLB, arMCC, AR]
- Corballis, M. C. & Beale, I. L. (1976) *The psychology of left and right*. Erlbaum. [rMCC]
- Corbetta, D. (2001) Dynamic interaction between posture, laterality, and bimanual coordination in human infants: Why stone knapping might be a uniquely hominid behavior. In: *Knapping stone: A uniquely hominid behavior?*, ed. V. Roux & B. Brill. McDonald Institute for Archaeological Research/ Cambridge University Press. [DC]
- Corbetta, D. & Bojczyk, K. G. (2002) Infants return to two-handed reaching when they are learning to walk. *Journal of Motor Behavior* 34:83–95. [DC]
- Corbetta, D. & Thelen, E. (1999) Lateral biases and fluctuations in infants' spontaneous arm movements and reaching. *Developmental Psychobiology* 34:237–55. [DC, AVP]
- (2002) Behavioral fluctuations and the development of manual asymmetries in infancy: Contributions of the dynamic systems approach. In: *Handbook of Neuropsychology, vol. 8: Child Neuropsychology*, ed. S. J. Segalowitz & I. Rapin. Elsevier Science. [DC]
- Coren, S. (1989) Southpaws – somewhat scrawnier. *Journal of the American Medical Association* 17:2682–83. [CF]
- (1996) Pathological causes and consequences of left-handedness. In: *Manual asymmetries in motor performance*, ed. E. Digby & E. A. Roy. CRC Press. [AR]
- Coren, S. & Halpern, D. F. (1991) Left-handedness: A marker for decreased survival fitness. *Psychological Bulletin* 109:90–106. [rMCC, CF]
- Coren, S. & Searleman, A. (1987) Left sidedness and sleep difficulty: The alinormal syndrome. *Brain and Cognition* 6:184–92. [AR]
- Corina, D. P., Bellugi, U. & Reilly, J. S. (1999) Neuropsychological studies of linguistic and affective facial expressions in deaf signers. *Language and Speech* 42:307–31. [BW]
- Corina, D. P., Poizner, H., Bellugi, U., Feinberg, T., Dowd, D. & O'Grady-Batch, L. (1992) Dissociation between linguistic and nonlinguistic gestural systems: A case for compositionality. *Brain and Language* 43:414–47. [BW]
- Cornish, K. M., Pigram, J. & Shaw, K. (1997) Do anomalies of handedness exist in children with Fragile-X syndrome? *Laterality* 2:91–101. [aMCC]
- Coulter, G., ed. (1993) *Phonetics and phonology, vol. 3: Current issues in sign language phonology*. Academic Press. [PFM]
- Cowell, S. F., Egan, G. F., Code, C., Harasty, J. & Watson, J. (2000) The functional neuroanatomy of simple calculation and number repetition: A parametric PET activation study. *NeuroImage* 12:565–73. [CC]
- Crow, T., ed. (2002) *The speciation of modern Homo sapiens*. British Academy, London. [NDC]
- Crow, T. J. (1993) Sexual selection, Machiavellian intelligence, and the origins of psychosis. *Lancet* 342:594–98. [aMCC]
- (1997) Schizophrenia as a failure of hemispheric dominance for language. *Trends in Neurosciences* 20:339–43. [MA]
- (1998) Sexual selection, timing and the descent of man: A theory of the genetic origins of language. *Current Psychology of Cognition* 17:1237–77. [arMCC, AR]
- Crystal, D. (1997) *The Cambridge encyclopedia of language*, 2nd edition. Cambridge University Press. [aMCC]
- Dagher, A., Owen, A. M., Boecker, H. & Brooks, D. J. (1999) Mapping the network for planning: A correlational PET activation study with the Tower of London task. *Brain* 122:1973–87. [GJ]
- Daly, M. & Wilson, M. (1989) *Homicide*. Aldine. [CF]
- Daniel, W. F. & Yeo, R. A. (1994) Accident proneness and handedness. *Biological Psychiatry* 35:499. [CF]
- Darwin, C. (1889/1998) *The expression of the emotions in man and animals*. Oxford University Press. [RSF]
- (1904) *The expression of the emotions in man and animals*, second edition. John Murray. [aMCC]
- Dassonville, P., Zhu, X. H., Ugurbil, K., Kim, S. G. & Ashe, J. (1998) Neurobiology – Functional activation in motor cortex reflects the direction and the degree of handedness. *Proceedings of the National Academy of Science of the United States of America* 95:11499. [GJ]
- Deacon, T. (1997) *The symbolic species*. Allen Lane/The Penguin Press. [arMCC]
- de Condillac, B. (1746/1947) *Essai sur l'origine des connaissances humaines, ouvrage ou l'on a seul principe tout ce concerne l'entendement*. In: *Oeuvres philosophiques de Condillac*. Georges LeRoy. [AR]
- DeGusta, D., Gilbert, W. H. & Turner, S. P. (1999) Hypoglossal canal size and hominid speech. *Proceedings of the National Academy of Sciences* 96:1800–1804. [JLB, RLH]
- Dehaene-Lambertz, G., Dehaene, S. & Hertz-Pannier, L. (2002) Functional neuroimaging of speech perception in infants. *Science* 298:2013–15. [rMCC]
- D'Esposito, M., Postle, B. R. & Rypma, B. (2000) Prefrontal cortical contributions to working memory: Evidence from event-related fMRI studies. *Experimental Brain Research* 133:3–11. [GJ]
- de Vries, J. I. P., Wimmers, R. H., Ververs, I. A. P., Hopkins, B., Savesberg, G. J. P. & van Geijn, H. P. (2001) Fetal handedness and head position preference: A developmental study. *Developmental Psychobiology* 39:171–78. [LR]
- de Waal, F. (1982) *Chimpanzee politics*. Johns Hopkins University Press/Harper and Row. [ACA, aMCC]
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. & Rizzolatti, G. (1992) Understanding motor events: A neurophysiological study. *Experimental Brain Research* 91:176–80. [SHJ-F]
- Diamond, A. S. (1959) *The history and origin of language*. Methuen. [arMCC]
- Dickins, T. E. (2002) A behaviourist's perspective on the origins of language. *History and Philosophy of Psychology* 4(1):31–42. [TED]
- Donald, M. (1991) *Origins of the modern mind: Three stages in the evolution of culture and cognition*. Harvard University Press. [aMCC, AR]
- (1999) Preconditions for the evolution of protolanguages. In: *The descent of mind*, ed. M. C. Corballis & S. E. G. Lea. Oxford University Press. [AR]
- Dronkers, N. F. (1996) A new brain region for coordinating speech articulation. *Nature* 384:159–61. [GJ]
- Ehert, G. (1987) Left hemisphere advantage in the mouse brain for recognizing ultrasonic communication calls. *Nature* 325:249–51. [aMCC, UJ]
- Ehrsson, H. H., Fagergren, E. & Forssberg, H. (2001) Differential fronto-parietal activation depending on force used in a precision grip task: An fMRI study. *Journal of Neurophysiology* 85:2613–23. [SHJ-F]
- Eilers, R., Oller, D. K., Levine, S., Basinger, D., Lynch, M. P. & Urbano, R. (1993) The role of prematurity and socioeconomic status in the onset of canonical babbling in infants. *Infant Behavior and Development* 16:297–315. [JMI]
- Ejiri, K. & Masataka, N. (2001) Co-occurrence of preverbal vocal behavior and motor action in early infancy. *Developmental Science* 4:40–48. [JMI]

- Elman, J., Bates, E. & Newport, E. (1996) *Rethinking innateness: A connectionist perspective on development*. MIT Press. [AR]
- Emmorey, E., Damasio, H., McCullough, S., Grabowski, T., Ponto, L. L. B., Hichwa, R. D. & Bellugi, U. (2002) Neural systems underlying spatial language in American Sign Language. *NeuroImage* 17(2):812–824. (doi:10.1006/nimg.2002.1187). [MAA]
- Emmorey, K. (2002) *Language, cognition, and the brain: Insights from sign language research*. Erlbaum. [DFA]
- Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S., Wiebe, V., Kitano, T., Monaco, A. P. & Pääbo, S. (2002) Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* 418:869–72. [rMCC, IECS, SFW]
- Fabre-Thorpe, M., Fagot, J., Lorincz, E., Levesque, F. & Vauclair, J. (1993) Laterality in cats: Paw preference and performance in a visuomotor activity. *Cortex* 29:15–24. [CF]
- Fadiga, L., Craighero, L., Buccino, G. & Rizzolatti, G. (2002) Speech listening specifically modulates the excitability of tongue muscles: A TMS study. *European Journal of Neuroscience* 15:399–402. [CB]
- Falk, D. (1983) Cerebral cortices of the East African early hominids. *Science* 221:1072–74. [AAB]
- Feyerherren, P. (1997) The competition between gesture and speech production in dual-task paradigms. *Journal of Memory and Language* 36:13–33. [PF]
- (1999) The neuropsychology of expressive movements. In: *Gesture, speech, and sign*, ed. L. Messing & R. Campbell. Oxford University Press. [PF]
- Feyerherren, P. & Havard, I. (1999) Mental imagery and production of hand gestures during speech by younger and older adults. *Journal of Nonverbal Behavior* 23:153–71. [PF]
- Finch, G. (1941) Chimpanzee handedness. *Science* 94:117–18. [aMCC]
- Fitch, R. H., Brown, C. P., O'Connor, K. & Tallal, P. (1993) Function lateralization for auditory temporal processing in male and female rats. *Behavioral Neuroscience* 107:844–50. [aMCC, UJ]
- Floel, A., Breitenstein, C. & Knecht, S. (2001) Speech enhances motor responses in both hands. *Brain and Language* 79:S55–S57. [CB]
- Floel, A., Ellger, T., Breitenstein, C. & Knecht, S. (2002) Language and the motor system. *Brain and Language* 83:S37–S39. [CB]
- (2003) *Language perception activates the hand motor cortex: Implications for evolutionary theories of language* (under review). [CB]
- Foerster, O. (1936) The motor cortex in the light of Hughlings Jackson's doctrines. *Brain* 59:135–59. [aMCC]
- Fogassi, L., Gallese, V., Fadiga, L. & Rizzolatti, G. (1998) Neurons responding to the sight of goal-directed hand/arm actions in the parietal area PF (7b) of the macaque monkey. *Society for Neuroscience Abstracts* 24:654. [SHJ-F]
- Fogel, A. & Hannan, T. E. (1985) Manual actions of nine to fifteen-week-old human infants during face-to-face interactions with their mothers. *Child Development* 56:1271–79. [JMI]
