When Did Directional Asymmetry Enter the Record?

JAMES STEELE

Summary. This chapter reviews evidence for the evolution of primate asymmetries in brain morphology and in behaviour, including the fossil and archaeological record of human evolution. This evidence suggests that, while morphological asymmetries are conserved features of the human brain, human functional asymmetries are derived, at least in their degree and consistency. A partial explanation is offered that takes account of allometric scaling in the evolution of brain size, neocortex size, and intra- and interhemispheric connectivity.

INTRODUCTION

LATERALITY OF FUNCTION is a well-described feature of human cognition, in language processing as well as in other tasks. Because human language has no obvious parallel in the cognitive and communication systems of other animals, it is reasonable to assume that there must be some derived feature of the organisation of the human cerebral hemispheres that reflects past selection for the language capacity. However, the issue is complicated by the existence of human polymorphisms both in aspects of behavioural laterality (such as handedness and language lateralisation), and in aspects of morphological asymmetry of the cerebral hemispheres (such as the larger side by volume, by surface area, or by some other dimension of shape in an area relevant to language processes). The rather low levels of heritability of such right–left asymmetries (best documented in the case of left-handedness) further complicate matters. There is therefore huge appeal in genetic models such as those of Annett (1995), Tim Crow (see the chapter in these *Proceedings*) and McManus (1999), which account for these polymorphisms and for observed levels of heritability of handedness while retaining selection for language (and for an optimal degree of lateralisation) as the evolutionary driving force.

At their current stage of development, however, these models all assume that human patterns of behavioural laterality and morphological brain asymmetry are unique and derived. There is an increasing body of evidence that this is not the case. If such evidence proves to be reliable, then we may need to modify these models significantly if they are to account for the appearance of human language as an adaptation. In this chapter I will review some of the most relevant comparative and evolutionary anatomical observations, and I will tentatively suggest an alternative account of the some of the more relevant aspects of human brain evolution.

FOSSIL AND COMPARATIVE DATA ON THE EVOLUTION OF HUMAN BRAIN ASYMMETRY

One of the keystones of the hypotheses of Crow, Annett and McManus is the premise that population-level right-handedness is a derived human trait reflecting an underlying brain adaptation for cognitive laterality (and, specifically, a population-level left-hemisphere dominance for speech processes). Certain key findings are cited recurrently; examples of such evidence from the period of human evolution prior to *Homo sapiens* include Holloway & de la Coste-Lareymondie's (1982) work on cerebral asymmetries in hominid skulls and endocasts, and Toth's (1985) experimental work on the preferential direction of rotation of the stone core by right-handed tool makers and his argument from archaeological evidence that this preference was characteristic of early Palaeolithic stone tool makers as well.

Although these genetic models identify lateralised brain processes as the focus of selection, their principal control data describe modern prevalence rates of right- and left-handedness. Similarly, when we conflate evidence of Palaeolithic right-handedness with that for morphological brain asymmetry, we are assuming that the one is somehow caused by the other. Studies have indeed shown a relationship between gross morphological asymmetries of the cerebral hemispheres and handedness, but the correlations are quite weak and are complicated by sex- and population-specific variation (Steele, 2000a). Steele (2000a: table 1) summarises observations of brain and skull asymmetry in human populations. It is apparent that there is a tendency for greater dimensions of the left occipital and right frontal poles, where these differ significantly from symmetry.

The clearest evidence from the fossil record relates to 'petalia' patterns. Following Cheverud *et al.* (1990: 368), petalias are defined as follows:

> the greater anterior or posterior protrusion of one cerebral lobe relative to the other. The protruding lobe may also be wider. In humans, both frontal and occip-

ital petalias are quite common, with the typical pattern consisting of a right frontal petalia and a left occipital petalia.

Steele (2000a: table 7) has summarised data from endocasts of hominid skulls. These indicate a preponderance of left occipital and right frontal width as well as length asymmetries in hominids as far back as early *Homo*, and perhaps including the later Australopithecines as well. If we accept that this pattern of brain morphology is associated with predominant right-handedness, then this too would be expected to have characterised these earlier species as long ago as 2–2.5 million years before the present.

