

1999a; Ehrsson et al. 2001). Like F5ab, BA45 is selectively activated during perceptual processing of graspable visual objects (Chao & Martin 2000). BAs 44 and 45 exhibit properties similar to mirror neurons in area F5c. More precisely, PET studies report activation of BA45 during observation of grasping (Grafton et al. 1996; Rizzolatti et al. 1996b) and meaningful hand actions (Grezes et al. 1998). Investigations with functional magnetic resonance imaging (fMRI) reveal activation in BA44 during observation of finger movements (Iacoboni et al. 1999) and grasping actions (Buccino et al. 2001). A similar finding has been reported using magnetoencephalography (MEG) during the observation of grasping actions (Nishitani & Hari 2000). These neuroimaging studies report activations primarily within the left ventral premotor cortex during action observation. As Corballis points out, this may indicate that the human mirror system is intimately tied into language processes in Broca's area. By contrast, this asymmetry may be related to confounding effects of subvocalization during task performance (Heyes 2001). A recent fMRI study in my lab that controlled for this possibility detected bilateral BA44/45 activation during observation of transitive prehensile actions (Johnson, under review).

In conclusion, despite the emergence of language processes in Broca's area, visuomotor functions of the rostral ventral premotor cortex have remained relatively unchanged over the millennia separating humans and macaques. These processes were and continue to be involved in constructing representations of transitive prehensile actions, not gestural communication. This continuity across species suggests that language came to this region not by co-opting existing visuomotor functions but rather as a separate and entirely unrelated adaptation. Corballis may be correct in suggesting that handedness arose from a bias originating with the lateralization of vocal communication to the left hemisphere. But, like the left-hemisphere bias for language production, the handedness asymmetry did not take root in a pre-existing gestural communication system.

Dual asymmetries in handedness

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Abstract: The possibility that two forms of asymmetry underlie handedness is considered. Corballis has proposed that right-handedness developed when gesture encountered lateralized vocalization but may have been superimposed on a preexisting two-thirds dominance. Evidence is reviewed here which suggests that the baseline asymmetry is even more substantial than this, with possible implications for brain anatomy and genetic theories of handedness.

At first sight, Corballis appears to be proposing that the high incidence of right-handedness among humans is a consequence of a single factor, namely, an association between manual gestures and vocalization (dominant in the left hemisphere) in the evolution of language. It becomes clear, however, that a second source of asymmetry is also envisioned, and it is observed (sect. 6) that the association with vocalization may have been responsible only for a "shift from a two-thirds to a 90% right-hand dominance." What is the evidence for this two-to-one "preexisting asymmetry" (sect. 5) in favor of using the right hand rather than the left? Corballis refers to an earlier article (Corballis 1997) in which he proposed a modification of the single-gene, two-allele model developed by McManus (1985a; 1999). According to the model, a dextral allele, D, codes for right-handedness, whereas a chance allele, C, leaves handedness open to chance. McManus's assumption that the DD

genotype would be associated always with right-handedness has not been challenged, but his proposal that the other homozygous genotype, CC, would be associated with equal incidences of right-handedness and of left-handedness (i.e., probability of right-handedness = .50) is open to question. Corballis (1997) proposed that the ratio of right-handedness to left-handedness for the CC genotype is not 1 to 1 but instead 2 to 1 (i.e., probability of right-handedness = .67) and showed that this improved the accuracy of predicting a person's handedness on the basis of their parents' handednesses.

It has since been shown (Jones & Martin 2000) that to provide a satisfactory unified account of all the major distributional features of handedness – in particular, the parent, grandparent, twin, and sex influences upon handedness – more drastic modifications are necessary, including the introduction of a ratio of right-handedness to left-handedness in the absence of the D allele of approximately 3.8 to 1 (i.e., probability of right-handedness = .79). The use of the same value of this parameter in accounting quantitatively for distributions in all four areas (i.e., parent, grandparent, twin, and sex effects) provided converging evidence of its appropriateness. Subsequently, extensive new data of McKeever (2000) have also been shown to be in good agreement with the same model (Jones & Martin 2001). This time, the independent estimate of the ratio of right-handedness to left-handedness in the absence of the D allele was approximately 3.5 to 1 (i.e., probability of right-handedness = .78), closely replicating the value estimated previously.

