

Distinctively human: cerebral lateralisation and language in *Homo sapiens*

Steven A. Chance & Timothy J. Crow

SANE POWIC, Warneford Hospital, Warneford Lane, Oxford, OX3 7JX, UK

e-mail: steven.chance@clneuro.ox.ac.uk

Summary - *Three lines of evidence: handedness, brain anatomy and cognition in great apes, extinct hominids and modern humans suggest that cerebral lateralisation underlies the human capacity for language. Chimpanzees do not show consistent population level handedness. Cultural artefacts and post-cranial anatomy allow some investigation of cerebral asymmetry and handedness in extinct hominids suggesting the presence of handedness in early Homo species. Directional handedness on a population basis is present and universal in modern Homo sapiens. In anatomical structure of the brain two components of macroscopic asymmetry are dissociable: i) "petalia", the protrusion of the right frontal and left posterior poles relative to their counterparts in the opposite hemisphere, seems to have an older evolutionary origin and be unrelated to language, ii) a "volume asymmetry" that may be Homo sapiens-specific and associated with the microscopic asymmetry of cell organisation in human language cortex that is not found in other apes. Sex differences in structural and functional asymmetry which are plausibly related to sex differences in verbal ability are found in human populations without established counterparts in chimpanzees and indicate a possible role of sexual selection in human lateralisation. The mapping of major elements from historical language models onto the asymmetric human brain is illustrated. The microscopic asymmetry of cell and minicolumn spacing is suggested as a neural basis for recursive processing.*

Keywords - *Human evolution, Cerebral torque, Handedness, Language, Minicolumn, Asymmetry.*

Introduction and scope

Language is arguably the pre-eminent function of the human brain. This singular species-specific communicative ability is supported by a brain similar in most respects to that of other mammals. Although relatively large and including some cells of a distinctive type, the human brain is neither the largest (Holloway, 1999) nor are its cells of a type unique to humans (Hof & Van Der Gucht, 2006). Perhaps the feature most salient with regard to language is the brain's asymmetrical structure. Here we evaluate the relationship between laterality, language and asymmetrical brain structure.

Language and complex tool-making are key elements in human culture. They are allied by the characteristic that is common to both - lateralization - in the asymmetry of language dominance (left hemisphere) and the handedness of the tool-maker (right handed). In 1877 the French neurologist and anthropologist, Paul Broca, wrote: "Man is, of all the animals, the one whose brain in the normal state is the most asymmetrical. He is also the one who possesses most acquired faculties. Among these the faculty of articulate language holds pride of place. It is this that distinguishes us the most clearly from the animals" (Broca, 1877, translated in Harrington, 1987:65-66).

The significance of asymmetry was largely overlooked until the discovery of the cerebral 'torque' in 1966 by Yakovlev and Rakic. In an abstract these authors described an asymmetry of the pyramidal tract of the motor system. Shortly thereafter asymmetry to the left of the planum temporale language cortex in two-thirds of individuals was reported by Geschwind & Levitsky (1968) in post-mortem brain.

A debate has followed concerning the thesis that cerebral asymmetry (reflected in a population bias toward the use of the right hand) is *Homo sapiens*-specific. On the one hand it is argued that asymmetry is determined by a single human gene (Annett, 1985, 2002) and that other mammals are equally often right and left-handed (McGrew & Marchant, 1997) and on the other that a bias toward the use of the right hand or paw is widespread across vertebrate species (Rogers & Andrew, 2002). The goal of the present review, close to Broca's original contention that humans have the *most* asymmetrical brain, is to identify those elements of asymmetry that do appear to be discontinuous between humans and other animals.

Three lines of evidence - handedness, brain anatomy and cognition - are each addressed in the three relevant phylogenetic groups: modern humans, great apes, and extinct hominids. By this system of triangulation we attempt to characterize the essential role that lateralization has played in human brain evolution.

Handedness

90% of the modern human population is right-handed. Movement of the hand is initiated by neurons of the primary motor cortex situated in the pre-central gyrus according to a somatotopic (mapping the topography of the body on to the brain surface) distribution. Fibres travelling from the cortex to the spinal cord pass down through the brain stem forming the "pyramids". It is these pyramidal tracts that were identified as asymmetrical by Yakovlev and Rakic. Since the brain tends to control muscles on the opposite side of the body, most

of the fibres cross to the contralateral side in the pyramidal decussation ("crossing over") and those destined to innervate muscles of the hand pass out of the spinal cord from cervical vertebrae C4 to T1. Comparative measures of the vertebral canal through which the cord passes reveal a cervical enlargement at this level in humans and in *Homo erectus* (MacLarnon, 1993).

The presence of handedness in *Homo* species is suggested by skeletal asymmetries, detectable in fossils, that reflect bias in the use of the upper limbs. Such asymmetries include differences of bone strength, cross-sectional area, functional shape change, and muscle attachments. The *Homo erectus* KNMWT-15000 fossil (the "Nariokotome boy") has a greater clavicular attachment for the right deltoid muscle and longer right ulna indicative of right-handedness. The right arms of Neandertal skeletons have been found to be more robust (Trinkaus *et al.*, 1994). Tooth wear due to tools gripped by teeth and hands is consistent with right-handedness in the mid-Pleistocene (Bermudez de Castro *et al.*, 1988). Stone flakes from tool making dated between 1.9 and 1.4mya indicate a statistical bias in the handedness of the stoneknappers. From the orientation of the flakes and remaining stone cores Toth (1985) concluded that some significant lateralisation of the hominid brain had already occurred by this time.