If these brain asymmetries reflect the underlying features that cause human patterns of behavioural laterality (including handedness), then we should expect their evolutionary appearance to coincide with that of population-level right-handedness. However, with respect to the origin of this brain morphological pattern, data from studies of great apes suggest that it has an even more ancient ancestry in the primate lineage. Table 1 summarises observations of the same variables in the great apes. These data suggest that left occipital and right frontal length petalias are conservative features of the human brain, shared with the apes [however, Zilles *et al.* (1996) found no significant directional asymmetry in the length petalia patterns of chimpanzees ($n = 9$)]. The low incidence of occipital width asymmetry (and the relatively low incidence of frontal width asymmetry) in the apes in the earlier studies recorded in Table 1 is notable, as occipital width asymmetry is the dimension which seems to be most significantly associated with hand preference in humans (Steele, 2000a). However, we should note also that this contrast in the data reflects the high percentage of cases of great ape endocasts where Holloway & de la Coste-Lareymondie (1982) could recognise no width asymmetry by visual inspection, whereas LeMay *et al.* (1982) were able to recognise its presence more often using quantitative analyses of outlines of great ape endocasts (which were computer-detected from telephotographs by thresholding). The absolute size of great ape brains is about one-third by volume of that of humans, which will make such asymmetries harder to detect by eye in the great ape material. In one recent study, Hopkins & Marino (2000) found significant directional asymmetry of the human pattern in occipital and frontal width in a larger pooled sample of 19 great apes (nine chimpanzees, four orang-utans, two gorillas and four bonobos) (see also Pilcher *et al.*, 2001). Clearly there is scope for additional work on further samples of great ape brains and crania in order to resolve this issue.

Although Hopkins & Marino (2000) found no significant directional asymmetries of width in the cerebral hemispheres of Old and New World monkeys, Heilbroner & Holloway (1988) did find more localised temporal lobe asymmetries, greater length of the Sylvian fissure in the left hemisphere, in four out of

Table 1. Incidences of great ape brain asymmetry (frontal and occipital poles)

Species and study	Frontal length			Frontal width			Occipital length			Occipital width		
	R↑	=	L↑	R>	=	L>	R↓	=	L↓	R>	=	L>
(a) BRAIN ASYMMETRIES												
Pongo pygmaeus												
LeMay (1976) (brains)	–	–	–	–	–	–	3	9	0	2	8	2
LeMay et al. (1982) (endocasts)	5	1	0	3	3	0	0	2	4	0	4	2
Holloway & de la Coste-Lareymondie (1982) (endocasts)	–	–	–	6	13	1	4	11	5	0	19	1
Gorilla gorilla												
LeMay (1976) (brains)	–	–	–	–	–	–	5	0	2	3	1	3
LeMay et al. (1982) (endocasts)	4	2	0	4	2	0	0	2	4	0	2	4
Holloway & de la Coste-Lareymondie (1982) (endocasts)	–	–	–	17	21	2	3	9	28	2	31	7
Pan troglodytes												
LeMay (1976) (brains)	–	–	–	–	–	–	3	6	0	1	2	6
LeMay et al. (1982) (endocasts)	3	2	1	1	4	1	0	3	3	0	3	3
Holloway & de la Coste-Lareymondie (1982) (endocasts)	–	–	–	8	21	5	9	13	12	3	31	0
Pan paniscus												
Holloway & de la Coste-Lareymondie (1982) (endocasts)	–	–	–	22	15	4	10	11	20	4	36	1
Total incidence	**12**	**5**	**1**	**61**	**79**	**13**	**37**	**66**	**78**	**15**	**137**	**27**
(b) CRANIAL VAULT ASYMMETRIES												
Pongo pygmaeus												
LeMay et al. (1982)	3	3	2	–	–	–	4	0	4	–	–	–
Gorilla gorilla												
LeMay et al. (1982)	8	2	3	–	–	–	2	2	7	–	–	–
Pan troglodytes												
LeMay et al. (1982)	6	4	2	–	–	–	2	3	7	–	–	–
Total incidence	**17**	**11**	**7**	**–**	**–**	**–**	**8**	**5**	**18**	**–**	**–**	**–**