- Foundas, A. L., Eure, K. F., Luevano, L. F. & Weinberger, D. R. (1998) MRI asymmetries of Broca's area: The *pars triangularis* and *pars opercularis*. *Brain and Language* 64:282–96. [AAB, UJ]
- Foundas, A. L., Leonard, C. M., Gilmore, R. L., Fennell, E. B. & Heilman, K. M. (1996) *Pars triangularis* asymmetry and language dominance. *Proceedings of the National Academy of Sciences USA* 93:719–22. [aMCC]
- Foundas, A. L., Leonard, C. M. & Heilman, K. M. (1995a) Morphological cerebral asymmetries and handedness – the *pars triangularis* and *planum temporale*. *Archives of Neurology* 52:501–508. [aMCC]
- Foundas, A. L., Macauley, B. L., Raymer, A. M., Maher, L. M., Heilman, K. M. & Rothi, L. J. G. (1995b) Gesture laterality in aphasic and apraxic stroke patients. *Brain and Cognition* 29:204–13. [PF]
- Fouts, R. S. (1987) Chimpanzee signing and emergent levels. In: *Language, cognition and consciousness: Integrative levels*, ed. G. Greenberg & E. Tobach. Erlbaum. [RSF]
- Fouts, R. S. & Mills, S. T. (1997) *Next of kin*. William Morrow. [RSF]
- Fouts, R. S. & Waters, G. (2001) Chimpanzee sign language and Darwinian continuity: Evidence for a neurology continuity of language. *Neurological Research* 23:787–94. [RSF]
- Fox, P. T., Ingham, R. J., Ingham, J. C., Hirsch, T. B., Downs, J. H., Martin, C., Jerabek, P., Glass, T. & Lancaster, J. L. (1996) A PET study of the neural systems of stuttering. *Nature* 382:158–62. [NDC]
- Frege, G. (1977) *Logical Investigations*, trans. P. Geach & R. Stoothoff. Blackwell. [GRG]
- Furlow, B., Gangestad, S. W. & Armijo-Prewitt, T. (1998) Developmental stability and human violence. *Proceedings of the Royal Society of London B* 265:1–6. [CF]
- Galaburda, A. M. & Pandya, D. N. (1982) Role of architectonics and connections in the study of primate brain evolution. In: *Primate brain evolution*, ed. E. Armstrong & D. Falk. Plenum Press. [UJ]
- Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P. C., Frith, U. & Frith, C. D. (2000) Reading the mind in cartoons and stories: An fMRI study of “theory of mind” in verbal and nonverbal tasks. *Neuropsychologia* 38:11–21. [MA]
- Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996) Action recognition in the premotor cortex. *Brain* 119(Pt. 2):593–609. [SHJ-F, AR]
- Gallese, V. & Goldman, A. (1998) Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences* 2:493–501. [SHJ-F]
- Gangestad, S. W. & Yeo, R. A. (1997) Behavioral genetic variation, adaptation and maladaptation: An evolutionary perspective. *Trends in Cognitive Sciences* 1:103–108. [CF]
- Gannon, P. J., Holloway, R. L., Broadfield, D. C. & Braun, A. R. (1998) Asymmetry of chimpanzee *planum temporale*: Human-like brain pattern of Wernicke's area homolog. *Science* 279:220–201. [aMCC, rMCC, RSF, GVJ]
- Gardner, P. M. (1976) Birds, words, and a requiem for the omniscient informant. *American Ethnologist* 3:446–68. [TMP]
- (2000) *Bicultural versatility as a frontier adaptation among Paliyan foragers of South India*. Edwin Mellen Press. [TMP]
- (2002) Rethinking foragers' handling of environmental and subsistence knowledge. Paper presented at the Ninth International Conference on Hunting and Gathering Societies, Edinburgh, Scotland, September 2002. [TMP]
- Gardner, R. A. & Gardner, B. T. (1969) Teaching sign language to a chimpanzee. *Science* 165:664–72. [aMCC]
- Gaur, A. (1984) *A history of writing*. British Library. [aMCC]
- Gazzaniga, M. S. (2000) Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain* 123:1293–326. [rMCC]
- Gazzaniga, M. S. & Smylie, C. S. (1990) Hemispheric mechanisms controlling voluntary and spontaneous facial expressions. *Journal of Cognitive Neuroscience* 2:239–45. [aMCC]
- Geffen, G., Traub, E. & Stierman, I. (1978) Language laterality assessed by unilateral ECT and dichotic monitoring. *Journal of Neurology, Neurosurgery, and Psychiatry* 41:354–60. [aMCC]
- Geschwind, N. & Galaburda, A. M. (1985a) Cerebral lateralization: Biological mechanisms, associations, and pathology: I. A hypothesis and a program for research. *Archives of Neurology* 42:428–59. [CF]
- (1985b) Cerebral lateralization: Biological mechanisms, associations, and pathology: II. A hypothesis and a program for research. *Archives of Neurology* 42:521–52. [CF]
- (1985c) Cerebral lateralization: Biological mechanisms, associations, and pathology: III. A hypothesis and a program for research. *Archives of Neurology* 42:634–54. [CF]
- Geschwind, N. & Levitsky, W. (1968) Human brain: Left-right asymmetries in temporal speech region. *Science* 161:186–87. [aMCC, GJ]
- Gesell, A. & Ames, L. B. (1947) The development of handedness. *Journal of Genetic Psychology* 70:155–75. [DC]
- Gibbons, A. (2002) In search of the first hominids. *Science* 295:1214–19. [aMCC]
- Gibson, K. R. & Jessee, S. (1999) Language evolution and expansions of multiple neurological processing areas. In: *The origins of language: What nonhuman primates can tell us*, ed. B. J. King. School of American Research Press. [aMCC]
- Gillett, G. (1992) *Representation, meaning and thought*. Clarendon. [GRG]
- Givón, T. (1995) *Functionalism and grammar*. Benjamins. [aMCC]
- Goel, V., Buchel, C., Frith, C. & Dolan, R. J. (2000) Dissociation of mechanisms underlying syllogistic reasoning. *NeuroImage* 12:504–14. [GJ]
- Goel, V., Gold, B., Kapur, S. & Houle, S. (1997) The seats of reason? An imaging study of deductive and inductive reasoning. *NeuroReport* 8:1305–10. [GJ]
- (1998) Neuroanatomical correlates of human reasoning. *Journal of Cognitive Neuroscience* 10:293–302. [GJ]
- Goldberg, E. (2001) *The executive brain*. Oxford University Press. [NDC]
- Goldin-Meadow, S. & McNeill, D. (1999) The role of gesture and mimetic representation in making language the province of speech. In: *The descent of mind*, ed. M. C. Corballis & S. E. G. Lea. Oxford University Press. [aMCC, RD]
- Goldin-Meadow, S., McNeill, D. & Singleton, J. (1996) Silence is liberating: Removing the handcuffs on grammatical expression and speech. *Psychological Review* 103:34–55. [aMCC, PF]
- Goldin-Meadow, S. & Mylander, C. (1998) Spontaneous sign systems created by deaf children in two cultures. *Nature* 391:279–81. [aMCC]
- Goldstein, S. R. & Young, C. A. (1996) “Evolutionary” stable strategy of handedness in Major League Baseball. *Journal of Comparative Psychology* 110:164–69. [CF]
- Good, C. D., Johnsrude, I., Ashburner, J., Henson, R. N. A., Friston, K. J. & Frackowiak, R. S. J. (2001) Cerebral asymmetry and the effects of sex and handedness on brain structure: A voxel-based morphometric analysis of 465 normal adult human brains. *NeuroImage* 14:685–700. [SFW]
- Goodall, J. (1968) A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In: *Primate patterns*, ed. P. Dolhinow. Holt, Rinehart and Winston. [ACA]
- (1986) *The chimpanzees of Gombe: Patterns of behavior*. Harvard University Press. [ACA, aMCC]

- Goodwyn, S. & Acredolo, L. (1998) Encouraging symbolic gestures: Effects on the relationship between gesture and speech. In: *The nature and function of gesture in children's communication*, ed. J. Iverson & S. Goldin-Meadow. Jossey-Bass. [rMCC]
- Goodwyn, S., Acredolo, L. & Brown, C. (in press) The impact of symbolic gesturing on early language development. *Journal of Nonverbal Behavior*. [rMCC]
- Gould, R. A. (1968) Chipping stones in the outback. *Natural History* 77:42–49. [TMP]
- Govind, C. K. (1989) Asymmetry in lobster claws. *American Scientist* 77:468–74. [rMCC]
- Grafton, S. T., Arbib, M. A., Fadiga, L. & Rizzolatti, G. (1996) Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research* 112:103–11. [SHJ-F]
- Grafton, S. T., Fadiga, L., Arbib, M. A. & Rizzolatti, G. (1997) Premotor cortex activation during observation and naming of familiar tools. *Neuroimage* 6:231–36. [AR]
- Graves, R. & Goodglass, H. (1982) Mouth asymmetry during spontaneous speech. *Neuropsychologia* 20:371–81. [aMCC]
- Graves, R. E. & Potter, S. M. (1988) Speaking from two sides of the mouth. *Visible Language* 22:129–37. [CC, arMCC]
- Grezes, J., Costes, N. & Decety, J. (1998) Top down effect of the strategy to imitate on the brain areas engaged in perception of biological motion: A PET study. *Cognitive Neuropsychology* 15:553–82. [SHJ-F]
- Groënen, M. (1997a) La latéralisation dans les représentations de mains négatives paléolithiques. *Manovre* 14:31–59. [CF]
- (1997b) *Ombre et lumières dans l'art des grottes*. Université Libre de Bruxelles. [CF]
- Grouios, G., Sakadami, N., Poderi, A. & Alevriadou, A. (1999) Excess of non-right handedness among individuals with intellectual disability: Experimental evidence and possible explanations. *Journal of Intellectual Disability Research* 43:306–13. [CF]
- Grouios, G., Tsorbatzoudis, H., Alexandris, K. & Barkoukis, V. (2000) Do left-handed competitors have an innate superiority in sports? *Perceptual and Motor Skills* 90:1273–82. [CF]
- Guilaine, J. & Zammit, J. (2001) *Les sentiers de la guerre – Visages de la violence préhistorique*. Le Seuil. [CF]
- Giüntürkiin, O. (2002) Adult persistence of head-turning asymmetry. *Nature* 421:712. [rMCC]
- Gur, R. C., Packer, I. K., Hungerbuhler, J. P., Reivich, M., Obrist, W. D., Amarnik, W. S. & Sackheim, H. A. (1980) Differences in the distribution of gray and white matter in human cerebral hemispheres. *Science* 207:1226–28. [RSF]
- Haas, J., ed. (1990) *The anthropology of war*. Cambridge University Press. [CF]
- Hadar, U., Burstein, A., Krauss, R. & Soroker, A. (1998a) Ideational gestures and speech in brain-damaged subjects. *Language and Cognitive Processes* 13:59–76. [PF]
