possible world argument in which prescientific hypotheses can be explored. This is not a process amenable to falsification, even though it borrows data from the natural sciences, but it is a process that helps us to think hard about hypotheses we might like to construct. It was this kind of thinking that Darwin put to great effect when constructing his natural history.

Handedness: Neutral or adaptive?

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Abstract: Corballis seems to have not considered two points: (1) the importance of direct selection pressures for the evolution of handedness; and (2) the evolutionary significance of the polymorphism of handedness. We provide arguments for the need to explain handedness in terms of adaptation and natural selection.

According to Michael C. Corballis, the brain lateralization for vocalization might precede the lateralized control of the hands. This certainly has to be taken seriously. However, we would like to comment on two points that he has apparently not considered: (1) the importance of natural selection for the evolution of handedness; and (2) the significance of the polymorphism of handedness.

In the theory presented by Corballis, handedness is described as a neutral character. Right-handedness is regarded as a direct consequence of the left-hemisphere dominance for vocalization. It is, however, difficult to consider handedness as a neutral character. For most manual tasks, especially those tasks involved in competitive activities, increasing performance by the specialization of one hand is certainly adaptive. For example, lateralized cats are faster at catching a virtual prey on a screen with one paw, compared to cats that have not specialized one of their paws (Fabre-Thorpe et al. 1991). In humans, hand or arm lateralization, whatever the side, is probably an adaptation for many activities, such as tool making and tool use (MacNeilage et al. 1987) or stone throwing (Calvin 1982; 1983a; 1987; 1993).

In fights, being lateralized certainly is an advantage. For example, many weapons are held with only one hand. Increasing the power, speed, and maneuverability of a particular arm or hand, that is, specializing it, is certainly pivotal. Aggressive interactions are responsible for fundamental selection pressures acting during primate and human evolution (e.g., Archer 1994; Bridges 1996; Daly & Wilson 1989; Furlow et al. 1998; Guilaine & Zammit 2001; Haas 1990; Wrangham & Peterson 1996; Zollikofer et al. 2002). The higher prevalence of right-handedness might well be due to a previously existing cerebral bias. But the specialization of one forelimb leading to right- or left-handedness is better viewed as the result of natural selection. The constitutive cerebral bias might well have driven the adaptive lateralization towards right-handedness. Nevertheless, it is unclear how the left-brain lateralization for vocalization alone, without natural selection for hand or arm specialization, would lead to the actual right-handedness.

An important problem is not tackled by Corballis's theory. The existence of a polymorphism of handedness remains unexplained. Yet, it is observed in all known human populations (Raymond & Pontier, in press) and described since the Palaeolithic (e.g., Bermùdez de Castro et al. 1988; Groënen 1997a; 1997b; Lalueza & Frayer 1997). Left handedness is associated with several fitness costs (e.g., Aggleton et al. 1993; Annett 1987a; Coren & Halpern 1991; Daniel & Yeo 1994; Gangestad & Yeo 1997; Geschwind & Galaburda 1985a; 1985b;1985c; Grouios et al. 1999; McManus & Bryden 1991). The persistence of an apparently stable proportion of left-handers implies the balancing of these costs by some advantages.

One of the observed costs is the smaller size and weight of left-handers (Coren 1989; O'Callaghan et al. 1987; Olivier 1978). Size is a component of the reproductive value, at least in males (Mueller & Mazur 2001; Pawlowski et al. 2000). However, smaller size and weight is probably not a disadvantage in weapon fights. This is indicated by the fact that weapon fighting sports, such as fencing, do not have weight categories for competitions, as opposed to hand fighting sports, such as boxing. Generally, all sports using an object mediating an interaction between two opponents – racket, sword, ball – do not have weight categories, as opposed to all other interactive sports without such objects. This suggests that when weapons were prevalent in hominids, the weight (and probably height) disadvantage of left-handers in fights was considerably reduced. In addition, a frequency-dependent advantage favours left-handers in interactive sports (Goldstein & Young 1996; Grouios et al. 2000; Raymond et al. 1996). The persistence of the polymorphism of handedness might well be partly explained by an advantage of left-handers in weapon manipulation and fights. This polymorphism, as well as handedness itself, needs to be understood in the view of adaptation and natural selection.