five Old and New World monkey species studied, where the study group consisted of large samples ($n = 20$–30) of formalin-fixed brain specimens. Gilissen (1992) made similar findings in capuchin monkeys, but not in spider monkeys. LeMay (1985) had earlier found a human-like pattern of asymmetry in Sylvian fissure length in great apes, but not in monkeys. These findings are relevant because the length of the Sylvian fissure is taken as an indicator of the surface area of the planum temporale, an area of the temporal lobe involved in speech processing (cf. Galaburda *et al.*, 1987). More recently, Gannon *et al.* (1998) have reported direct surface area measurements showing a larger planum temporale in the left hemisphere of 17 out of 18 chimpanzee brains studied, and Hopkins *et al.* (1998) [using magnetic resonance imaging (MRI) scan data] have reported a significant size bias towards the left hemisphere in a sample of 21 great apes (of whom 16 had greater planum temporale length in the left hemisphere). A similar result has also been reported by Gilissen *et al.* (1998) for common chimpanzees, while Gannon & Kheck (1999) also found a larger left planum temporale in the majority of a small sample of both gorilla and orangutan brains ($n = 6$ and $n = 7$, respectively). Finally, Gannon *et al.* (2000) have also reported a significant left over right asymmetry for volume of the planum temporale (defined cytoarchitectonically) in an Old World monkey (*Macaca fascicularis*).

These observations of morphological brain asymmetries in humans, in our hominid ancestors, and in other living primates suggest continuity rather than discontinuity. It is certainly hard to sustain the view that morphological brain asymmetry in these dimensions is a unique derived human trait representing a speciation event in the appearance of *H. sapiens*. Other more subtle morphological features of the human brain may indeed represent novel, derived, traits. At the macroscopic level, Holloway (1996) has suggested that the third inferior frontal convolution (which includes Broca's area) has distinctive characteristics in the human brain that can also be recognised in the endocast of KNM-ER 1470 [*Homo rudolfensis*, or *Australopithecus rudolfensis* according to Wood & Collard's (1999) taxonomic revision]. Holloway also notes that the endocast evidence for later hominids is insufficient to enable us to identify any new features of the convolutional pattern of the brain with the appearance of anatomically modern humans. However, Cantalupo & Hopkins (2001) have found human-like Broca's area asymmetry in great apes. At the microscopic level, Buxhoeveden and collaborators (Buxhoeveden *et al.*, 1996, 2001) have found differences in cortical cell-packing in human and non-human primate brains in Tpt (auditory association cortex), including differences in the degree of left–right asymmetry in cell density, which may indicate derived human patterns of connectivity. Others have found that the ratio of grey matter to neuropil is lower in the left hemispheres of human brains, suggesting that 'the dominant hand is controlled by a cortical region with a greater amount of connectivity

than found in the homologous area of the other hemisphere' (Amunts *et al*., 1997: 400). However, we should note that both cerebral convolutedness and cell packing density vary systematically with absolute size of the primate cerebral cortex, making it hard to distinguish changes in the human brain that are definitely not explicable by allometric scaling associated with size increase.

FOSSIL, ARTEFACTUAL AND COMPARATIVE DATA ON THE EVOLUTION OF HUMAN HANDEDNESS

Despite the apparent continuities in human and great ape brain morphological asymmetry, behavioural evidence of handedness in non-human primates is perplexingly equivocal. Perhaps there is a directional bias to the use of the right hand in precise manipulative tasks at the population level in primates, but even in chimpanzees this has proved extremely hard to verify (Hopkins & Morris, 1993; McGrew & Marchant, 1996, 1997; Hopkins & Fernández-Carriba, 2000). The most comprehensive attempt to demonstrate continuities between human and non-human primate behavioural laterality has come from MacNeilage and collaborators (MacNeilage *et al*., 1987; MacNeilage, 1993). But even MacNeilage (1993: 325) acknowledges that:

> it cannot be denied that … the [functional] asymmetries are for the most part, though not entirely … inherently weaker and less consistent in their direction in other primates than in humans.