Among modern great apes, by contrast to humans, chimpanzees (Finch, 1941) and gorillas (Annett & Annett, 1991) do not show directional lateralisation on a population basis. The studies of Marchant and McGrew (1996) of chimpanzees in the Gombe National Park and of Holder (1999) comparing chimpanzee, red colobus, redtail monkey, grey-checked mangabey and mountain gorilla are also in agreement that no species level left- or right-handedness was observed (Fig. 1). In a meta-analysis McGrew and Marchant (1997) concluded that nonhuman primate hand function "has not been shown to be lateralized at the species level". Claims by Hopkins and Cantalupo (2003) for population level right-handedness in captive chimpanzees have been subjected to statistical

criticism by Palmer (2003) and are complicated by later reports from the same group (Lonsdorf & Hopkins, 2005) of population level left-handedness for ant foraging in chimpanzees in the wild. Thus the null hypothesis that directional handedness on a population basis is absent in non-human primates has not been disproved.

In 1920 F. Wood-Jones argued that the difference in dexterity between the hands of monkeys and men “lies not so much in the movements which the arrangement of muscle, bone and joints makes it possible for either animal to perform, but in the purposive volitional movements which ... the animal habitually exercises”. fMRI investigation in modern humans reveals that planning for tool use occurs in the left hemisphere (Johnson-Frey *et al.*, 2005). Consequently, although handedness constitutes an observable behavioural lateralisation, its significance depends on the degree to which it is associated with lateralisation of higher cognitive tasks including language.

In an examination of the data collected from 12,000 children in the UK National Child Development Cohort, Crow *et al.* (1998) found that those close to “hemispheric indecision” (equal hand skill) were disadvantaged with respect to verbal and non-verbal ability, reading and mathematical skill (Fig. 2). The essential findings in this study have recently been replicated in a

much larger human adult population in the BBC Internet survey (Peters *et al.*, 2006). The general conclusion is that a major genetic influence associated with lateralisation determines variation across a wide range of human ability.

Cerebral anatomy

The presence of asymmetry in the human cerebral hemispheres is detectable at both the macroscopic and microscopic scales. An association between these asymmetries is inferred but not yet supported by statistical analysis – frequently measurements performed at different levels of scale are not performed on the same material. The evidence for discontinuity between humans and other apes is complicated by methodological variations at the macroscopic level but is, so far, consistent at the microscopic level. Here we begin with the macroscopic.

The modern human cerebral hemispheres are asymmetrical: right frontal regions are larger than left, and left occipital regions are larger than right; (Bear *et al.*, 1986; Witelson and Kigar, 1992). Two components of this brain “torque” are dissociable (Chance *et al.*, 2005). The first is a horizontal shift of one hemisphere with respect to the other that we have found to be associated with petalia (this term describes the greater asymmetrical protrusion of one hemisphere beyond the other). The second is a differential distribution of tissue within each hemisphere along the antero–posterior axis, that we have described as “volume torque” (see Fig. 3 and 4).

Most evidence for anatomical cerebral asymmetry in hominid evolution depends on assessment of petalia. Endocasts from fossil hominid skulls indicate right frontal and left occipital asymmetries in early *Homo* probably continuous with late Australopithecines. Some comparative data suggest that petalia are present in modern great apes (Holloway & De La Coste-Lareymondie 1982), although Zilles *et al.* (1996) found no directional asymmetry in the length petalia pattern of chimpanzees. If present, the great ape asymmetry appears to be

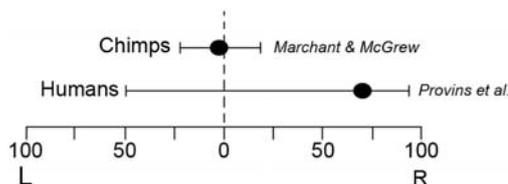


Fig. 1 - Hand preference for everyday activities in chimpanzees and *Homo sapiens* compared. Data for chimpanzees refer to a community of 38 animals (*Pan troglodytes schweinfurthii*) observed by Marchant and McGrew (1996). Data for *Homo sapiens* were collected by questionnaire from populations of undergraduates by Provins et al. (1982). Medians and boundary values for 95% have been extracted from graphs in the original publications.

greater anteriorly, in contrast to modern human patterns in which the occipital asymmetry is most prominent. The contrast is notable, as Steele (2002) has pointed out, since the occipital width asymmetry is the dimension most significantly associated with hand preference in humans.