- Hadar, U., Wenkert-Olenik, D., Krauss, R. & Soroker, N. (1998b) Gesture and the processing of speech: Neuropsychological evidence. *Brain and Language* 62:107–26. [PF]
- Hamada, H., Meno, C., Watanabe, D. & Saijoh, Y. (2002) Establishment of vertebrate left-right asymmetry. *Nature Reviews Genetics*, 3(2):103–13. [SFW]
- Hanlon, R. E., Brown, J. W. & Gerstman, L. J. (1990) Enhancement of naming in nonfluent aphasia through gesture. *Brain and Language* 38:298–314. [CB]
- Harrington, F. & Mech, L. David (1978) Wolf vocalization. In: *Wolf and Man*, ed. R. Hall & H. Sharp. Academic Press. [ACA]
- Harris, L. J. (1993) Do left handers die sooner than right handers? Commentary. *Psychological Bulletin* 114:203–34. [rMCC]
- Harris, L. J. & Carlson, D. F. (1988) Pathological left-handedness: An analysis of theories and evidence. In: *Brain lateralization in children*, ed. D. L. Molfese & S. J. Segalowitz. Guilford. [rMCC]
- Hast, M. H., Fischer, J. M., Wetzel, A. B. & Thompson, V. E. (1974) Cortical motor representation of the laryngeal muscles in *Macaca mulatta*. *Brain Research* 73:229–40. [UJ]
- Hauser, M. D. (1996) *The evolution of communication*. Bradford Books/MIT Press. [aMCC]
- Hauser, M. D. & Anderson, K. (1994) Functional lateralization for auditory temporal processing in adult, but not infant rhesus monkeys: Field experiments. *Proceedings of the National Academy of Sciences USA* 91:3946–48. [aMCC]
- Hauser, M. D., Chomsky, N. & Fitch, W. T. (2002) The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1569–79. [AAB, CB, CJ, JLB]
- Hauser, M. D., Teixidor, P., Field, L. & Flaherty, R. (1993) Food-elicited calls in chimpanzees: Effects of food quantity and divisibility. *Animal Behaviour* 45:817–19. [aMCC]
- Hauser, M. D. & Wrangham, R. W. (1987) Manipulation of food calls in captive chimpanzees. A preliminary report. *Folia Primatologica* 48:207–10. [aMCC]
- Hautzel, H., Mottaghy, F. M., Schmidt, D., Zemb, M., Shah, N. J., Muller-Gartner, H. W. & Krause, B. J. (2002) Topographic segregation and convergence of verbal, object, shape and spatial working memory in humans. *Neuroscience Letters* 323:156–60. [GJ]
- Hayaki, H. (1990) Social context of pant-grunting in young chimpanzees. In: *The chimpanzees of the Mahale mountains*, ed. T. Nishida. University of Tokyo Press. [ACA]
- Hayes, C. (1952) *The ape in our house*. Gollancz. [aMCC]
- Heffner, H. E. & Heffner, R. S. (1984) Temporal lobe lesions and perception of species-specific vocalizations by Japanese macaques. *Science* 226:75–76. [aMCC]
- (1990) Role of primary auditory cortex in hearing. In: *Comparative perception, vol. 2: Complex signals*, ed. M. A. Berkely & W. C. Stebbins. Wiley. [aMCC]
- Hepper, P. G., McCartney, G. R. & Shammone, I. A. (1998) Lateralised behaviour in the first trimester human fetuses. *Neuropsychologia* 36:531–34. [LR]
- Hepper, P. G., Shahidullah, S. & White, R. (1991) Handedness in the human fetus. *Neuropsychologia* 29:1107–11. [LR]
- Hewes, G. W. (1973a) An explicit formulation of the relationship between tool-using, tool-making and the emergence of language. *Visible Language* 7:101–27. [AR]
- (1973b) Primate communication and the gestural origin of language. *Current Anthropology* 14:5–24. [aMCC, RSF, AR]
- Heyes, C. (2001) Causes and consequences of imitation. *Trends in Cognitive Science* 5:253–61. [SHJ-F]
- Hickok, G., Love-Geffen, T. & Klima, E. S. (2002) Role of the left hemisphere in sign language comprehension. *Brain and Language* 82:167–78. [BW]
- Hobert, O., Johnston, R. J. & Chang, S. (2002) Left-right asymmetry in the nervous system: The *Caenorhabditis elegans* model. *Nature Reviews Neuroscience* 3:629–40. [SFW]
- Hollman, S. D. & Hutchison, J. B. (1994) Is sexual-aggressive communication related to asymmetrical mechanisms in the brain? *Aggressive Behavior* 20:223–34. [aMCC, UJ]
- Holloway, R. L. (1967) The evolution of the human brain: Some notes toward a synthesis between neural structure and the evolution of complex behavior. *General Systems* XII:3–19. [RLH]
- (1969) Culture: A human domain. *Current Anthropology* 10(4):395–412. [RLH]
- (1981) Culture, symbols, and human brain evolution: A synthesis. *Dialectical Anthropology* 5:287–303. [RLH]
- (1983) Human paleontological evidence relevant to language behavior. *Human Neurobiology* 2:105–14. [AAB, aMCC]
- (1996) Evolution of the human brain. In: *Handbook of human symbolic evolution*, ed. A. Lock & C. R. Peters. Oxford University Press. [DC, RLH]
- Holloway, R. L. & de LaCoste-Lareymondie, M. C. (1982) Brain endocast asymmetry in pongids and hominids: Some preliminary findings of the paleontology of cerebral dominance. *American Journal of Physical Anthropology* 58:101–10. [RLH]
- Holowka, S. & Petitto, L. A. (2002) Left hemisphere cerebral specialization for babies while babbling. *Science* 297:1515. [rMCC]
- Hommel, B., Muesseler, J., Aschersleben, G. & Prinz, W. (2001) The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences* 24:849–937. [RD]
- Hook-Costigan, M. A. & Rogers, L. J. (1998) Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia* 36:1265–73. [aMCC, RSF, UJ]
- Hopkins, B., Lems, W., Janssen, B. & Butterworth, G. (1987) Postural and motor asymmetries in newborns. *Human Neurobiology* 6:153–56. [LR]
- Hopkins, B. & Rönnqvist, L. (1998) Human handedness: Developmental and evolutionary perspectives. In: *The development of sensory, motor and cognitive capacities in early infancy: From sensation to cognition*, ed. F. Simion & G. F. Butterworth. Psychology Press. [LR]
- (2002) Facilitating postural control: Effects on reaching behavior of 6-month-old infants. *Developmental Psychobiology* 40:168–82. [LR]
- Hopkins, W. D. (1993) Posture and reaching in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology* 107:162–68. [AVP]
- (1996) Chimpanzee handedness revisited: 55 years since Finch (1941). *Psychonomic Bulletin and Review* 3:449–57. [aMCC, AVP]
- Hopkins, W. D. & Cantalupo, C. (in press) Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): A critical analysis and some alternative explanations. *Laterality*. [WDH]
- Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B. & Pilcher, D. L. (2002) Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology: General* 131:412–23. [JLB]
- Hopkins, W. D. & Cantero, M. (in press) From hand to mouth in the evolution of

- language: The influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Developmental Science*. [WDH, DAL]
- Hopkins, W. D., Dahl, J. F. & Pilcher, D. (2001) Genetic influence on the expression of hand preferences in chimpanzees (*Pan troglodytes*): Evidence in support of the right shift theory and developmental instability. *Psychological Science* 12:299–303. [aMCC]
- Hopkins, W. D., Hook, M., Braccini, S. & Schapiro, S. J. (in press) Population-level right handedness for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): Replication and extension in a second colony of apes. *International Journal of Primatology*. [WDH]
- Hopkins, W. D. & Leavens, D. A. (1998) Hand use and gestural communication in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 112:95–99. [aMCC, WDH, DAL]
- Hopkins, W. D., Marino, L., Rilling, J. K. & MacGregor, L. A. (1998) *Planum temporale* asymmetries in great apes as revealed by magnetic resonance imaging (MRI). *Neuroreport* 9:2913–18. [aMCC, WDH]
- Hopkins, W. D. & Pilcher, D. A. (2001) Neuroanatomical localization of the motor hand area with magnetic resonance imaging: The left hemisphere is larger in great apes. *Behavioral Neuroscience* 115:1159–64. [WDH]
- Hopkins, W. D. & Wesley, M. J. (2002) Gestural communication in chimpanzees (*Pan troglodytes*): Influence of experimenter position on gesture type and hand preference. *Laterality* 7:19–30. [DAL]
- Hostetter, A. B., Cantero, M. & Hopkins, W. D. (2001) Differential use of vocal and gestural communication in response to the attentional status of a human. *Journal of Comparative Psychology* 115:337–43. [DAL]
- Hostetter, A. B. & Hopkins, W. D. (2002) The effect of thought structure on the production of lexical movements. *Brain and Language* 82:22–29. [PF]
- Houdé, O., Zago, L., Mellet, E., Moutier, S., Pineau, A., Mazoyer, B. & Tzourio-Mazoyer, N. (2000) Shifting from the perceptual brain to the logical brain: The impact of cognitive inhibition training. *Journal of Cognitive Neuroscience* 12:721–28. [GJ]
- Hunt, G. R., Corballis, M. C. & Gray, R. D. (2001) Species-level laterality in crow tool manufacture. *Nature* 414:707. [rMCC]
- Hurford, J. R. (2003) Language beyond our grasp: What mirror neurons can, and cannot do, for language evolution. In: *The evolution of communication systems: A comparative approach*, ed. D. Kimbrough Oller, U. Griebel & K. Plunkett. MIT Press. [TED]
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. & Rizzolatti, G. (1999) Cortical mechanisms of human imitation. *Science* 286:2526–28. [SHJ-F, GJ]
- Ingman, M., Kaessmann, H., Pääbo, S. & Gyllenstein, U. (2000) Mitochondrial genome variation and the origin of modern humans. *Nature* 208:708–13. [aMCC]
- Ingmanson, E. (1996) Hand use preference among *Pan paniscus* at Wamba, Zaire. *American Journal of Physical Anthropology* 22:129. [WDH]
- Inoue-Nakamura, N. & Matsuzawa, T. (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111:159–73. [ACA, aMCC]
- Iverson, J. M. (2003) Infant vocal-motor coordination: Precursor to the gesture-speech system? (under review). [JMI]