There is evidence, therefore, that not only does the phenotypic baseline deviate from the position of symmetry with regard to the right and left hands, which has been assumed by McManus (1985a; 1999), but also that the deviation is even more extreme than Corballis's proposed 2 to 1 ratio of right-handedness to left-handedness, though of course still considerably less than the overall ratio in the population of approximately 9 to 1 (i.e., probability of right-handedness = .9). What are the consequences of the baseline asymmetry being in fact more extreme than the ratio of 2 to 1 which is assumed by Corballis? Two kinds of implication may be distinguished. First, there are relatively specific knock-on consequences if the same degree of asymmetry is assumed to be manifest in related structures. For example, Corballis notes that Gannon and colleagues (1998) reported a leftward bias in the size of the planum temporale in all but one member of a group of 18 chimpanzees, a result which he describes (sect. 5.1) as "curiously" greater than the 12 cases out of 18 expected on the basis of an asymmetry of two to one ($p < .01$ on a binomial test). However, the apparent anomaly is resolved if the present more extreme asymmetry is adopted, because this produces an acceptable prediction of at least 14 cases of leftward bias out of 18 ($p > .05$ on a binomial test).

A second and particularly interesting implication of the greater degree of baseline asymmetry is a corresponding diminution in the available range of variation in asymmetry that can be attributed to other factors. Within the context of genetic theories of handedness, the phylogenetic contrast between different alleles is thus blunted. This means, for example, that a satisfactory explanation can at last be provided for the relatively low levels of concordance in handedness observed among pairs of twins (see Jones & Martin 2000; 2001; McManus & Bryden 1992). Alternatively, in the context of Corballis's present hypothesis, a higher baseline of asymmetry for language gestures would serve to reduce the magnitude of the putative task of lateralized vocalization in driving up the incidence of right-handedness to its present 90% level, and this could perhaps be explored in the future in the shape of a quantitative model of the proposed shift. Comparing Corballis's present hypothesis more directly with recent genetic approaches to handedness, it would be interesting also to consider how it might accommodate converging theoretical indications of linkage to the X chromosome, irrespective of whether the phenotypic relation is assumed to be recessive (Jones & Martin 2000; 2001) or additive (Corballis 2001).

Finally, an attractive aspect of Corballis's present hypothesis is the central role within the gestural origin of language that is ascribed to mirror neurons (e.g., Nishitani & Hari 2000; Rizzolatti et al. 1996a) in Broca's area and its monkey homologue. Jeannerod (1994; 1997) has used the general term of motor imagery for those patterns of neural activation that occur in the absence of movement but that nevertheless resemble the patterns accompanying actual movements. Relatively small but consistent associations between handedness and level of cognitive performance have been observed for a number of tasks in the laboratory, appearing to provide evidence for the involvement of motor imagery in processes that include those of memory and perception (e.g., Martin & Jones 1998; 1999) and categorization (e.g., Viggiano & Vannucci 2002). The identification of motor imagery as mediating the interaction between characteristic patterns of motor behavior and relatively abstract cognitive processes would appear to fit well with Corballis's hypothesized nexus for gesture, language, and vocalization.

What functional imaging of the human brain can tell about handedness and language

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Abstract: Anatomic-functional studies in humans point out that handedness and language-related functional laterality are not correlated – except during language production; and that the convergence of language and hand control is located in the precentral gyrus, whereas executive functions required by movement imitation and phonological and semantic processing converge onto Broca's area. Multiple domains are likely to be actors in language evolution.

Corballis's hypothesis is based on the co-occurrence in humans of right-handedness and left-hemispheric specialization for language. We want to point out that this co-occurrence does not imply that handedness and language-related asymmetries are correlated, even in our species. The exact nature of this relation has yet to be understood. Functional imaging provides a unique opportunity to investigate hemispheric specialization for different language components in distinct brain areas and is beginning to shed some light on this issue. This approach has so far provided results confirming the heterogeneity of left-handers compared to right-handers (Szaflarski et al. 2002; Tzourio et al. 1998a), but the relation between handedness and hemispheric language specialization may not go beyond this group difference.

