

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

Louise Rönnqvist

Department of Psychology, Umeå University, Umeå, Sweden 90187.

[louise.ronnqvist@psy.umu.se](mailto:louise.ronnqvist@psy.umu.se)

[http://www.psy.umu.se/staff/louise\\_ronnqvist\\_eng.html](http://www.psy.umu.se/staff/louise_ronnqvist_eng.html)

**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

Iris E. C. Sommer and René S. Kahn

*Rudolf Magnus Institute of Neuroscience, Department of Psychiatry, University Medical Centre Utrecht, 3584CX Utrecht, The Netherlands.*  
I.Sommer@azu.nl R.Kahn@azu.nl

**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