- Iverson, J. M. & Goldin-Meadow, S. (1998) Why people gesture when they speak. *Nature* 396:228. [rMCC]
- Iverson, J. M. & Thelen, E. (1999) Hand, mouth, and brain: The dynamic emergence of speech and gesture. *Journal of Consciousness Studies* 6:19–40. [JMI]
- Jackendoff, R. (2002) *Foundations of language: Brain, meaning, grammar, evolution*. Oxford University Press. [DFA]
- Jäncke, L. & Steinmetz, H. (1993) Auditory lateralization and *planum temporale* asymmetry. *NeuroReport* 5:169–72. [aMCC]
- Jeannerod, M. (1994) The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences* 17:187–245. [GVJ]
- (1997) *The cognitive neuroscience of action*. Blackwell. [GVJ]
- Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S. & Grafton, S. G. (in press). Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron*. [SHJ-F]
- Jones, G. V. & Martin, M. (2000) A note on Corballis (1997) and the genetics and evolution of handedness: Developing a unified distributional model from the sex-chromosomes gene hypothesis. *Psychological Review* 107:213–18. [GVJ]
- (2001) Confirming the X-linked handedness gene as recessive, not additive: Reply to Corballis (2001). *Psychological Review* 108:811–13. [GVJ]
- Jones, R. K. (1966) Observations on stammering after localized cerebral injury. *Journal of Neurology and Neurosurgical Psychiatry* 29:192–95. [RSF]
- Jonides, J., Smith, E. E., Marshuetz, C., Koeppe, R. A. & Reuter-Lorenz, P. A. (1998) Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Science of the USA* 95:8410–13. [GJ]
- Josse, G., Crivello, F., Mazoyer, B. & Tzourio-Mazoyer, N. (2002) Left *planum temporale* surface correlates with cortical activated network during language comprehension and production. Paper presented at the 8th International Conference on Functional Mapping of the Human Brain. *Neuroimage* 10:151. [GJ]
- Jürgens, U., Kirzinger, A. & von Cramon, D. (1982) The effect of deep-reaching lesions in the cortical face area on phonation: A combined case report and experimental monkey study. *Cortex* 18:125–40. [aMCC]
- Jürgens, U. & Zwirner, P. (2000) Individual hemispheric asymmetry in vocal fold control of the squirrel monkey. *Behavioural Brain Research* 109:213–17. [rMCC, UJ]
- Karnath, H.-O., Ferber, S. & Himmelbach, M. (2001) Spatial awareness is a function of the temporal lobe not the posterior parietal lobe. *Nature* 411:950–53. [aMCC]
- Kay, R. F., Cartmill, M. & Barlow, M. (1998) The hypoglossal canal and the origin of human vocal behavior. *Proceedings of the National Academy of Sciences USA* 95:5417–19. [aMCC, RLH]
- Ke, Y., Su, B., Song, X., Lu, D., Chen, L., Li, H., Qi, C., Marzuki, S., Deka, R., Underhill, P., et al. (2001) African origin of modern humans in East Asia: A tale of 12,000 Y chromosomes. *Science* 292:1151–53. [aMCC]
- Kelly, S. D. (2001) Broadening the units of analysis in communication: Speech and nonverbal behaviours in pragmatic comprehension. *Journal of Child Language* 28:325–49. [SDK]
- (2003) Putting language back in the body: The influence of hand gesture on language production and comprehension. Paper presented at the Acoustic Ecology Conference at the University of British Columbia in Vancouver, Canada, January 2003. [SDK]
- Kelly, S. D., Barr, D., Church, R. B. & Lynch, K. (1999) Offering a hand to pragmatic understanding: The role of speech and gesture in comprehension and memory. *Journal of Memory and Language* 40:577–92. [SDK]
- Kendon, A. (1991) Some considerations for a theory of language origins. *Man* 26:199–221. [RD]
- Kennedy, D. N., Lange, N., Makris, N., Bates, J., Meyer, J. & Caviness, V. S. (1998) Gyri of the human neocortex: An MRI-based analysis of volume and variance. *Cerebral Cortex* 8:372–84. [SFW]
- Kennedy, D. N., O'Craven, K. M., Ticho, B. S., Goldstein, A. M., Makris, N. & Henson, J. W. (1999) Structural and functional brain asymmetries in human *status inversus totalis*. *Neurology* 53:1260–65. [SFW]
- Kimura, D. (1973a) Manual activity while speaking: I. Right-handers. *Neuropsychologia* 11:45–50. [aMCC]
- (1973b) Manual activity while speaking: II. Left-handers. *Neuropsychologia* 11:51–55. [aMCC]
- (1976) The neural basis of language qua gesture. In: *Studies in neurolinguistics, vol. 2*, ed. H. Whitaker & H. A. Whitaker. Academic Press. [CC]
- (1982) Left hemisphere control of oral and brachial movements and their relationship to communication. *Philosophical Transactions of the Royal Society of London, Series B* 298:135–49. [CC]
- (1993) *Neuromotor mechanisms in human communication*. Oxford University Press. [LR]
- Kimura, D. & Archibald, Y. (1974) Motor functions of the left hemisphere. *Brain* 97:337–50. [CC]
- Kinsbourne, M. (1971) The minor cerebral hemisphere as a source of aphasic speech. *Archives of Neurology* 254:302–306. [IECS]
- Klima, E. & Bellugi, E. (1979) *The signs of language*. Harvard University Press. [PFM]
- Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., Ringelstein, E.-B. & Henningsen, H. (2000) Handedness and hemispheric language dominance in healthy humans. *Brain* 123:2512–18. [aMCC, IECS]
- Knecht, S., Dräger, B., Floel, A., Lohmann, H., Breitenstein, C., Deppe, M., Henningsen, H. & Ringelstein, E. B. (2001) Behavioural relevance of atypical language lateralization in healthy subjects. *Brain* 124:1637–65. [SFW]
- Knecht, S., Floel, A., Dräger, B., Breitenstein, C., Sommer, J., Henningsen, H., Ringelstein, E. B. & Pascual-Leone, A. (2002) Degree of language lateralization determines susceptibility to unilateral brain lesions. *Nature Neuroscience* 5:695–99. [CB, SFW]
- Knight, C. (1998) Ritual/speech coevolution: A solution to the problem of deception. In: *Approaches to the evolution of language*, ed. J. R. Hurford, M. Studdert-Kennedy, & C. Knight. Cambridge University Press. [aMCC, CK]
- (1999) Sex and language as pretend-play. In: *The evolution of culture*, ed. R. Dunbar, C. Knight & C. Power. Edinburgh University Press. [CK]
- (2000) Play as precursor of phonology and syntax. In: *The evolutionary emergence of language. Social function and the origins of linguistic form*, ed. Knight, C. D., M. Studdert-Kennedy & J. R. Hurford. Cambridge University Press. [CK]
- (2002) Language and revolutionary consciousness. In: *The transition to language*, ed. A. Wray. Oxford University Press. [CK]
- Kobayashi, H. & Kohshima, S. (2001) Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the human eye. *Journal of Human Evolution* 40:419–35. [aMCC, CK]

- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V. & Rizzolatti, G. (2002) Hearing sounds, understanding actions: Action representation in mirror neurons. *Science* 297:846–48. [UJ, AR, LR]
- Konishi, S., Hayashi, T., Uchida, I., Kikyo, H., Takahashi, E. & Miyashita, Y. (2002) Hemispheric asymmetry in human lateral prefrontal cortex during cognitive set shifting. *Proceedings of the National Academy of Science of the United States of America* 99:7803–808. [GJ]
- Konishi, S., Nakajima, K., Uchida, I., Kameyama, M., Nakahara, K., Sekihara, K. & Miyashita, Y. (1998a) Transient activation of inferior prefrontal cortex during cognitive set shifting. *Nature Neuroscience* 1:80–84. [GJ]
- Konishi, S., Nakajima, K., Uchida, I., Kikyo, H., Kameyama, M. & Miyashita, Y. (1999) Common inhibitory mechanism in human inferior prefrontal cortex revealed by event-related functional MRI. *Brain* 122:981–91. [GJ]
- Konishi, S., Nakajima, K., Uchida, I., Sekihara, K. & Miyashita, Y. (1998b) No-go dominant brain activity in human inferior prefrontal cortex revealed by functional magnetic resonance imaging. *European Journal of Neuroscience* 10:1209–13. [GJ]
- Krause, M. A. & Fouts, R. S. (1997) Chimpanzee (*Pan troglodytes*) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology* 111:330–36. [DAL]
- Krauss, R. M., Dushay, R. A., Chen, Y. & Rauscher, F. (1995) The communicative value of conversational hand gestures. *Journal of Experimental Social Psychology* 31:533–52. [RD]
- Kutas, M. & Hillyard, S. A. (1980) Reading senseless sentences: Brain potentials reflect semantic incongruities. *Science* 207:203–205. [SDK]
- Kuypers, H. G. J. M. (1985) The anatomical and functional organization of the motor system. In: *Scientific basis of clinical neurology*, ed. M. Swash & C. Kennard. Churchill Livingstone. [LR]
- Lai, C. S., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F. & Monaco, A. P. (2001) A novel forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413:519–23. [rMCC]
- Laland, K. N., Kumm, J., van Horn, J. D. & Feldman, M. W. (1995) A gene-culture model of human handedness. *Behavior Genetics* 25:433–45. [AAB]
- Lalueza, C. & Frayer, D. W. (1997) Non-dietary marks in the anterior dentition of the *Krapina neanderthals*. *International Journal of Osteoarchaeology* 7:133–49. [CF]
- Larsen, B., Skinhoj, E. & Lassen, N. (1978) Variations in regional cortical blood flow in the right and left hemispheres during automatic speech. *Brain* 101:193–209. [CC]
- Lausberg, H., Davis, M. & Rothenhäusler, A. (2000) Hemispheric specialization in spontaneous gesticulation in a patient with callosal disconnection. *Neuropsychologia* 38:1654–63. [PF]
- Leakey, L. S. B., Tobias, P. V. & Naiber, J. R. (1964) A new species of the genus *Homo* from Olduvai gorge. *Nature* 202:7–9. [LR]
- Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. (1995) New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565–71. [AAB]
