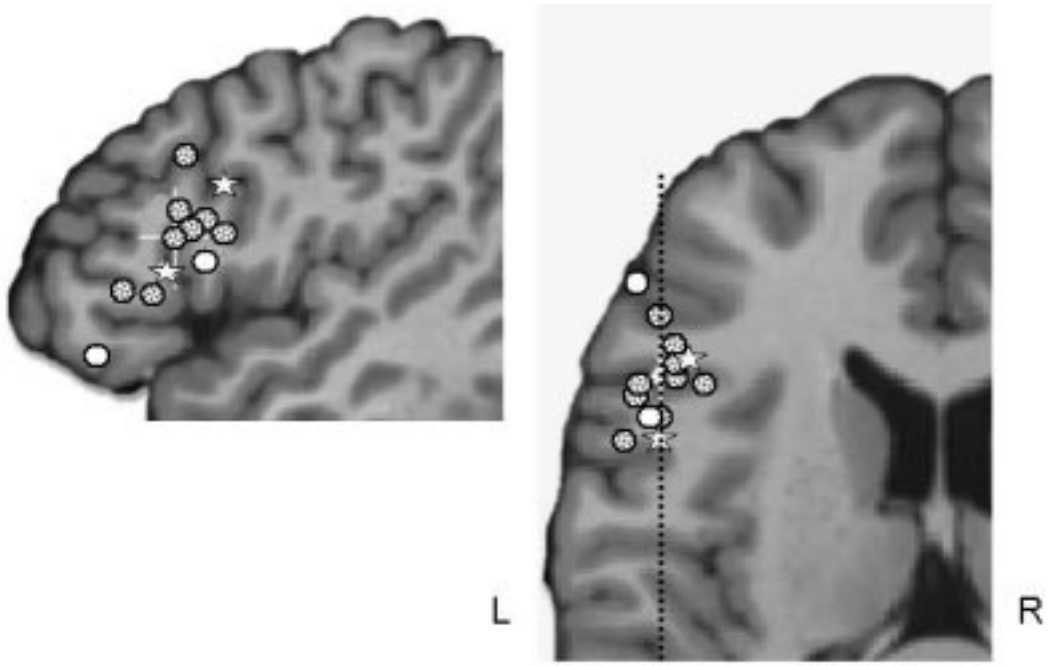


Figure 1 (Josse & Tzourio-Mazoyer). Plots of activity in BROCA during movement imitation (white dot: Chaminade; Iacoboni), working memory (stars: Hautzel; Braver) and executive control tasks (mainly inhibition, grey dots: Dagher; Goel; Houdé; Jonides; Konishi). The sagittal (left) and axial (right) slices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

Uwe Jürgens

German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany.
ujuerge@gwdg.de

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 phylogenetic 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.

https://doi.org/10.1017/S0140525X03450061 Published online by Cambridge University Press

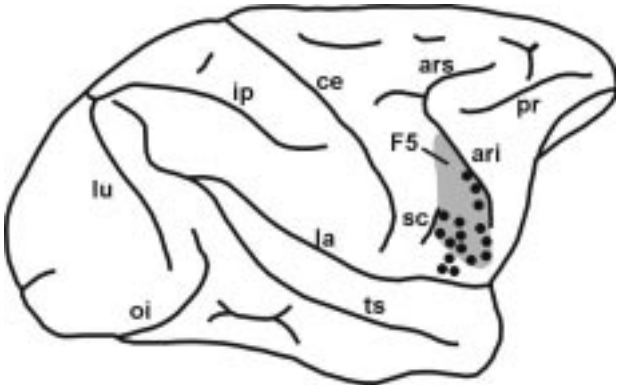


Figure 1 (Jürgens). Lateral view of the rhesus monkey brain with delineation of area F5 according to Matelli and colleagues (1985). Black circles indicate sites yielding vocal fold movements when electrically stimulated (Hast et al. 1974). Abbreviations: *ari*, sulcus arcuatus inferior; *ars*, sulcus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

Spencer D. Kelly

Psychology Department – Neuroscience Program, Colgate University, Hamilton, NY 13346. **skelly@mail.colgate.edu**
http://departments.colgate.edu/psychology/web/kelly.htm

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.

https://doi.org/10.1017/S0140525X03450061 Published online by Cambridge University Press