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.

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