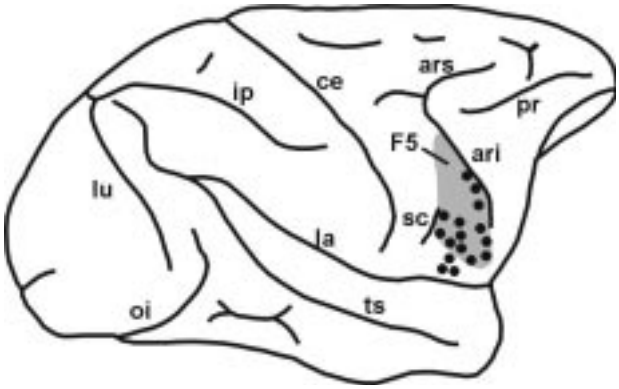


Figure 1 (Jürgens). Lateral view of the rhesus monkey brain with delineation of area F5 according to Matelli and colleagues (1985). Black circles indicate sites yielding vocal fold movements when electrically stimulated (Hast et al. 1974). Abbreviations: *ari*, sulcus arcuatus inferior; *ars*, sulcus 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 audiovocal 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.

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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

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