- Leavens, D. A. (2001) Communicating about distal objects: An experimental investigation of factors influencing gestural communication by chimpanzees (*Pan troglodytes*). Unpublished doctoral dissertation, University of Georgia. [DAL]
- Leavens, D. A. & Hopkins, W. D. (1998) Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology* 34:813–22. [DAL]
- Leavens, D. A., Hopkins, W. D. & Bard, K. A. (1996) Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 110:346–53. [DAL]
- Leavens, D. A., Hostetter, A. B., Wesley, M. J. & Hopkins, W. D. (in press) Tactical use of unimodal and bimodal communication by chimpanzees (*Pan troglodytes*). *Animal Behaviour*. [DAL]
- Lehner, P. (1978) Coyote communication. In: *Coyotes: Biology, Behavior, and Management*, ed. M. Bekoff. Academic Press. [ACA]
- Lessell, S. (1986) Handedness and esotropia. *Archives of Ophthalmology* 104:1492–94. [AR]
- Levelt, W. J. M., Richardson, G. & La Heij, W. (1985) Pointing and voicing in deictic expressions. *Journal of Memory and Language* 24:133–64. [PF]
- Levin, M. & Mercola, M. (1998) The compulsion of chirality: Toward an understanding of left-right asymmetry. *Genes and Development* 6:763–69. [IECS]
- Lew, A. R. & Butterworth, G. (1997) The development of hand-mouth coordination in 2- to 5-month-old infants: Similarities with reaching and grasping. *Infant Behavior and Development* 20:59–69. [JMI]
- Lewin, R. (1998) *Principles of human evolution: A core textbook*. Blackwell Science. [DC]
- Lieberman, A. M. & Whalen, D. H. (2000) On the relation of speech to language. *Trends in Cognitive Sciences* 4:187–96. [aMCC, IECS]
- Lieberman, D. (1998) Sphenoid shortening and the evolution of the modern human cranial shape. *Nature* 393:158–62. [aMCC]
- (1999) *Learning, behavior, and cognition*, 3rd edition. Wadsworth. [LW]
- Lieberman, P. (1998) *Eve spoke: Human language and human evolution*. Norton. [aMCC]
- Lieberman, P., Crelin, E. S. & Klatt, D. H. (1972) Phonetic ability and related anatomy of the new-born, adult human, Neanderthal man, and the chimpanzee. *American Anthropologist* 74:287–307. [aMCC]
- Liepmann, H. (1913/1979) Motorisch Aphasie und Apraxie. *Monatschrift für Psychiatrie und Neurologie* 34. (Translated by G. H. Eggert and reproduced in *Aphasia-Apraxia-Agnosia* 1:53–59.) [CC]
- Lock, A. J. (1980) *The guided reinvention of language*. Academic. [aMCC]
- Locke, J. L., Bekken, K. E., McMinn-Larson, L. & Wein, D. (1995) Emergent control of manual and vocal-motor activity in relation to the development of speech. *Brain and Language* 51:498–508. [JMI]
- Loew, R., Kegl, J. A. & Poizner, H. (1997) Fractionation of the components of roleplay in a right-lesioned signer. *Aphasiology* 11:263–81. [BW]
- Luppino, G., Murata, A., Govoni, P. and Matelli, M. (1999) Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Experimental Brain Research* 128:181–87. [SHJ-F]
- Luschei, E. S. & Goldberg, L. J. (1981) Neural mechanisms of mandibular control: Mastication and voluntary biting. In: *Handbook of physiology: The nervous system, vol. 2*. American Physiological Society. [aMCC]
- MacLarnon, A. & Hewitt, G. (1999) The evolution of human speech: The role of enhanced breathing control. *American Journal of Physical Anthropology* 109:341–63. [aMCC, RLH]
- Maclean, P. D. (1980) The triune brain evolving. *American Journal of Physical Anthropology* 52:251. [rMCC]
- MacNeilage, P. F. (1998) The frame/content theory of evolution of speech production. *Behavioral and Brain Sciences* 21:499–546. [MAA, aMCC, RSF, PFM]
- MacNeilage, P. F. & Davis, B. L. (2000a) On the origin of internal structure of word forms. *Science* 288:527–31. [PFM]
- (2000b) Evolution of speech: The relation between ontogeny and phylogeny. In: *The evolutionary emergence of language*, ed. C. Knight & J. R. Hurford. Cambridge University Press. [PFM]
- (2001) Motor mechanisms in speech ontogeny: Phylogenetic, neurobiological and linguistic implications. *Current Opinion in Neurobiology* 11:696–700. [PFM]
- MacNeilage, P. F., Studdert-Kennedy, M. G. & Lindblom, B. (1987) Primate handedness reconsidered. *Behavioral and Brain Sciences* 10:247–303. [aMCC, CF]
- MacSweeney, M., Calvert, G. A., Campbell, R., McGuire, P. K., David, A. S., Williams, S. C. R., Woll, B. & Brammer, M. J. (2002) Speechreading circuits in people born deaf. *Neuropsychologia* 40:801–807. [BW]
- MacSweeney, M., Campbell, R., Calvert, G. A., McGuire, P. K., David, A. S., Suckling, J., Andrew, C., Woll, B. & Brammer, M. J. (2001) Dispersed activation in the left temporal cortex for speech-reading in congenitally deaf people. *Proceedings of the Royal Society Series B* 268:451–57. [BW]
- Maess, B., Koelsch, S., Gunter, T. C. & Friederici, A. D. (2001) Musical syntax is processed in Broca's area: An MEG study. *Nature Neuroscience* 4:540–45. [aMCC]
- Malcolm, N. (1958) *Ludwig Wittgenstein: A memoir*. Oxford University Press. [AC-M]
- Marks, J. (2002) *What it means to be 98% chimpanzee: Apes, people, and their genes*. University of California Press. [ACA]
- Marler, P. & Tenaza, R. (1977) Signaling behavior of apes with special reference to vocalization. In: *How animals communicate*, ed. T. A. Sebeok. Indiana University Press. [ACA]
- Marshall, A. J., Wrangham, R. W. & Arcadi, A. C. (1999) Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour* 58:825–30. [ACA, aMCC]
- Marshall, J., Atkinson, J. A., Smulovich, E., Thacker, A. & Woll, B. (in press) Aphasia in a user of British Sign Language: Dissociation between sign and gesture. *Cognitive Neuropsychology*. [BW]
- Martin, M. & Jones, G. V. (1998) Generalizing everyday memory: Signs and handedness. *Memory and Cognition* 26:193–200. [GVJ]
- (1999) Motor imagery theory of a contralateral handedness effect in recognition memory: Toward a chiral psychology of cognition. *Journal of Experimental Psychology: General* 128:265–82. [GVJ]
- Marx, K. & Engels, F. (1939) *The German ideology*, ed. C. J. Arthur. Lawrence and Wishart. [GRG]
- Marzke, M. W. & Shackley, M. S. (1986) Hominid hand use in the Pliocene and Pleistocene: Evidence from experimental archaeology and comparative morphology. *Journal of Human Evolution* 15:439–60. [AAB]
- Matelli, M., Luppino, G. & Rizzolatti, G. (1985) Patterns of cytochrome oxidase activity in the frontal agranular cortex of macaque monkey. *Behavioural Brain Research* 18:125–36. [UJ]
- Mayberry, R. I., Jaques, J. & Dede, G. (1998) What stuttering reveals about the

- development of the gesture-speech relationship. *New Directions for Child Development* 79:77–87. [CB]
- McBrearty, S. & Brooks, A. S. (2000) The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39:453–563. [rMCC]
- McCune, L., RougHellichius, L., Vihman, M. M., Delery, D. B. & Gogate, L. (1996) Grunt communication in human infants (*Homo sapiens*). *Journal of Comparative Psychology* 110:27–37. [rMCC]
- McGrew, W. C. & Marchant, L. F. (1997) On the other hand: Current issues in a meta-analysis of the behavioural laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology* 40:201–32. [aMCC, UJ, AVP]
- (2001) Ethological study of manual laterality in the chimpanzees of the Mahale Mountains, Tanzania. *Behaviour* 138:329–58. [aMCC]
- McGurk, H. & MacDonald, J. (1976) Hearing lips and seeing voices. *Nature* 264:746–48. [aMCC]
- McKeever, W. F. (2000) A new family handedness sample with findings consistent with X-linked transmission. *British Journal of Psychology* 91:21–39. [GVJ]
- McManus, I. C. (1985a) Handedness, language dominance and aphasia: A genetic model. *Psychological Medicine*, Monograph Supplement 8. [AAB, rMCC, GVJ]
- (1985b) Right- and left-hand skill: Failure of the right shift model. *British Journal of Psychology* 76:1–34. [AR]
- (1999) Handedness, cerebral lateralization, and the evolution of language. In: *The descent of mind: Psychological perspectives on hominid evolution*, ed. M. C. Corballis & S. E. G. Lea. Oxford University Press. [arMCC, GVJ]
- (2002a) *Left hand, right hand*. Weidenfeld and Nicolson. [rMCC]
- (2002b) Right hand, left hand. In: *Folk physics for apes: The chimpanzee's theory of how the world works*, ed. D. J. Povinelli. Oxford University Press. [LW]
- McManus, I. C. & Bryden, M. P. (1991) Geschwind's theory of cerebral lateralization: Developing a formal, causal model. *Psychological Bulletin* 110:237–53. [CF]
- (1992) The genetics of handedness, cerebral dominance and lateralization. In: *Handbook of neuropsychology*, vol. 6, ed. I. Rapin & S. J. Segalowitz. Elsevier. [GVJ]
- McManus, I. C., Murray, B., Doyle, K. & Baron-Cohen, S. (1992) Handedness in childhood autism shows a dissociation of skill and preference. *Cortex* 28:373–81. [aMCC]
- McManus, I. C., Sik, G., Cole, D. R., Mellon, A. F., Wong, J. & Kloss, J. (1988) The development of handedness in children. *British Journal of Developmental Psychology* 6:257–73. [DC]
- McNeill, D. (1985) So you think gestures are nonverbal? *Psychological Review* 92:350–71. [arMCC, SDK]
- (1992) *Hand and mind: What gestures reveal about thought*. Chicago University Press. [PF]
- Meaburn, E., Dale, P. S., Craig, I. W. & Plomin, R. (2002) Language-impaired children: No sign of the FOXP2 mutation. *NeuroReport* 13:1075–77. [SFW]
- Meier, R. P. & Newport, E. L. (1990) Out of the hands of babes: On a possible sign language advantage in language acquisition. *Language* 66:1–23. [arMCC]