Petalia are reversed in humans who have situs inversus – a reversal of the asymmetry of the organs of the body. Yet, individuals with situs inversus appear to show normal language dominance, normal asymmetry of the planum temporale (posterior auditory cortex forming part of Wernicke's posterior language area - see Fig. 5) (Kennedy *et al.*, 1999), and are mostly right-handed (Matsumoto *et al.*, 1997). This evidence suggests that the physical shift of the hemispheres that is the main constituent of petalia is un-related to lateralization of language. Similarly, continuity of the pattern of petalia between *Australopithecus* and *Homo* (Holloway & De La Coste Lareymondie, 1982) indicates that this feature has an evolutionary origin earlier than modern *Homo sapiens*. However, the

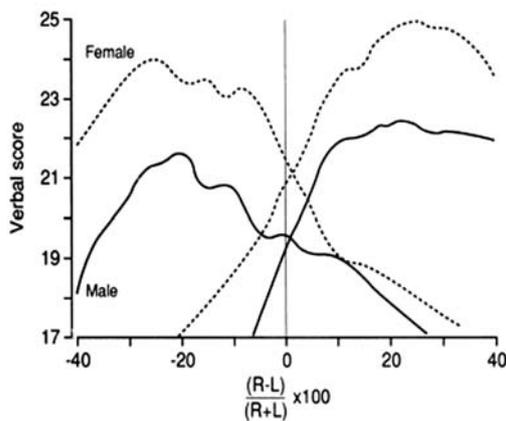


Fig. 2 - Relative hand skill predicts academic ability; verbal ability deficits at the point of hemispheric indecision at age 11 (after Crow *et al.*, 1998). Solid lines depict males, dotted lines depict females (females have higher scores in general). Right handers have a peak relative hand skill value above zero, left handers have a peak relative handskill below zero. Equal handskill ("hemispheric indecision") occurs at zero on the x-axis where verbal ability declines.

second component of torque, the asymmetrical antero-posterior distribution of tissue within the hemispheres ("volume torque"), responds differently to pathology in modern humans and is correlated with the volume of the superior temporal gyrus (Chance *et al.*, 2005) that forms the inferior boundary of the Sylvian fissure, containing auditory language cortex, including the planum temporale, and therefore may be linked to lateralization of language. The two morphometrically distinct components of torque may thus have different evolutionary significance.

The evolutionary continuity of regional (as opposed to global) asymmetries is also unclear. On the one hand, Holloway and De La Coste Lareymondie (1982) report cerebral asymmetry in *Australopithecines*; on the other, Falk (1983) has claimed that the local sulco-gyral patterns of early *Homo* are similar to modern humans' and unlike *Australopithecines*'. As noted above, the distinction between anterior and posterior regions is of interest because the frontal lobe is similarly expanded in all hominoids (Semendeferi *et al.*, 1997) whereas more posterior regions such as the temporal (Semendeferi & Damasio 2000) and parietal lobes (Bruner *et al.*, 2003) are selectively larger in modern humans. In particular, whilst an expansion of frontal breadth and vertical size accompanies encephalization (increased brain size) across several hominid species, the posterior parietal expansion distinguishes modern *Homo sapiens* from other lineages including that of the Neandertals (Bruner *et al.*, 2003). This extended posterior expansion (and associated asymmetry) may therefore be of particular interest for the acquisition of linguistic capabilities thought to be specific to *Homo sapiens*.

An argument for evolutionary discontinuity of regional structure developed by Schenker *et al.* (2005) identifies two elements of white matter (the connective, fat-insulated tracts that link regions of grey matter); a local measure delimited within gyri ("gyral" white matter) that is relatively expanded in modern humans, and a more global measure of the remaining "core" white matter that is proportional to that of other apes. This places an emphasis on the expansion of gyri,

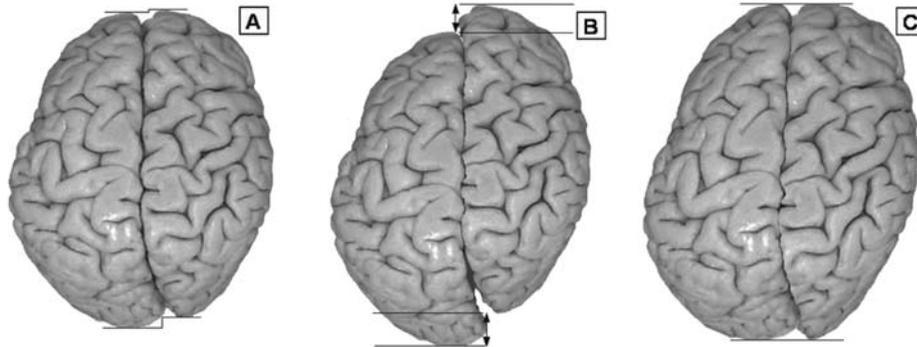


Fig. 3 - In its simplest definition petalia refers to the appearance of more tissue at the poles of the hemispheres on one side than the other. This usually takes the form of greater protrusion of the pole of one hemisphere in front or behind the other hemisphere. Definitions of petalia vary, and may take more or less account of the width of the polar regions. Figure A shows a human brain from above (front at top, posterior at bottom) with marginal rightwards frontal petalia and clear leftwards occipital (posterior) petalia. Hemisphere shift can be exaggerated, by shifting the hemisphere positions (B), or diminished, leaving only an asymmetry of tissue distribution (volume torque) augmented in this image for illustrative purposes (C).