Direct evidence of the hand preferences of Palaeolithic hominids comes in two forms: skeletal modifications that reflect the unequal loading history of the two upper limbs during life, and biases in the production and use of artefacts that reflect the ergonomics of technological actions involving a preferred hand. A large number of studies in recent years have demonstrated the range of adaptive responses of the skeleton to patterns of mechanical loading *in vivo* (Steele, 2000a, b). These responses can include increases in bone strength due to increased bone density and/or cross-sectional area, increases in mechanical efficiency by shape change, and resistance to avulsion by increasing the surface area of the sites of attachment of muscles and ligaments on a bone's surface. Evidence suggests that, in any particular case, the effect of muscle strength and mechanical loading on bone mineral formation is localised to the specific site of muscle–bone interaction. Because a consistent hand preference leads to lateral asymmetry in the mechanical loading experienced by the two hands, arms and shoulders during life, we can detect handedness by studying right–left differences in the degree of skeletal response to loading strains.

Fossil hominid remains have been studied from this perspective. It is evident that predominant right-handedness extends back in time to at least the early

members of our own genus *Homo*. The skeleton of the Nariokotome boy, WT-15000 (early African *Homo erectus*, also called *Homo ergaster*), has greater development of the clavicular area of attachment of the right deltoid muscle and greater length of the right ulna, consistent with right-handedness (Walker & Leakey, 1993). Humeral shaft asymmetry consistent with right-arm dominance is also prevalent in Neanderthal skeletons: of six skeletons in which the relevant measurements could be taken bilaterally, all were more robust in the right arm (Trinkaus *et al.*, 1994).

Schultz (1937) recorded asymmetries of the lengths of arm bones (humerus and radius) in a large sample of ape skeletons (including 130 gorillas, 82 chimpanzees, eight orang-utans and 21 gibbons). In marked contrast with the 722 human skeletons in his sample, he found no tendency for the right arm to be dominant in apes as assessed by this measure. He also found that the mean degree of asymmetry (unsigned) in apes was about half that found in the arm bones of humans. These findings suggest that apes do not exhibit either the population-level right-handedness seen in humans, or the degree of loading of the individually dominant side that is seen in human bones.

A variety of artefactual data is available that confirms a predominance of right-handedness throughout the Palaeolithic period. A number of aspects of object manipulation (such as direction of rotation and grip orientation) are influenced by the anatomical structure of the hand, such that use of left or right hand for these actions will follow a characteristic and asymmetric pattern. This has enabled archaeologists to infer hand preference from tool-making debris, and from wear patterns on hand-held artefacts they can establish whether the hand used in each task was the preferred or the non-preferred one. The latter type of inference is usually based on ethnographic observation and on experimental reproduction of similar artefacts or wear traces by individuals with different hand preferences.

Toth (1985) found that there was a preferential direction of rotation of the stone core by knappers, who hold it in their non-dominant hand while using the preferred hand to strike the knapping blows. This preferential direction of core rotation varies according to which hand holds the core, with the result that the rotation bias can be detected in archaeological waste material from stone tool making. The pattern which he found in right-handed knappers was also found in the stone flakes recovered from the sites of Koobi Fora, Kenya (dating to about 1.9–1.4 million years ago), and from Ambrona, in Spain (dating to about 0.3–0.4 million years ago). While this indicates a preponderance of the right-handed phenotype at these sites, it is difficult to say exactly what proportion of earlier hominid tool makers (probably genus *Homo* in both cases) was right-handed. This is not just because Toth's (1985) estimation technique is 'noisy'. It is also because more recent experimental work suggests that the proportions found of stone flakes showing traces of clockwise and counter-clockwise core