- Meister, I. G., Boroojerdi, B., Foltys, H., Sparing, R., Huber, W. & Töpper, R. (2003) Motor cortex hand area and speech: Implications for the development of language. *Neuropsychologia* 41:401–406. [rMCC]
- Mellars, P. (1989) Major issues in the emergence of modern humans. *Current Anthropology* 30:349–85. [aMCC]
- (2002) Archaeology and the origins of modern humans: European and African perspectives. In: *The speciation of modern Homo Sapiens*, ed. T. J. Crow. Oxford University Press. [rMCC]
- Meltzoff, A. N. & Moor, M. K. (1992) Early imitation within a functional framework: The importance of personal identity, movement and development. *Infant Behavior and Development* 15:479–505. [LR]
- Mercola, M. & Levin, M. (2001) Left-right asymmetry determination in vertebrates. *Annual Review of Cell and Developmental Biology* 17:779–805. [SFW]
- Michel, G. F. (1981) Right handedness: A consequence of infant supine head-orientation preference? *Science* 212:685–87. [GFM, LR]
- (1998) A lateral bias in the neuropsychological functioning of human infants. *Developmental Neuropsychology* 14:445–69. [GFM]
- (2003) Development of intermanual transfer of the texture, shape, and temperature of objects from seven to eleven months of age. Paper presented at the *New Data and Techniques in Developmental Psychobiology Symposium* conducted at the 18th Annual Winter Conference on Current Issues in Developmental Psychobiology, Ocho Rios, Jamaica, January 2003. [GFM]
- Michel, G. F. & Harkins, D. A. (1986) Postural and lateral asymmetries in the ontogeny of handedness during infancy. *Developmental Psychobiology* 19:247–58. [GFM]
- Michel, G. F. & Moore, C. L. (1995) *Developmental psychobiology: An interdisciplinary science*. MIT Press. [GFM]
- Michel, G. F., Sheu, C.-F. & Brumley, M. R. (2001) Evidence of a right-shift factor affecting hand-use preferences from seven- to eleven-months of age as revealed by latent class analysis. *Developmental Psychobiology* 41:1–12. [GFM]
- Michel, G. F., Sheu, C.-L. & Hinojosa, T. (2003) *The distribution of hand-use preferences for obtaining objects for 7- to 13-month-old infants* (under review). [GFM]
- Miles, H. L. (1990) The cognitive foundations for reference in a signing orangutan. In: *Language and intelligence in monkeys and apes*, ed. S. T. Parker & K. R. Gibson. Cambridge University Press. [aMCC]
- Milner, B. (1974) Hemispheric specialization: Scopes and limits. In: *The neurosciences*, vol. 3, ed. F. O. Schmidt & F. Worden. MIT Press. [CC]
- (1975) Psychological aspects of focal epilepsy and its neurosurgical management. In: *Advances in neurology*, vol. 8, ed. D. P. Purpura & R. D. Walters. Raven. [aMCC]
- Milner, B., Branch, C. & Rasmussen, T. (1966) Evidence for bilateral speech representation in some non-righthanders. *Transactions of the American Neurological Association* 91:306–308. [CC]
- Mitani, J. C. & Brandt, K. L. (1994) Social factors influence the acoustic variability in the long-distance calls of male chimpanzees. *Ethology* 96:233–52. [ACA]
- Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P. & Byrne, R. (1992) Dialects in wild chimpanzees? *American Journal of Primatology* 27:233–43. [ACA]
- Mitani, J. C., Hunley, K. L. & Murdoch, M. E. (1999) Geographic variation in the calls of wild chimpanzees: A reassessment. *American Journal of Primatology* 47:133–51. [ACA, arMCC]
- Mitani, J. C. & Nishida, T. (1993) Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour* 45:735–46. [ACA]
- Mohr, J. P., Pessin, M. S., Finkelstein, S., Funkenstein, H. H., Duncan, G. W. & Davis, K. R. (1978) Broca aphasia: Pathologic and clinical. *Neurology* 28:311–24. [AAB]
- Monk, R. (1990) *Ludwig Wittgenstein: The duty of genius*. Penguin. [GRG]
- Morford, M. & Goldin-Meadow, S. (1992) Comprehension and production of gesture in combination with one-word speakers. *Journal of Child Language* 19:559–80. [SDK]
- Morgan, M. J. (1991) The asymmetrical genetic determination of laterality: Flatfish, frogs and human handedness. In: *Biological asymmetry and handedness*, ed. G. R. Bock & J. Marsh. Wiley. [aMCC]
- Morgan, M. J. & Corballis, M. C. (1978) On the biological basis of human laterality: II. The mechanisms of inheritance. *Behavioral and Brain Sciences* 2:269–77. [aMCC]
- Morrow, P. (1990) Symbolic actions, indirect expressions: Limits to interpretations of Yup'ik society. *Inuit Studies* 14:141–58. [TMP]
- Mueller, U. & Mazur, A. (2001) Evidence of unconstrained directional selection for male tallness. *Behavioral Ecology and Sociobiology* 50:302–11. [CF]
- Neidle, C., Kegl, J., MacLaughlin, D., Bahan, B. & Lee, R. G. (2000) *The syntax of American Sign Language*. MIT Press. [arMCC]
- Neville, H. J., Bavelier, D., Corina, D., Rauschecker, J., Kami, A., Lalwani, A., Braun, A., Clark, V., Jezzard, P. & Turner, R. (1997) Cerebral organization for deaf and hearing subjects: Biological constraints and effects of experience. *Proceedings of the National Academy of Sciences USA* 95:922–29. [aMCC]
- Newell, K. M. (1986) Constraints on the development of coordination. In: *Motor development in children: Aspects of coordination and control*, ed. M. G. Wade & H. T. A. Whiting. Nijhoff. [AVP]
- Nishida, T. (1980) The leaf-clipping display: A newly discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution* 9:117–28. [ACA]
- Nishitani, N. & Hari, R. (2000) Temporal dynamics of cortical representation for action. *Proceedings of the National Academy of Science USA* 97:913–18. [aMCC, SHJ-F, GVJ]
- (2002) Viewing lip forms. Cortical dynamics. *Neuron* 36:1211–20. [CB]
- Noble, W. & Davidson, I. (1996) *Human evolution, language and mind: A psychological and archaeological inquiry*. Cambridge University Press. [AAB, MAA]
- Nottebohm, F. (1977) Asymmetries for neural control of vocalization in the canary. In: *Lateralization in the nervous system*, ed. S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer. Academic. [aMCC, UJ]
- Oakley, K. P. (1972) *Skill as a human possession*. In: *Perspectives on human evolution* 2, ed. S. L. Washburn & P. Dolhinow. Holt, Rinehart and Winston. [AAB]
- O'Callaghan, M. J., Tudehope, D. I., Dugdale, A. E., Mohay, H., Burns, Y. & Cook, F. (1987) Handedness in children with birthweights below 1,000g. *Lancet* 1:1155. [CF]
- Ohnuma, K., Kenichi, A. & Akazawa, T. (1997) Transmission through verbal and non-verbal communication: Preliminary experiments in Levallois Flake production. *Journal of Anthropological Science* 105:159–68. [TMP]
- Oldfield, R. C. (1971) The assessment and analysis of handedness: The Edinburgh Handedness Inventory. *Neuropsychologia* 9:97–113. [aMCC]
- Olivier, G. (1978) Anthropometric data on left-handed. *Biométrie Humaine* 13:13–22. [CF]

- Olson, D. A., Ellis, J. E. & Nadler, R. D. (1990) Hand preferences in captive gorillas, orangutans, and gibbons. *American Journal of Primatology* 20:83–94. [AVP]
- Oztop, E. & Arbib, M. A. (2002) Schema design and implementation of the grasp-related mirror neuron system. *Biological Cybernetics* 87:116–40. [SHJ-F]
- Oztop, E., Bradley, N. & Arbib, M. A. (2003) Infant grasp learning: A computational model (submitted). [MAA]
- Passingham, R. E. (1981) Broca's area and the origin of human vocal skills. *Philosophical Transactions of the Royal Society B* 29:167–75. [rMCC, NDC]
- Patterson, F. (1978) Conversations with a gorilla. *National Geographic* 154:438–65. [aMCC]
- Paulesu, E., Frith, C. D. & Frackowiak, R. S. J. (1993) The neural correlates of the verbal component of working memory. *Nature* 362:342–45. [GJ]
- Pawlowski, B., Dunbar, R. I. M. & Lipowicz, A. (2000) Tall men have more reproductive success. *Nature* 403:156. [CF]
- Paxinos, G., Huang, X.-F. & Toga, A. W. (2000) *The rhesus monkey brain in stereotaxic coordinates*. Academic Press. [UJ]
- Pedersen, A. V., Størksen, J. H. & Vereijken, B. (2002) Lateral biases in the development of infant walking. Poster presentation at the Seventh European Workshop on Ecological Psychology, Bendor, France, July 2002. [AVP]
- Pedersen, P. M., Jørgensen, H. S., Nakayama, H., Raaschou, H. O. & Olsen, T. S. (1995) Aphasia in acute stroke: Incidence, determinants and recovery. *Annals of Neurology* 38:659–66. [MA]
- Peters, M. (1988) Footedness: Asymmetries in foot preference and skill and neuropsychological assessment of foot movement. *Psychological Bulletin* 103:179–92. [AVP]
- Petrides, M. (1994) Frontal lobes and behaviour. *Current Opinion in Neurobiology* 4:207–11. [SHJ-F]
- Petrides, M. & Pandya, D. N. (1999) Dorsolateral prefrontal cortex: Comparative cytoarchitectonic analysis in the human and macaque brain and corticocortical connection patterns. *European Journal of Neuroscience* 11:1011–36. [UJ]
- Pettito, L. A. S., Holowka, S., Sergio, L. E. & Ostry, D. (2001) Language rhythms in baby hand movements. *Nature* 413:35–36. [rMCC]
- Pilcher, D. L., Hammock, E. A. D. & Hopkins, W. D. (2001) Cerebral volumetric asymmetries in non-human primates: A magnetic resonance imaging study. *Laterality* 6:165–79. [SFW]
- Pinker, S. (1994) *The language instinct*. Morrow. [arMCC]
- Pinker, S. & Bloom, P. (1990) Natural language and natural selection. *Behavioral and Brain Sciences* 13:707–84. [arMCC]
- Place, U. T. (2000) The role of the hand in the evolution of language. *Psycoloquy* 11. [AR]
- Ploog, D. (2002) Is the neural basis of vocalization different in non-human primates and *Homo sapiens*? In: *The speciation of modern Homo Sapiens*, ed. T. J. Crow. Oxford University Press. [rMCC]