Are human gestures in the present time a mere vestige of a former sign language? Probably not

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Abstract: Right-hand preference for conversational gestures does not imply close connections between the neural systems controlling manual and vocal communication. Use of speech and gestures may dissociate in some cases of focal brain damages. Furthermore, there are limits in the ability to combine spoken words and concurrent hand movements. These findings suggest that discourse production depends on multiple components which probably have different evolutionary origins.

Numerous theories have been advanced in an attempt to explain the manual asymmetry observed in many human activities. Corballis argues for a new evolutionary scenario on the basis of evidence from palaeontology, comparative psychology, and behavioural neuroscience. According to his account, right-handedness in genus Homo derives from an association of gestures and vocal signals in the communicative behaviour of our direct ancestors, whereby the dominant mode of communication progressively shifted from a manual to vocal modality. The hypothesis is intended to be falsifiable and indeed, several aspects of the theory deserve discussion. This commentary aims to examine the relevance of the specific argument concerning present-day human gestural activity. There is no doubt that people gesture as they talk and that in right-handers, these gestures are predominantly performed by the right hand. It does not follow, however, that the primitive language of humankind used the gestural modality and that present-day gestures are merely the remainder of that earlier stage. The alternative view favoured by other investigators is that spoken language derives from vocal communication or, more exactly, that gestures and speech coevolved in parallel from the beginning and that there are only limited connections between the two production systems.

Why do speakers gesture while talking? There is no simple answer to this question because different kinds of gestures probably depend on different mechanisms involved in discourse production. Some hand movements are called *iconic* or *representational* gestures because, like a drawing in the air, they depict the concept they express. Other gestures, sometimes called *beat* or *batonic* gestures, have simpler forms, no meaning, and relate to phrasal stress to emphasise some parts of speech. *Deictic* or *pointing* gestures constitute a third category in which reference is achieved through spatial contiguity. That classification is not complete and it is possible to further subdivide conversational gestures according to a range of discourse functions. As far as representational gestures are concerned, recent observations indicate that the performance of this kind of movement relates to the mental activation of motor images (Beattie & Shovelton 2002; Feyereisen & Havard 1999). In that sense, these conversational gestures derive from action and the right hand is probably preferred because it is the dominant hand during interactions with objects, not the other way around.

Gesture laterality varies with gesture form and meaning. The right hand is preferred for performing representational gestures, but no asymmetry is found as far as beat gestures are concerned (Hostetter & Hopkins 2002; unpublished study of Debra Stephens quoted by McNeill 1982, p. 332). Thus, the claim that vocalisation created right-handedness is not true for all types of gestures: The beat gestures are simple, nonfigurative movements that are closely related to speech but are performed by the two hands in the same proportions.

Unilateral brain damages affect gestures and speech in different ways, and in agreement with Corballis's view, left-hemisphere dominance is stronger for language than for manual activity. Left hemispheric stroke patients were found to perform the same amount of conversational gestures as control subjects: fewer right-hand gestures but more left-hand and bilateral gestures (Foundas et al. 1995b). It was concluded that the right hemisphere contributes to the production of speech-related gestures (see also the complex pattern of lateralization described in a split-brain patient by Lausberg et al. 2000). In a picture description task, the rate of representational gesture production was higher in aphasic patients suffering from naming or repetition impairments than in control subjects, or in aphasics suffering from conceptual impairments (Hadar et al. 1998a). This rate of representational gesture production was lower in right-hemisphere patients suffering from visuo-spatial impairments (Hadar et al. 1998b). Therefore, some aspects of speech production (lexical access, phonological encoding) depend on different brain structures from those controlling the production of representational gestures, which entail visuo-spatial processing. Motor and verbal representations may be combined on another, preverbal level, during the conceptualisation of the message.