rotation varies not just with hand use, but also with experience and skill level. Ludwig & Harris (1994) report that experimental knapping by experienced stone tool makers showed a much higher proportion of flakes produced by core rotation in the 'preferred' direction (*c.* 90%) than was reported either by Toth (1985) or by Ludwig & Harris (1994) in their own experiments with novices (about 60%). This is because the greater skill of the experienced knappers gives them more control over their procedures, and the ability to reduce a core much more systematically. Ludwig & Harris (1994) argue that this kind of skill level appeared in hominid stone tool-making traditions as early as 1.7 million years ago. Thus the proportions of flakes at Koobi Fora and Ambrona that were produced by core rotation in the counter-clockwise directions could indicate either a lower level of skill among right-handed tool makers, or a higher than expected prevalence of the left-handed phenotype among skilled tool makers (Pobiner, 1999). Future work may differentiate the effects of these factors; at present, while we can say that there was a preponderance of right-handed tool making in the Lower Palaeolithic, we cannot quantify the degree of such preponderance with any precision using this method.

Bermudez de Castro *et al.* (1988) discuss striations on the anterior teeth of several individuals from the Middle and early Upper Pleistocene in Europe, which were probably caused inadvertently by stone tools (used to cut meat or other material gripped between the individuals' own teeth). Of these individuals, the great majority showed a right-handed use pattern, one showed a left-handed use pattern, and one could not be assigned to either category. Cornford (1986) found evidence of handedness in stone tools found at various levels of the Cotte de St Brelade site in Jersey (dating from periods 130,000–240,000 years ago), and estimated a frequency of right-handed tool production of 71–84% (weighted average = 81.7%; Callow & Cornford, 1986: table D.1). Cornford (1986) argues that the task would strongly favour use of the preferred hand, thus making these data a good guide to the original frequency of right-handedness among successive occupants of the site. Semenov (1961; 1964: 173) found a pattern of right-handed use of bone retouchers for working blade edges on stone tools at two Neanderthal sites, Kiik-Koba (Crimea) and Teshik-Tash (Uzbekistan). He also suggested that about 80% of end-scraper tools from the Upper Palaeolithic of Europe and North Africa show wear patterns consistent with right-handed use (Semenov, 1964: 87; cf. Takeoka, 1991).

In summary, the fossil evidence, both of differences in right and left arm bones and of handedness in tool manufacture and use, supports the generalisation that humans have been predominantly right-handed since the dawn of flaked stone technology. It thus becomes puzzling that our brain asymmetry patterns should also appear in other living primates, while our behaviour shows a population-level bias towards right-handedness that is not nearly so apparent in these other living species.

HUMAN BRAIN EVOLUTION: HOW CAN WE EXPLAIN INCREASED EVIDENCE FOR LATERALITY WITHOUT SALTATIONS?

Evidence of continuity in morphological asymmetries does not tell the whole story of human brain evolution. One other major trend in this story is the absolute size increase of the hominid brain (the arguments in this section have been presented in an earlier form in Steele, 1998). We can infer a great deal from this latter trend, because comparative studies have demonstrated very significant developmental constraints on the evolution of relative sizes of the major brain structures, constraints that account for the scaling of human brain structure volumes as well as of those of other primates (Finlay & Darlington, 1995). For example, comparisons across primate genera demonstrate that in taxa with absolutely larger brains, a higher proportion of total brain volume is made up by neocortex. The following regression models illustrate this scaling relationship for each of the two major subdivisions of the primate order, strepsirhines and haplorhines. The two regression formulae (reduced major axis technique) describing these relationships are as follows (equations from Steele, 1996; data from Stephan *et al.*, 1981).

