

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; Plooi (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 exponential 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