Combining words and gestures in discourse has a cost, however, and it constitutes a particular instance of dual-task performance. Vocal responses were delayed in a choice reaction time task when a representational or deictic gesture was to be performed concurrently (Feyereisen 1997; Levelt et al. 1985). Similarly, temporal characteristics of speech were altered when manual signs and spoken words were combined in simultaneous communication, a procedure aimed at augmenting the input available to deaf listeners (e.g., Whitehead et al. 1997). Thus, we see that there is competition between the two production systems and there are constraints in the development of a integrated bimodal system. In natural conversations, representational gestures are often performed during silent pauses to reduce such interference.

There are also limits to the combination of words and gestures on a morpho-syntactic level. Unlike manual signs, conversational hand gestures do not display the dual patterning found in spoken language. They are not built from elementary, meaningless units (kinemes) and they do not combine to form larger phrasal units. Nonetheless, in some circumstances, when speakers are prevented from using language to communicate, more complex manual signs can be invented (Goldin-Meadow et al. 1996). Similarly, during language acquisition, there is a transition phase during which hearing children combine a word and a gesture but provide no instances of gesture sequences (e.g., pointing to a bottle of milk and miming the act of drinking: Capirci et al. 1996). The development of vocal communication prevents manual gestures from developing into a full-fledged sign language, as happens in deaf communities. As a result, conversational gestures lack syntactic properties, and it is somewhat difficult to imagine that during evolution, syntax first appeared in a proto-sign language and then disappeared in the manual modality when vocal communication became dominant.

Analyses of conversational gestures in normal and brain-damaged individuals are consistent with the hypothesis of piecemeal evolution of separate components of language and action (Feyereisen 1999). In its broad sense, language use, be it vocal or manual, involves several specialised subsystems, some of which operate on distinct parameters and depend in part on specific brain regions.

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Unbalanced human apes and syntax

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Abstract: We propose that the fine discrete movements of the tongue as used in speech are what account for the extreme lateralization in humans, and that handedness is a mere byproduct of tongue use. With regard to syntax, we support the Armstrong et al. (1995) proposition that syntax derives directly from gestural motor movements as opposed to facial expressions.

We will discuss two areas in which we disagree with Corballis with regard to his hypothesis concerning the gestural origin of language. They are: (1) the importance of the tongue in lateralization, and (2) the importance of gesture as the prime mechanism for the evolution of syntax.

With regard to lateralization, Corballis places too much emphasis on handedness. He advances a gestural theory for the origin of language, yet he focuses on vocalization as a driving force for lateralization. It is this focus that perhaps led him astray on two accounts. First, it is possible that the trend toward lateralization for vocalization that Corballis suggests, is merely a side-effect of a general trend toward a lateralization for communication. For example, Hook-Costigan and Rogers (1998) found similar individual tendencies toward lateralization as those reported for group level handedness in primates in the hemi-mouth comparisons of marmosets when making communicative versus emotional vocalization and facial gestures.

Second, when nonhuman apes vocalize they do not move their tongues. However, we humans move our tongues extensively when we speak. The problem is to explain how we evolved from not moving our tongues during vocalizations to doing it all the time. As Corballis suggests, the neurological association between the motor movements of the tongue and hand are close; but even Darwin (1889/1998) saw the critical connection between the fine discrete movements of the hand and sympathetic movements of the tongue. For Hewes (1973b), via Darwin, the solution was that the fine discrete movements of the hand facilitated similar movements, with the tongue, of the type we use during speech. Waters and Fouts (2002) found that such sympathetic movements of the tongue and lips accompany the fine motor manipulations performed by chimpanzees to a greater degree than with gross motor movements. Such research, when coupled with theories regarding basic syllabic frames consisting of lip and tongue movements (MacNeilage 1998), provides a better proposal for basic human phonation. Also, it provides a mechanism for the association and transfer of more complex information across modalities.

Once the tongue started moving during speech, it presented a whole new situation with regard to motor control. The tongue is a single medial organ, and we have two competing hemispheres.