> For strepsirhines ($n = 12$ genera)
> $\log_{10}$ neocortex (mm^3) $= 1.125 \log_{10}$ (rest of brain, mm^3) $- 0.460$, $r^2 = 0.985$
> For haplorhines ($n = 25$ genera, excluding *Homo*)
> $\log_{10}$ neocortex (mm^3) $= 1.20 \log_{10}$ (rest of brain, mm^3) $- 0.523$, $r^2 = 0.992$

In each case, the slope in the regression model indicates that larger brained taxa have relatively more neocortex. *Homo sapiens* has neither more nor less neocortex than would be expected for a typical haplorhine primate of our brain size (Steele, 1996). We are the most 'neocorticalised' primate species, but only by virtue of being the largest-brained.

Let us also note another scaling constant, this time as observed more generally among mammals. This is the tendency for the relative amount of white matter to increase in larger brained taxa, and is described by a standard major axis model of the relationship between volumes of cortical grey matter and of cortical white matter in mammals (from Hofman, 1989):

> $\log V_{grey}$ (cm^3) $= 0.773 \log V_{white}$ (cm^3) $+ 0.732$
> [95% confidence interval (CI) for slope $= 0.741 - 0.806$, $r^2 = 0.992$]

Rilling & Insel (1999) have inverted this relation by regressing volume of cerebral white matter on volume of cerebral grey matter in a separate series of primate brains, finding a slope of 1.12 (95% CI 1.05–1.19), which tells a

similar story. Now if we take these grey and white matter volumes as crude surrogates for neurone and axon numbers, respectively (a naive assumption given the contribution of axons to grey matter volume, but one which may serve), then we can see that the mammalian scaling trend, for a relative increase in white matter in larger brains, is none the less insufficient to maintain the same 'percent global connectivity' among all cortical neurones (which would necessitate a parabolic increase in axon number with any increase in neurone number; cf. Deacon, 1990: 226–31; Ringo, 1991). It follows from this that as absolute brain size increased in the course of hominid evolution, there was a parallel increase in the relative volume of the neocortex, and a decrease in the overall degree of direct global connectivity among its neurones (cf. Ringo, 1991).

What are the functional implications of this? Ringo (1991) points out most specifically that the scaling of callosal area to cortical surface area in a range of smaller-brained species, and also in humans, indicates that percentage connectedness of neurones across the callosum falls with increasing brain size, and he suggests that this might relate to efficiency savings on processing power (given the increased conduction time of signals transmitted along long fibre connections). More generally, he suggests that the processing inefficiencies of retaining the same degree of interconnectedness in larger brains mean that lateral and regional specialisation of function will be strongly correlated with absolute brain size. Ringo *et al.* (1994) have developed this hypothesis, arguing that in large brains the conduction delay involved in interhemispheric transfer has important implications for the efficiency of interhemispheric integration of processing for 'time-critical' tasks. They show that in tasks like phoneme processing in speech, such a delay would critically constrain the efficiency of processing when it involved the activation of transcortical cell assemblies. The implication is that, as the absolute size of the hominid brain expanded, many cognitive and motor processes became more constrained to intrahemispheric networks due both to the allometric reduction in overall cortical connectivity, and to time delays in the integration of cell assemblies characterised by long fibre interconnections. More recently, Rilling & Insel (1999) have also reported a decrease in corpus callosum area relative to brain volume and to neocortical surface area with larger brains, in a primate series extending from squirrel monkeys to humans (see also Hopkins & Rilling, 2000). They observe that 'results suggest that interhemispheric connectivity via the corpus callosum is reduced in larger primate brains, whereas intrahemispheric connectivity is augmented' (Rilling & Insel, 1999: 1457), and that:

> in view of evidence that interhemispheric connectivity is inversely related to functional laterality, our results suggest that lateralisation of function may be an emergent property accompanying brain enlargement in primate evolution. Moreover, the human brain should be the most functionally lateralised anthropoid

> brain because it has the least amount of interhemispheric connectivity between neocortical neurons. (Rilling & Insel, 1999: 1459)