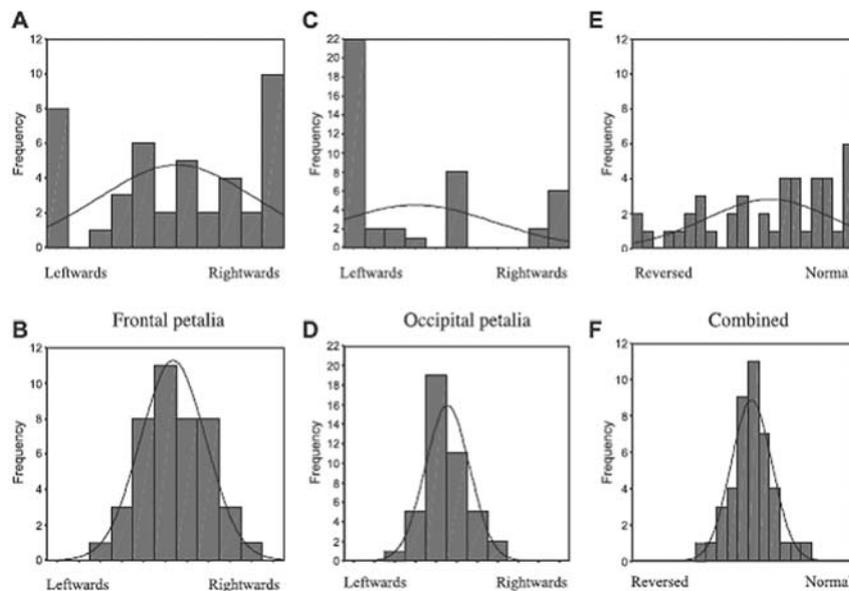


Fig. 4 - Human petalia depend on hemisphere shift (after Chance et al., 2005). Histograms of the distribution of frontopetalia values (A and B) at the front of the brain, occipitopetalia values (C and D) at the back of the brain, and "combined" torque statistics (E and F) - that is the degree to which rightward frontal asymmetry is associated with leftward posterior asymmetry. The histograms in the top row (A, C, and E) include antero-posterior hemisphere shift in the measures, and the histograms in the bottom row (B, D, and F) exclude hemisphere shift. The distributions with shift show drifts in the expected directions (ie. rightward frontopetalia, leftward occipitopetalia), those without shift cluster around zero, suggesting that antero-posterior shift is the main component of asymmetry in petalia measures.

which are the cortical convolutions on whose surface cognitive functions are mapped, in the discontinuity between humans and other apes.

The expansion of white matter within a gyrus is consistent with a relative expansion of cortical surface area as proposed by Harasty *et al.* (2003). The horizontal expansion of cortical surface is largely due to the proliferation and spacing of radial minicolumns of cells that form the cortex during development (Rakic, 1995). These are microscopic structures that span the 3-4mm depth of the mature cortex and have a horizontal width of approximately 50 micrometres (see Fig. 6). Intra- and inter-cortical connections are organised according to these basic units of cortical organisation. Minicolumns emerge by radial migration of cells towards the brain's surface during embryonic formation of the cerebral cortex. Column-like radial organization is found for cell bodies, and their axonal and dendritic connections. The functional role of columns is not fully understood but they appear to form the basis of functional organization across the brain's surface. In the human planum temporale, minicolumn width asymmetry is associated with surface area asymmetry (Chance *et al.*, 2006). Critically, this asymmetry of minicolumn spacing in the human planum temporale is absent in the

brains of other apes (Buxhoeveden *et al.*, 2001).

The functional role of cortical columns is not identical across animal species. Among the best studied columnar organisation is that of the visual cortex, at the posterior of the brain. Ocular dominance columns (neighbouring columns are activated preferentially by stimulation of different eyes) are present in the cat, ferret, mink and more than a dozen primate species (reviewed in Horton & Hocking, 1996) but are absent in the mouse, rat, squirrel, rabbit, possum, sheep and goat. Another columnar organisation in visual cortex - the orientation preference columns - has junctions between columns that are called "pinwheels". The distribution of these varies among the species which have columns and the relative density of pinwheels suggests a phylogenetic ordering. Tree shrews have the lowest relative density, with ferrets exhibiting a higher value, followed by cats, squirrel monkeys and then macaques in order of increasing relative density (Wolf & Geisel, 1998). The distribution of these columnar features is thought to depend on the efficient minimization of connective distance between cortical areas that is of increasing importance with increasing brain size (Koulakov & Chklovskii, 2001).

Horton and Adams (2005) observe that the "...salient point to emerge is that species with ocular dominance columns are predators." It is notable that the predatory status of several species is associated with another brain measure that has evolutionary implications - the encephalization quotient, EQ, represents the degree to which brain size in a species exceeds or falls below the brain size of typical mammals of similar body size. EQ correlates with feeding behaviour in various mammalian taxa. Carnivores have larger EQs than herbivores, and primates have larger EQs than insectivores or foliovores (Jerison, 1973; Gibson *et al.*, 2001). *Homo sapiens* has an unusually high EQ, greater than that of other apes, and the argument has been made (Jerison, 1973) that high EQ is also associated with greater intelligence.

Increased brain size and enlarged cortical surface will occur as a result of minicolumn proliferation and expansion. We (Chance *et al.*, 2006) have suggested that there are two phases

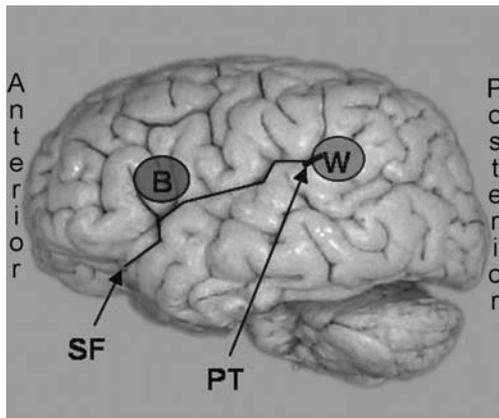


Fig. 5 - Language associated cerebral cortex. A view of the left hemisphere of a human brain. B = Broca's area, W = Wernicke's area, SF = Sylvian fissure, PT = planum temporale.

in minicolumn development; first proliferation and secondly expansion, that contribute to cortical surface asymmetry to different degrees in different regions. The asymmetries are amplified in more recently evolved association cortex where the phase of expansion has greater influence on region size and asymmetry.