- Plooi, F. X. (1978) Some basic traits of language in wild chimpanzees? In: *Action, gesture and symbol: The emergence of language*, ed. A. Lock. Academic Press. [ACA, RSF]
- Popper, K. R. (1959) *The logic of scientific discovery*. Unwin Hyman. [TED]
- Povinelli, D. J. (1993) Reconstructing the evolution of mind. *American Psychologist* 48:493–509. [SDK]
- Povinelli, D. J. & Eddy, T. J. (1996) What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development* 62(3), Serial No. 247. [DAL]
- Pratt, R. T. C. & Warrington, E. K. (1972) The assessment of cerebral dominance with unilateral ECT. *British Journal of Psychiatry* 121:327–28. [aMCC]
- Premack, D. (1986) *Gavagai! Or the future history of the animal language controversy*. MIT Press. [SFW]
- Previc, F. H. (1991) A general theory concerning the prenatal origins of cerebral lateralization in humans. *Psychological Review* 98:299–334. [AAB, aMCC, LR]
- Provins, K. A. (1997) Handedness and speech: A critical appraisal of the role of genetic and environmental factors in the cerebral lateralization of function. *Psychological Review* 104:554–71. [aMCC]
- Pujol, J., Deus, J., Losilla, J. M. & Capdevila, A. (1999) Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology* 52:1038–43. [aMCC]
- Pulvermüller, F. (1999) Words in the brain's language. *Behavioral and Brain Sciences* 22:253–79. [CB]
- Pulvermüller, F., Härle, M. & Hummel, F. (2001) Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain and Language* 78:143–68. [SDK]
- Pulvermüller, F., Neining, B., Elbert, T., Mohr, B., Rockstroh, B., Koebbel, P. & Taub, E. (2001) Constraint-induced therapy of chronic aphasia after stroke. *Stroke* 32:1621–26. [CB]
- Ramsay, D. S. (1984) Onset of duplicated syllable babbling and unimanual handedness in infancy: Evidence for developmental change in hemispheric specialization? *Developmental Psychology* 20:64–71. [JMI]
- (1985) Fluctuations in unimanual hand preference in infants following onset of duplicated syllable babbling. *Developmental Psychology* 21:318–24. [JMI]
- Ramsay, D. S. & Willis, M. P. (1984) Organization and lateralization of reaching in infants: An extension of Bresson et al. *Neuropsychologia* 22:639–41. [JMI]
- Rauscher, F. H., Krauss, R. M. & Chen, Y. S. (1996) Gesture, speech, and lexical access: The role of lexical movements in speech production. *Psychological Science* 7:226–31. [rMCC]
- Raymond, M. & Pontier, D. (in press) Is there a geographical variation of human handedness? *Laterality*. [CF]
- Raymond, M., Pontier, D., Dufour, A.-B. & Möller, A. P. (1996) Frequency-dependent maintenance of left handedness in humans. *Proceedings of the Royal Society of London B* 263:1627–33. [CF]
- Rimpau, J. B., Gardner, R. A. & Gardner, B. T. (1989) Expression of person, place, and instrument in ASL utterances of children and chimpanzees. In: *Teaching sign language to chimpanzees*, ed. R. A. Gardner, B. T. Gardner & T. E. van Cantfort. SUNY Press. [RSF]
- Rizzolatti, G. & Arbib, M. A. (1998) Language within our grasp. *Trends in Neuroscience* 21:188–94. [CC, aMCC, TED, RD, RSF, SHJ-F, UJ, SDK, LR]
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G. & Matelli, M. (1988) Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research* 71:491–507. [SHJ-F]
- Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. (1996a) Premotor cortex and the recognition of motor actions. *Cognitive Brain Research* 3:131–41. [aMCC, SHJ-F, GVJ]
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D. & Fazio, F. (1996b) Localization of grasp representation in humans by PET: Observation versus execution. *Experimental Brain Research* 111:246–52. [AAB, aMCC, SHJ-F]
- Rizzolatti, G., Fogassi, L. & Gallese, V. (2000) Mirror neurons: Intentionality detectors? *International Journal of Psychology* 35:205. [SHJ-F]
- Rizzolatti, G. & Luppino, G. (2001) The cortical motor system. *Neuron* 31:889–901. [SHJ-F]
- Rizzolatti, G., Luppino, G. & Matelli, M. (1998) The organization of the cortical motor system: New concepts. *Electroencephalography and Clinical Neurophysiology* 106:283–96. [SHJ-F]
- Rizzolatti, G., Scandolara, C., Gentilucci, M. & Camarda, R. (1981) Response properties and behavioral modulation of “mouth” neurons of the postarcuate cortex (area 6) in macaque monkeys. *Brain Research* 255:421–24. [UJ]
- Roberts, W. W. (1949) The interpretation of some disorders of speech. *Journal of Mental Science* 95:567–88. [aMCC]
- Rochat, P. (1989) Object manipulations and exploration in 2- to 5-month-old infants. *Developmental Psychology* 25:871–84. [JMI]
- Rogalewski, A., Floel, A., Breitenstein, C. & Knecht, S. (2003) *From mouth to hand: Prosody in spoken language activates the hand motor system* (under review). [CB]
- Rogers, L. J. (2000) Evolution of side biases: Motor versus sensory lateralization. In: *Side bias: A neuropsychological perspective*, ed. M. K. Mandal, M. B. Bulman-Fleming & G. Tiwara. Kluwer. [aMCC]
- Rogers, L. J. & Bradshaw, J. L. (1996) Motor asymmetries in birds and nonprimate mammals. In: *Manual asymmetries in motor performance*, ed. E. Digby & E. A. Roy. CRC Press. [AR]
- Romanes, G. J. (1888) *Mental evolution in man: Origin of human faculty*. Keegan Paul, Trench and Company. [JMI]
- Romanski, L. M. & Goldman-Rakic, P. S. (2002) An auditory domain in primate prefrontal cortex. *Nature Neuroscience* 5:15–16. [UJ]
- Rönnqvist, L. (1995) A critical examination of the Moro response in newborn infants – symmetry, state relation, underlying mechanisms. *Neuropsychologia* 33:713–26. [LR]
- Rönnqvist, L. & Hopkins, B. (1998) Head position preference in human newborn: A new look. *Child Development* 69:13–23. [LR]
- Rönnqvist, L., Hopkins, B., van Emmerik, R. & de Groot, L. (1998) Lateral biases in spontaneous head turning and the Moro response in the human newborn: Are they both vestibular in origin? *Developmental Psychobiology* 33:339–49. [AVP, LR]
- Ross, E. D. & Mesulam, M.-M. (1979) Dominant language functions of the right hemisphere? Prosody and emotional gesturing. *Archives of Neurology* 36:144–48. [UJ]
- Rossi, G. F. & Rosadini, G. (1967) Experimental analyses of cerebral dominance in man. In: *Brain mechanisms underlying speech and language*, ed. C. H. Milliken & F. L. Darley. Grune and Stratton. [aMCC]
- Ryding, E., Bradvik, B. & Ingvar, D. (1987) Changes in regional cerebral bloodflow measured simultaneously in the right and left hemispheres during automatic speech and humming. *Brain* 110:1345–58. [CC]
- Sandler, W. & Lillo-Martin, D. (2000) Natural sign languages. In: *The Blackwell handbook of linguistics*, ed. M. Aronoff & J. Rees-Miller. Blackwell. [PFM]

- Savage-Rumbaugh, S., Shanker, S. G. & Taylor, T. J. (1998) *Apes, language, and the human mind*. Oxford University Press. [aMCC]
- Sekiyama, K., Miyauchi, S., Imaruoka, T., Egusa, H. & Tashiro, T. (2000) Body image as a visuomotor transformation device revealed in adaptation to reversed vision. *Nature* 407:374–77. [aMCC]
- Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N. & Mowbray, K. (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–36. [aMCC]
- Semino, O., Passarino, G., Oefner, P. J., Lin, A. A., Arbuzova, S., Beckman, L. E., De Benedictis, G., Francalacci, P., Kouvatsi, A., Limborska, S., et al. (2000) The genetic legacy of Paleolithic *Homo sapiens* in extant Europeans: A Y chromosome perspective. *Science* 290:1155–59. [aMCC]
- Senghas, A. & Coppola, M. (2001) Children creating language: How Nicaraguan Sign Language acquired a spatial grammar. *Psychological Science* 12:323–28. [aMCC]
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, C. & Coppens, Y. (2001) First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus des Séances de l'Académie des Sciences* 332:137–44. [AAB]
- Seyal, M., Mull, B., Bhullar, N., Ahmad, T. & Gage, B. (1999) Anticipation and execution of a simple reading task enhance corticospinal excitability. *Clinical Neurophysiology* 110:424–29. [rMCC]
- Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Constable, R. T., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Fletcher, J. M., Shankweller, D. P., Katz, L. & Gore, J. C. (1995) Sex differences in the functional organisation of the brain for language. *Nature* 373:607–609. [CK]
- Sherwood, C. S., Broadfield, D. C., Holloway, R. L., Gannon, P. J. & Hof, P. R. (2003) Variability of Broca's area homologue in great apes: Implications for language evolution. *The Anatomical Record* 217A:276–85. [RLH]
- Sieratzki, J. S. & Woll, B. (2002) Neuropsychological and neuropsychiatric perspectives on maternal cradling preferences. *Epidemiologia e Psichiatria Sociale* 11:170–76. [BW]
- Singh, M., Manjary, M. & Dellatolas, G. (2001) Lateral preferences among Indian school children. *Cortex* 37:231–41. [AVP]
- Skinhøj, E. & Larsen, B. (1980) The pattern of cortical activation during speech and listening in normals and different types of aphasic patients as revealed by regional cerebral blood flow (rCBF). In: *Aphasia: Assessment and treatment*, ed. M. T. Samo & O. Hook. Masson. [CC]
- Skoyles, J. R. (2000) Gesture, language origins, and right handedness. *Psycoloquy* 11. [rMCC, AR]
- Sommer, I. E. C., Ramsey, N. F., Mandl, R. C. W. & Kahn, R. S. (2002) Language lateralization in monozygotic twins concordant and discordant for handedness. *Brain* 125:2710–18. [IECS]
- Speedie, L. J., Wertman, E., T'air, J. & Heilman, K. M. (1993) Disruption of automatic speech following a right basal ganglia lesion. *Neurology* 43:1768–74.