These scaling laws of human brain evolution do not account for all the pieces in the puzzle of human laterality. But they may account for the paradox whereby our brain morphological asymmetry is conserved from a distant primate common ancestor, while our behavioural asymmetries are (in their degree and consistency) evolutionarily novel. Perhaps we became more lateralised as an inevitable by-product of the need to make the most efficient use of our enlarged neocortex, with the typical pattern of right–left differences in functional specialisation simply amplifying pre-existing morphological asymmetries and wiring biases. It is extremely hard to sustain the alternative argument, that human laterality arose as a result of the evolution of novel brain morphological asymmetries restricted to the hominid line. But this resolution would raise new questions as well as provide new answers. Is there a quantitative threshold in hominid brain enlargement beyond which functional laterality was fully human, or did the degree and consistency of such functional laterality gradually increase with brain expansion throughout the Palaeolithic? What are the implications for language lateralisation? Answering these new questions will require, among other things, some very careful mathematical modelling of the properties of neural networks with differing degrees of connectivity.

DISCUSSION

McManus: Many of these asymmetries that people have been studying for years are really quite small and they are really on top of a very asymmetric body. Of course the heart of most individuals is on the left side. In fact if you take a fetal brain and pump blood into it from a highly asymmetric vascular system, it is not too surprising to also find minor asymmetries. So to demonstrate that any of the brain asymmetries are related to language, you must first demonstrate that they are independent of situs inversus (heart on right side) and secondly you need to actually demonstrate that they are related to language lateralisation. If you go back to the planum temporale data of Geschwind and Galaburda, really all they showed was that there was a large asymmetry and because there was another large asymmetry in language they assumed that the two must be related. They never demonstrated a relationship between the two and no one ever has since. There is no evidence that someone who has a larger right planum temporale has reversed language asymmetry. Thus it is not surprising that the asymmetries are now found in the great apes and other non-humans.

Wolpert: Isn't someone addressing this using scanning techniques?

Crow: Yes they are. In fact there does not seem to be a volume asymmetry of the whole hemispheres in humans. There really is not a volume asymmetry of the brain in humans.

McManus: There was just a large study done in the functional imaging lab at Queens Square where they looked at about 480 structural MRI scans done prior to functional analysis. They know that about 80 of them are left-handed and they couldn't find any differences in the structure of the brains in the right- and left-handers no matter what they measured. It is not because the techniques are not sensitive because they are finding sex differences interestingly. My strong suspicion is that there is no difference in left- and right-handers in their morphological asymmetries.

Questioner: I thought Marjorie LeMay has found differences between left- and right-handers?

McManus: Yes she did, but a number of other studies were not able to replicate this. Handedness is a relatively weak correlate of language lateralisation. What we need are studies of structural scans with corresponding functional MRI scans to see what is actually correlated.

Comment: We must not forget that brain asymmetries are widely spread throughout the animal kingdom. They are not just present in humans.

Crow: But they are not there in the chimpanzee, which is what we are really concerned with. Marchant and McGrew, who are in conflict with Hopkins, have very carefully reviewed the literature (McGrew & Marchant, 1996, 1997) and did a comprehensive study in the Gombe National Park (Marchant & McGrew, 1996). The conclusion is that there is no overall asymmetry in chimpanzees (for anatomical data on the planum temperale, see Buxhoeveden *et al.*, 2001).

Comment: There is a difference between handedness in the morphological sense and handedness in the functional sense. This is actually important because in primates vocalisations are localised on one side.

Crow: There is a problem with that literature. What you are talking about is a lesion literature which is not compatible with the literature on anatomical and functional asymmetries.

McManus: People want to find these asymmetries. Many studies are not blind. Asymmetries are publishable, symmetries are not. There was a recent publication that sheep have an asymmetric brain for recognising conspecifics and that they have right hemisphere specialisation.

Comment: Left-handedness has been associated with all kinds of things, for example autoimmunity and weakly associated with atrophy.

McManus: This was another one of Geschwind's observations, but meta-analyses don't replicate this. There are so many artefacts that we have to be very careful in reviewing these data.

Comment: What can we reasonably not doubt?

McManus: Probably, Broca's original observation that the vast majority of patients who have unilateral damage to their brain, if it's on the left, lose speech. That's the only thing I think is clear from the whole literature.

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