Functional imaging allows the direct testing of the correlation between handedness and brain activity during various tasks. This approach has led to evidence of a significant correlation between a handedness score and functional cerebral asymmetry of the motor cortex during a manual task. This result attests the strong proximity between handedness and the functional lateralization of the motor cortex (Dassonville et al. 1998). Such proximity does not exist between handedness and functional brain asymmetry for language. No correlation (in the statistical sense) was observed between handedness and speech listening (Josse et al. 2002; Tzourio et al. 1998b). Szaflarski reported a significant although weak correlation ($R^2 = 0.1$ at most) between the degree of handedness and the degree of lateralization associated with a semantic task (Szaflarski et al. 2002). However, most subjects pertaining to this study did not fit this linear relation (see Fig. 4 in that article). In our view such a correlation rather reflects the group difference described above. In other words, no results so far have really supported the assumption that the stronger the right-handedness is, the stronger is the leftward asymmetry of language areas during speech processing. Rather, the consensus seems to be limited to

the fact that a right-handed person is more likely to have a left hemisphere dominant for language, than is a left-handed person.

Actually, because handedness seems to rely on a functional asymmetry of the frontal motor region, it may well be that handedness is more closely related to frontal language regions and to motor aspects of language than to its perceptive components. Some recent results support this hypothesis. Indeed, although we could not find evidence of any handedness effect on speech-listening functional data, we did find in the same subjects such an effect on functional data related to verb generation (Josse et al. 2002). Interestingly, one of the differences between these two language tasks is that verb generation relies more on frontal motor regions than does speech listening. Note also that Szaflarski and collaborators observed that the effect of handedness on semantic-related data was more pronounced on frontal regions.

A stronger relationship emerges from the study of neuro-anatomical asymmetries and language hemispheric specialization evaluated with functional imaging. For example, subjects with a larger left planum temporale recruited more of some of the left hemisphere regions while listening to speech (Josse et al. 2002; Tzourio et al. 1998b), which partly supports Geschwind's hypothesis that anatomical asymmetries are markers of functional hemispheric specialization for language (Geschwind & Levitsky 1968). This can be linked to a theory by Zatorre stating that language hemispheric specialization emerged from constraints imposed by the processing of language sounds (cf. Zatorre et al. 2002), which proposes another scenario for language evolution focused on perceptive aspects.

Another part of the author's argument about the emergence of language left-hemisphere specialization in humans is founded on the close topographical relationship of mouth and hand sensorimotor cortices, which supposedly allowed interactions between vocalization and manual control during evolution. The author suggests that the seat of the convergence of manual and vocal control would be located within Broca's area (BROCA). This hypothesis needs to be qualified with respect to the anatomical location of BROCA. Recalling that BROCA includes the pars opercularis and the pars triangularis of the left inferior frontal gyrus, it must be underlined that functional imaging has challenged Broca's original observation (Broca 1861a) and demonstrated that BROCA is involved neither in simple motor control of manual activity nor in speech articulation. Rather, the convergence of these functions lies posterior to BROCA, in cortical motor and premotor areas within the precentral gyrus (with the anterior insula for speech articulation; Dronkers 1996). As a matter of fact, an attentive reading of language functional imaging studies reveals a robust and constant involvement of precentral areas not only during speech production but also during language comprehension and reading, consistent with the idea that speech production and manual control interacted during the evolution process.

BROCA is involved in the executive control of phonological processing (Paulesu et al. 1993) and semantic knowledge (Thompson-Schill et al. 1997). Its implication during movement imitation is in line with such an executive role, also evidenced during working memory and executive tasks. In order to document this statement, we conducted a short survey of several functional imaging studies dealing with movement imitation (Chaminade et al. 2002; Iacoboni et al. 1999), working memory (Braver & Bongiolatti 2002; Hautzel et al. 2002), and executive control, including inhibition (Dagher et al. 1999; Goel et al. 1997; 1998; 2000; Houdé et al. 2000; Jonides et al. 1998; Konishi et al. 1998a; 1998b; 1999; 2002). All studies reported an activation of BROCA (labeled ventral prefrontal in working memory studies), whether the material was verbal or not (see Fig. 1 here, and the review by D'Esposito et al. 2000). This convergence of language control, executive functions, and movement imitation in prefrontal areas, dedicated to higher-order cognition in monkeys, may also be part of the emergence of human syntax.

This evidence suggests that the emergence of language could