Thus we propose the following dichotomy: early phase minicolumn proliferation linked to primary sensory cortex size, somatic and cerebrovascular asymmetry, hemisphere shift, core white matter distribution and petalia with an older evolutionary origin, contrasted with late phase minicolumn expansion linked to surface area expansion of association cortex, language lateralisation, handedness, volume torque, gyral white matter increase, temporal and parietal lobe enlargement, greater posterior asymmetry and a recent human evolutionary origin.

Language cortex

Following the work of Broca and Wernicke the language areas of the human brain are relatively well established. Damage to Broca's area in the posterior inferior gyrus of the left and surrounding prefrontal cortex is associated with expressive (nominal) aphasia – failure or impairment of speech - whereas damage to Wernicke's area in the left posterior Sylvian fissure (including the planum temporale) is associated with receptive (fluent) aphasia – failure to understand speech. Consequently the left frontal area is linked to speech production and the left posterior temporal cortex and parietal junction is linked to speech perception. (Fig. 5)

Ploog (2002) has reviewed primate studies and human clinical findings. These indicate that whereas the neural basis of vocalisation in other

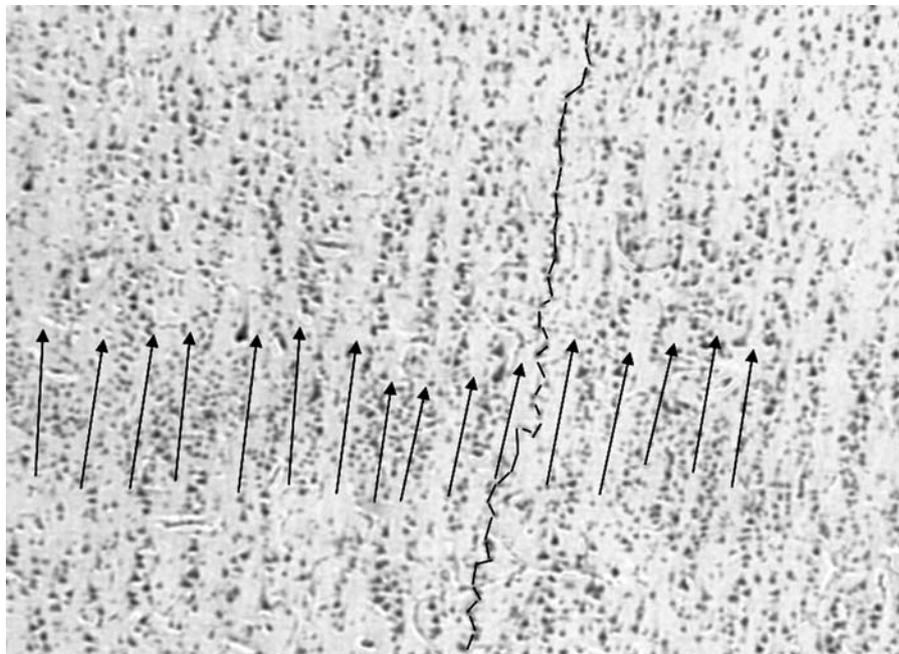


Fig. 6 - A representative sample of human temporal lobe association cortex. Columnarity can be seen in the approximately vertical clusters of dark stained cell bodies (against the light background). Arrows in the gaps between minicolumns identify the vertical axis at the edge of the minicolumns in cortical layer IV. A single minicolumn has been illustrated stretching through layers V, IV and III, up towards the cortical surface by joining neighbouring cell bodies with black lines.

primates is located in the cingulate cortex, in humans it includes the prefrontal neocortex in the left hemisphere (Broca's area) consistent with greater involvement of association cortex and a crucial role of lateralisation in human speech production. The neurons in prefrontal cortex are greater in number (Uylings *et al.*, 2006) and more widely spaced in the left hemisphere (Cullen *et al.*, 2006) and the largest cells (the magnopyramidal cells) are larger on the left (Hayes & Lewis, 1995). In addition, the role of the cingulate cortex in human vocalisation may be modified by the presence of spindle neurones, which, although they are found in great apes are not present in the cortex of other primates (Allman *et al.*, 2001).

Posteriorly, in the auditory receptive region, Gannon *et al.*, (1998) have claimed to demonstrate gross region size asymmetry of the planum temporale in chimpanzees, although two early studies (Pfeifer, 1936; Von Economo & Horn, 1930) reported a lack of planum temporale asymmetry in apes. Asymmetry of the Sylvian fissure has been variously reported as present in orang utans and gorillas (LeMay & Geschwind, 1975), and chimpanzees (Yeni-Komshian & Benson, 1976) but absent in lesser apes and inconsistent in Old World monkeys (Falk *et al.*, 1986; Heilbronner & Holloway, 1988) where the planum temporale itself may be absent (Pfeifer, 1936). Perisylvian asymmetries have been identified in fossil endocasts attributed to *Homo* and *Australopithecus* (Holloway, 1980; LeMay, 1976; Tobias, 1987) although the reliability of such measures is not certain, since fossil endocasts are prone to qualitative interpretation. Because Sylvian fissure measurements only indirectly reflect the size of auditory cortex, including the planum temporale, the implications of Sylvian fissure asymmetries for language capacity in fossil humans and apes are unclear.