- Spinozzi, G., Castorina, M. G. & Truppa, V. (1998) Hand preference in unimanual and coordinated-bimanual tasks by Tufted Capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 112:183–91. [DC]
- Steele, J. (1999) Stone legacy of skilled hands. *Nature* 399:24–25. [LR]
- (2000) Handedness in past human populations: Skeletal markers. *Laterality* 5:193–220. [AAB, DC]
- Steklis, H. D. & Harnad, S. R. (1976) From hand to mouth: Some critical stages in the evolution of language. In: *Origins and evolution of language and speech*, ed. S. R. Harnad, H. D. Steklis & J. Lancaster. Annals of the New York Academy of Sciences. [aMCC]
- Stokoe, W. C. (1991) Semantic phonology. *Sign Language Studies*. 71:107–14. [DFA]
- (2001) *Language in hand: Why sign came before speech*. Gallaudet University Press. [MAA]
- Stout, D. (2002) Skill and cognition in stone tool production. *Current Anthropology* 43:693–722. [RLH]
- Studdert-Kennedy, M. (1998) The particulate origins of language generativity: From syllable to gesture. In: *Approaches to the evolution of language*, ed. J. R. Hurford, M. Studdert-Kennedy & C. Knight. Cambridge University Press. [CC, aMCC]
- Suddendorf, T. & Corballis, M. C. (1997) Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs* 123:133–67. [TMP]
- Sundara, M., Namasivayam, A. K. & Chen, R. (2001) Observation-execution matching system for speech: A magnetic stimulation study. *NeuroReport* 12:1341–44. [CB]
- Supalla, T. & Newport, E. (1978) How many seats in a chair? The derivation of nouns and verbs in American Sign Language. In: *Understanding language through sign language research*, ed. P. Siple. Academic Press. [MAA]
- Szaflarski, J. P., Binder, J. R., Possing, E. T., McKiernan, K. A., Ward, B. D. & Hammeke, T. A. (2002) Language lateralization in left-handed and ambidextrous people: fMRI data. *Neurology* 59:238–44. [CJ]
- Tan, U. & Tan, M. (1999) Incidences of asymmetries for the palmar grasp reflex in neonates and hand preference in adults. *NeuroReport* 10:3253–56. [AVP]
- Tanaka, S., Kanzaki, R., Yoshibayashi, M., Kamiya, T. & Sugishita, M. (1999) Dichotic listening in patients with situs inversus: Brain asymmetry and situs asymmetry. *Neuropsychologia* 37:869–74. [SFW]
- Tanner, J. E. & Byrne, R. W. (1996) Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology* 37:162–73. [ACA, aMCC, RSF]
- Tattersall, I. (1997) Out of Africa again . . . and again? *Scientific American* 276(4):60–70. [aMCC]
- Temple, C. M. (1990) Academic discipline, handedness and immune disorders. *Neuropsychologia* 28:303–308. [AR]
- Ten Houten, W. (1976) Discussion and criticism: More on split-brain research, culture and cognition. *Current Anthropology* 77:503–506. [CK]
- Terrace, H. S., Pettito, L. A., Sanders, R. J. & Bever, T. G. (1979) Can apes create a sentence? *Science* 206:891–902. [SFW]
- Thelen, E. (1979) Rhythmical stereotypies in normal human infants. *Animal Behaviour* 27:699–715. [JMI]
- (1991) Motor aspects of emergent speech: A dynamic approach. In: *Biobehavioral foundations of language*, ed. N. Krasnegor. Erlbaum. [JMI]
- Thelen, E., Corbetta, D., Kamm, K., Spencer, J. P., Schneider, K. & Zernicke, R. (1993) The transition to reaching: Mapping intention and intrinsic dynamics. *Child Development* 64:1058–98. [JMI]
- Thelen, E., Schöner, G., Scheier, C. & Smith, L. B. (2001) The dynamics of embodiment: A field theory of infant perseverative reaching. *Behavioral and Brain Sciences* 24:1–34. [AVP]
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K. & Farah, M. J. (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Science USA* 94:14792–97. [GJ]
- Tobias, P. V. (1987) The brain of *Homo habilis*: A new level of organization in cerebral evolution. *Journal of Human Evolution* 16:741–61. [aMCC]
- (1998) Water and human evolution. *Out There* 35:38–44. [aMCC]
- Toga, A. W. & Thompson, P. M. (2003) Mapping brain asymmetry. *Nature Reviews Neuroscience* 4:37–48. [AR]
- Tokimura, H., Tokimura, Y., Oliviero, A., Asakura, T., & Rothwell, J. C. (1996) Speech-induced changes in corticospinal excitability. *Annals of Neurology* 40:628–34. [rMCC]
- Tomasello, M. (1999) *The cultural origins of human cognition*. Harvard University Press. [CK, DAL]
- Tomasello, M. & Call, J. (1997) *Primate cognition*. Oxford University Press. [aMCC, DAL]
- Tomasello, M., Call, J., Nagell, K., Olguin, R. & Carpenter, M. (1994) The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates* 35:137–54. [DAL]
- Tomasello, M., Call, J., Warren, J., Frost, G., Carpenter, M. & Nagell, K. (1997) The ontogeny of chimpanzee gestural signals: A comparison across groups and generations. *Evolution of Communication* 1:223–59. [ACA, aMCC]
- Toth, N. (1985) Archeological evidence for preferential right handedness in the lower and middle Pleistocene and its possible implications. *Journal of Human Evolution* 14:607–14. [aMCC]
- Tzourio, N., Crivello, F., Mellet, E., Nkanga-Ngila, B. & Mazoyer, B. (1998a) Functional dominance for speech comprehension in left handers versus right handers. *NeuroImage* 8:1–17. [GJ]
- Tzourio, N., Nkanga-Ngila, B. & Mazoyer, B. (1998b) Left *planum temporale* surface correlates with functional dominance during story listening. *NeuroReport* 9:829–33. [GJ]
- Underhill, P. A., Shen, P. D., Lin, A. A., Jin, L., Passarino, G., Yang, W. H., Kauffman, E., Bonne-Tamir, B., Bertranpetit, J., Francalacci, P., et al. (2000) Y chromosome sequence variation and the history of human populations. *Nature Genetics* 26:358–61. [aMCC]
- Van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. (2003) Orangutan cultures and the evolution of material culture. *Science* 299:102–105. [DAL]
- Veà, J. J. & Sabater-Pi, J. (1998) Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatologica* 69:289–90. [ACA, aMCC]
- Viggiano, M. P. & Vannucci, M. (2002) Drawing and identifying objects in relation to semantic category and handedness. *Neuropsychologia* 40:1482–87. [GVJ]
- Wada, J. A., Clarke, R. & Hamm, A. (1975) Cerebral hemispheric asymmetry in humans. *Archives of Neurology* 32:239–46. [arMCC]
- Walker, A. & Leakey, R. (1993) The postcranial bones. In: *The Nariokotome Homo erectus skeleton*, ed. A. Walker & R. Leakey. Harvard University Press. [AAB]
- Walker, S. F. (1980) Lateralization of functions in the vertebrate brain. *British Journal of Psychology* 71:329–67. [SFW]
- Warrington, E. K. & Pratt, R. T. C. (1973) Language laterality in left handers assessed by unilateral ECT. *Neuropsychologia* 11:423–28. [aMCC]

- Waters, G. & Fouts, R. S. (2002) Sympathetic mouth movements accompanying fine motor movements in five captive chimpanzees (*Pan troglodytes*) with implications toward the evolution of language. *Neurological Research* 24:174–80. [RSF]
- Watkins, K. E., Dronkers, N. F. & Vargha-Khadem, F. (2002) Behavioural analysis of an inherited speech and language disorder: Comparison with acquired aphasia. *Brain* 125:452–64. [rMCC]
- Watson, N. V. (2001) Sex differences in throwing: Monkeys having a fling. *Trends in Cognitive Sciences* 5:98–99. [LR]
- Westergaard, G. C., Kuhn, H. E. & Suomi, S. J. (1998) Bipedal posture and hand preference in humans and other primates. *Journal of Comparative Psychology* 112:55–64. [DC]
- White T. D., Suwa, G. & Asfaw, B. (1994) Australopithecus ramidus, a new species of hominid from Aramis, Ethiopia. *Nature* 371:306–12. [AAB]
- Whitehead, R. L., Schiavetti, N., Whitehead B. H. & Metz, D. E. (1997) Effect of sign task on speech timing in simultaneous communication. *Journal of Communication Disorders* 30:439–55. [PF]
- Wiessner, P. (1982) Risk, reciprocity and social influences in !Kung San economics. In: *Politics and history in band societies*, ed. E. Leacock & R. Lee. Cambridge University Press. [TMP]
- Williams, J. H. G., Whiten, A., Suddendorf, T. & Perrett, D. I. (2001) Imitation, mirror neurons and autism. *Neuroscience and Behavioural Reviews* 25:287–95. [rMCC, AR]
- Wilson, M. L., Hauser, M. D. & Wrangham, R. W. (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour* 61:1203–16. [DAL]
- Wiltschko, W., Traudt, J., Güntürkün, O., Prior, H. & Wiltschko, R. (2002) Lateralization of magnetic compass orientation in a migratory bird. *Nature* 419:467–70. [LW]
- Wise, R. J. S., Greene, J., Büchel & Scott, S. K. (1999) Brain regions involved in articulation. *The Lancet* 353. [CC]
- Witelson, S. F. & Pallie, W. (1973) Left hemisphere specialization for language in the newborn: Neuroanatomical evidence of asymmetry. *Brain* 96:641–46. [rMCC]
- Wittgenstein, L. (1953) *Philosophical Investigations*. Oxford: Blackwell.
- Woll, B. (2001) The sign that dares to speak its name: Echo phonology in British Sign Language (BSL). In: *The hands are the head of the mouth*, ed. P. Boyes-Braem & R. L. Sutton-Spence. Signum Press. [BW]
- Wolpert, L. (1993) *The unnatural nature of science*. Harvard University Press. [rMCC]
- (2003) Causal belief and the origins of technology. *Philosophical Transactions of the Royal Society of London* (in press). [LW]
- Wood, B. A. (1992) Evolution of australopithecines. In: *The Cambridge encyclopedia of human evolution*, ed. S. Jones, R. Martin & D. Pilbeam. Cambridge University Press. [aMCC]
- Wood, B. A. & Collard, M. (1999) The human genus. *Science* 284:65–71. [aMCC]
- Woodruff, G. & Premack, D. (1979) Intentional communication in the chimpanzee: The development of deception. *Cognition* 7:333–62. [DAL]
- Wrangham, R. W. & Peterson, D. (1996) *Demonic males. Apes and the origins of human violence*. Mariner Books/Houghton Mifflin Company. [CF]
- Wray, A. (1998) Protolanguage as a holistic system for social interaction. *Language and Communication* 18:47–67. [MAA]
- Yellen, J. E., Brooks, A. S., Cornelissen, E., Mehlman, M. J. & Stewart, K. (1995) A Middle Stone Age worked bone industry from Katanda, Upper Semliki Valley, Zaire. *Science* 268:553–56. [aMCC]
- Yeo, R. A., Thoma, R. J. & Gangestad S. W. (2002) Human handedness: A biological perspective. In: *Handbook of Neuropsychology*, ed. S. J. Segalowitz & I. Rapin. Elsevier Science. [WDH]
- Zahavi, A. (1993) The fallacy of conventional signalling. *Philosophical Transactions of the Royal Society of London* 340:227–30. [CK]
- Zahavi, A. & Zahavi, A. (1997) *The handicap principle. A missing piece in Darwin's puzzle*. Oxford University Press. [CK]
- Zatorre, R. J., Belin, P. & Penhune, V. B. (2002) Structure and function of auditory cortex: music and speech. *Trends in Cognitive Sciences* 6:37–46. [GJ]
- Zollikofer, C. P. E., Ponce de León, M. S., Vandermeersch, B. & Lévêque, F. (2002) Evidence for interpersonal violence in the St. Césaire Neanderthal. *Proceedings of the National Academy of Sciences USA* 99:6444–48. [CF]