In humans, the left hemisphere auditory cortex is dominant for speech perception due, in part, to a capacity for processing temporal transitions in the speech signal (Efron, 1963; Tallal *et al.*, 1993; Zatorre *et al.*, 2002; Shtyrov *et al.*, 2000). It is plausible that the minicolumn asymmetry not seen in other non-human apes

and the greater surface area on the left contribute to a right ear advantage for simple auditory tasks (Jerger & Martin, 2004) (consistent with the brain's tendency to preferentially process and respond to stimuli on the opposite side of the body). The concept of "asymmetric sampling in time" (Friederici, 2006) is useful. Right auditory cortex advantages are seen with other tasks, for example slow spectral sound processing (Zatorre & Belin, 2001), which probably requires a longer sampling window. Zatorre and Belin propose that the alternative processing benefit emerging from the different neural organization on the right side is based on the columnar organisation of cells. However, sign language is also lateralised which is presumably not dependent on the speed of "acoustic" processing. More likely the difference in scale of the sampling windows is not specific to a sensory domain, much as the elements of working memory may be temporal or spatial. For example, the region of the brain associated with visuo-spatial processing also exhibits asymmetry in the spacing of cells and minicolumns in humans (Di Rosa *et al.*, 2006).

It has been suggested that greater spacing of minicolumns in human association cortex results in less overlapping dendritic trees and allows more independent minicolumn function (Seldon, 1981a, b). Harasty *et al.* (2003) have proposed that this is consistent with greater surface area and the wider spacing of evoked electrophysiological activity peaks in the left hemisphere (Yvert *et al.*, 2001). Furthermore, one can speculate that in the generation of "meaning" the left occipito-parieto-temporal cortex (Wernicke's area) activates more discrete, whereas, the right hemisphere activates more distributed semantic fields appropriate to its greater sensitivity to context (Rodel *et al.*, 1992). The accumulation of microscopic asymmetries into larger scale asymmetries of connected patches or fields is supported because, just as there is an asymmetry of minicolumn (approx 50 μm diameter) spacing (Buxhoeveden *et al.*, 2001; Chance *et al.*, 2006), larger macrocolumn patches (approx 500 μm diameter) are also more widely spaced in the left than in the right auditory association cortex (Galuske *et al.*, 2000).

Minicolumn spacing appears to depend on the extent of the connective processes of the cells that fill the space between them, termed "neuropil". The neuropil space around neurons is maintained to preserve the minicolumnar structure throughout the human lifespan (Casanova *et al.*, 2007). Amunts *et al.* (1999) have reported asymmetry of neuropil in human Broca's area and Anderson *et al.* (1999) have reported asymmetry of neuropil in human planum temporale which is presumably concomitant with the minicolumn asymmetries already described (Chance *et al.*, 2006) and contrasts with the absence of minicolumn (Buxhoeveden, 2001) and neuropil (Sherwood *et al.*, 2007) asymmetries found in chimpanzees and other primates. Sherwood *et al.* (2007) propose that the human cortical phenotype differs from chimpanzees in showing a fundamental structural asymmetry in the space occupied by neuropil versus cell bodies.

Structural plasticity of neuropil is likely to vary with fluctuating demand, depending on labile expression of nerve growth factors and proteins essential for synaptic connections. The lifetime course of neuropil spacing and regional differences in column and dendritic arbor size suggest an ongoing variation of protein expression rates in different regions that is specific to the human brain (Chance, 2006). Several genes involved in brain development exhibit different rates of expression in humans compared to chimpanzees (Khaitovich *et al.*, 2006).

In summary, there is evolutionary discontinuity for cytoarchitectural asymmetry but continuity is sometimes claimed for macroscopic asymmetry. This dissociation reflects uncertainty concerning the relationships between different measures of asymmetry. For example, 90% of the modern human population are right handed. Approximately 67% have normal rightward frontal petalia. 73% show a bias in the extent to which the left corticospinal tract (controlling the right hand) crosses over first at the pyramidal decussation of the brain stem (Kertesz & Geschwind, 1971), and in the spinal cord 56% of subjects have a larger right

corticospinal tract (controlling the right hand) compared to only 19% who have it larger on the left (Nathan *et al.*, 1990). The lack of a simple relationship between asymmetry from one level to the next is a challenge to the asymmetry thesis. However, there are limitations to the methods so far developed and further advances may be expected to clarify the core element.

Asymmetry is established early, continues to develop in infancy and adolescence, and is maintained throughout life. As demonstrated by the relationship of primary auditory and planum temporale association cortex, it is likely that later maturing regions will reflect amplification of asymmetry along the hierarchy from primary sensory/motor to heteromodal association cortex. Although not always quantitative, associations have been found between 1) torque, planum temporale asymmetry and language laterality, 2) minicolumn and macrocolumn asymmetry, 3) connective dendrite expansion, magnopyramidal cell size and development of the fatty axon insulation, myelin.

Language

Most arboreal monkeys employ simple 'discrete' call systems, while more derived terrestrial monkeys are characterised by more complex 'graded' vocalisation systems (Falk, 1980). Work with apes has found that they can be taught language using signs more easily than speech, and can acquire a relatively large 'vocabulary' of signs (Savage-Rumbaugh, 1984). In general such sign language involves minimal grammar (Terrace *et al.*, 1979). Generativity and the understanding of deictic reference are lacking. A chimp may learn to understand finger pointing but will not point itself (Woodruff & Premack, 1979). By contrast, humans understand by 12 months old and will point themselves by about 14 months (Schaffer, 1984).

If we equate the capacity for language with representational ability, the archaeological evidence (rock art and other graphic artefacts (Noble & Davidson, 1996; Mellars, 2002))

suggests a recent origin at around 90 to 100 thousand years ago. Christiansen and Kirby (2003, p. 64) identify the origin of human language with the emergence of modern humans. Universal grammar has been proposed as the core element that characterizes language (Chomsky, 1995). The current task is to identify how laterality facilitates the essential features of human language.

De Saussure (1916) argued that what is characteristic of human language is that the linguistic sign consists of two parts - the signifier (a phonological engram or "word"), and its associations (the signifieds or concepts and meanings). Later linguists, e.g. Paivio (1991) and Wray (2002) have spoken of a duality of patterning or "a duality of representation in the brain". However few theories have been related to hemispheric asymmetry.

Some authors have postulated that language is bi-hemispheric. Cook (2002) for example asks - if language is localised (in the form of Broca's and Wernicke's areas) to the left hemisphere, what is the right hemisphere doing? Beeman and Chiarello (1998) have developed the theme that the right hemisphere plays a role in prosody, pragmatics and affect, and that the more remote associations of phonological engrams are stored in the right hemisphere.

Crow (1998; 2004) has proposed a four-quadrant model reflecting the fact that cerebral torque constitutes a bias across the anteroposterior axis such that left and right prefrontal cortices are asymmetric and have the reverse asymmetry of posterior occipito-parieto-temporal cortex. He argues that De Saussure's signifier is located in the left hemisphere and that it has two representations, one motor in Broca's and one sensory in Wernicke's areas. He locates Lichtheim's (1885) "abstract concept" centre in the right hemisphere and divides it into an anterior motor component ("intentions") and a posterior sensory component ("meanings"). Crow suggests that these represent the "signifieds" in the right hemisphere, although it is arguable that aspects of the signifieds are present in both hemispheres - the right hemisphere may be described as the home of the abstract (or pragmatic) elements of the signified.

The four-quadrant scheme is consistent with Chomsky's (1995, p. 168) distinction in The Minimalist Program between articulatory-perceptual and conceptual-intentional, with the specification that the articulatory component is anterior as also is the intentional component but on the opposite side, and the conceptual component is posterior and on the right. Figure 7 illustrates the asymmetric circuit derived from the combination of Crow's four quadrant model (1998) with Chomsky's Minimalist Program (1995), De Saussure's "signifier/signified" dichotomy (1916) and Lichtheim's (1885) "abstract concept" centre represented by the conceptual ("meaning") and intentional ("plans for speech and action") quadrants in the non-dominant hemisphere.

The four quadrant scheme takes as its inspiration the macroscopic asymmetry of

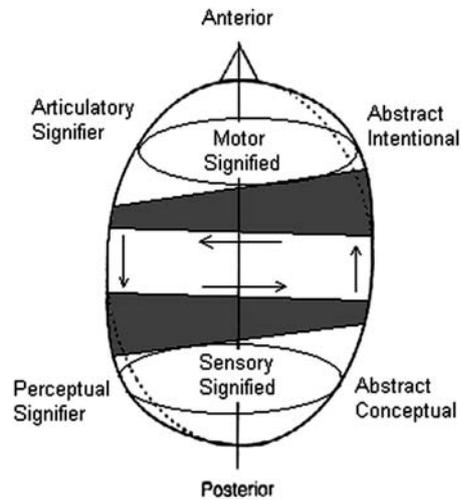


Fig. 7 - The derived four-quadrant model of language lateralisation. A dominant directionality of connections is illustrated by the arrows. Each compartment is assumed to have a distinct function; here "conceptual" and "intentional" are in the right hemisphere (in an alternative version (Crow, 2000) "meaning" and "thought"). Essential elements of evolved language can be characterised; for example concept naming is proposed as output from the loop via articulation of the signifier (left-anterior), and rehearsal may be achieved by repeatedly completing the circuit from articulation to perception.

the human cerebral hemispheres in order to model language. But what element of language is reflected in the microscopic asymmetry for which there is, arguably, stronger evidence for evolutionary discontinuity between other apes and humans? A review of theories considers that a combination of two elements are essential for universal grammar: recursion and concept naming (Crow, 2005). The first of these, recursion, may be facilitated by the cumulative effect of many repeated processes. The asymmetry in the spacing of many repeated cells or minicolumns suggests just such cumulative differences with an emergent functional lateralisation.

To characterise the functional difference, in the sensory domain, the hemispheric distinction that most of the proposed dichotomies wrestle with concerns hemispheric preference for processing stimuli at different levels of scale – global features such as remote associations and context (right hemisphere), versus local features such as close associations and phonology (left hemisphere) (Corballis, 1991). Similarly, for motor function, right handedness suggests a more detailed organisation of motor programs in the left hemisphere.

As discussed above, it is suggested that asymmetry in the spacing of minicolumns relates to asymmetry in the size of activated semantic fields (broadly distributed in the right hemisphere, narrowly focussed in the left). The two streams of processing occur in parallel – global processing in broad activation fields of the right hemisphere and local processing in focussed fields of the left hemisphere. In isolation these streams simply represent two separate levels of detail, but by cross-referencing the differences between the active fields of the two hemispheres the relationship of local features to global features may be encoded. The emergent hierarchy of features within features is a recursive structure. Therefore the integration of global and local features, mediated by inter-hemispheric connections in the normal human brain, is a means to facilitate recursive processing.

It has been proposed that recursion depends on working memory capacity that was enhanced

in the evolution of *Homo sapiens* (Coolidge & Wynn, 2007). It is plausible that enlarged phonological working memory will benefit linguistic embedding and this has been linked to the posterior cerebral enlargement distinctive in modern humans (Bruner *et al.*, 2003). However, in addition to an enlarged working memory, recursion involves generativity – the ability to perceive and express layers of structure and their relations to each other. The asymmetric expansion of neuropil space between minicolumns has the benefit of achieving both enlarged cortex and asymmetric activated fields that may encode layers of global and local structure.

Sex differences

In the UK National Child Development Cohort study already described (Crow *et al.*, 1998), there were sex differences - females had an advantage with respect to verbal ability and were more strongly deviated toward the right hand, while males had a modest advantage in reading except at the point of hemispheric indecision where they were disadvantaged. The presence of human sex differences associated with laterality were replicated in the BBC Internet survey (Peters *et al.*, 2006)

Postmortem (Highley *et al.*, 1999) and MRI (Westerhausen *et al.*, 2004) studies of the main interhemispheric tract, the corpus callosum, indicate fewer but thicker myelinated fibers in men and more densely packed fibers in women. Women have larger callosa relative to brain size than men. De Lacoste-Utamsing and Holloway (1982) first identified a larger and more bulbous splenium (the posterior subregion of the corpus callosum) in women. Similar sex differences in corpus callosum size or shape have been reported by post-mortem and neuroimaging (Bermudez & Zatorre 2001; Clarke *et al.*, 1989; Witelson, 1989). In contrast, chimpanzee data do not show sex differences in handedness (Marchant, 1996) or in the size of the corpus callosum (Dunham & Hopkins, 2006).

In humans, with minicolumn asymmetries unlike other apes, minicolumn number correlates

with callosal axon number and echoes the sex difference. We have found minicolumn number in region planum temporale more asymmetrical in men than women although mean planum temporale volume relative to brain weight was 11% larger in women than in men. This is consistent with data suggesting greater anatomical asymmetry in mature males, but relatively better verbal processing in females (Maccoby & Jacklin, 1974; Halpern, 2000). Witelson *et al.* (1995) found that women have a greater density of neurons in posterior planum temporale. Asymmetric expansion of planum temporale minicolumn spacing in males accounted for an estimated 27% of their asymmetry in region size (surface area) whereas in females it accounted for only 11% of the asymmetry (Chance *et al.*, 2006).

Sex differences therefore exist in the development of lateralised functions including verbal skills that are associated with handedness. Sex differences are also found in the connections between the cerebral hemispheres and in the spacing of minicolumns and their constituent cells. While we have not addressed the issue of selective pressure, assuming, in general, that language and its associated asymmetries are advantageous, the presence of sex differences and their absence in chimpanzees provide scope to suggest that sexual selection has played a role in the evolution of the lateralised human phenotype.

Conclusions

Although the evidence is incomplete, and some contradictory, most can be interpreted as consistent with the conclusion that directional handedness on a population basis and the form

of cerebral asymmetry distinguish modern *Homo sapiens* from the great apes and other primates. These indices are putative correlates of the capacity for language. We distinguish these correlates of a later developing asymmetric expansion of the cortex from an earlier developing hemisphere shift associated with somatic asymmetry which complicates interpretation of the anatomical literature.

Lateralisation is central to both language and handedness in *Homo sapiens*. Handedness appears to be different between humans and chimpanzees, with 90% of modern humans being right handed for a range of tasks, whereas chimpanzees as a species do not show consistent asymmetries of hand use across a range of tasks. There is evidence for right handedness in earlier species of *Homo*. Recent studies in humans indicate that handedness is correlated with the development of verbal ability. Why can apes not learn human language? The homologues of language areas in the chimpanzee brain are smaller than *Homo sapiens*, may not show such clear macroscopic asymmetries and do not show asymmetries of cytoarchitecture – the microscopic spacing of cells and their connective structures. We have discussed how asymmetry may facilitate the essential features of human language and outlined the possible neural basis of the association between cerebral asymmetry and language in terms of minicolumn structure, region size and inter-hemispheric connectivity.

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Info on the web

<http://www.icea.ox.ac.uk>

Evolution of cognition unit at University of Oxford.

<http://www.tandf.co.uk/journals/pp/1357650X.html>

Laterality: asymmetries of body, brain and cognition.

<http://powic.sane.org.uk>

Language, evolution and psychosis.

<http://www.virtual-anthropology.com/>

Virtual Anthropology, Vienna.

<ftp://ftp.cordis.europa.eu/pub/nest/docs/4-nest-what-it-290507.pdf>

EU project, Paul Broca II: The evolution of cerebral asymmetry in Homo sapiens.

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