The International Journal of Comparative Psychology, Vol. 3, No. 1, Fall 1989

LATERAL ASYMMETRIES IN HUMAN EVOLUTION

John L. Bradshaw
Norman C. Nettleton
Monash University

ABSTRACT: Lateral asymmetries are not confined to humans. Palaeozoic trilobites and calcichordates are now known to have been asymmetrical; song control in passerines is vested in the left cerebral hemisphere; learning which is lateralized to the left forebrain of chicks includes imprinting, visual discrimination learning and auditory habituation, while responses to novelty, attack and copulation are activated by the right; in rats the right hemisphere is involved in emotional behavior and spatial discriminations, and there are numerous other behavioral, anatomical and pharmacological asymmetries; the left hemisphere of the female mouse is superior at processing its pups' calls, and there are reports of behavioral asymmetries in impala, cats and dogs. Anatomical asymmetries in the primate brain, from monkeys upwards, are matched by increasing evidence of behavioral asymmetries in visual pattern discrimination, discrimination of species-specific calls, and handedness. We discuss the interaction of preexisting behavioral and brain asymmetries with the evolution in hominids of an upright bipedal posture and tool use, and the origins of language, and conclude that there may be a continuity with earlier species of our two most obvious asymmetries, language lateralization and hand preferences. There may be an ancient left-brain specialization for sensory and motor discrimination learning, which is complemented by a relegation to the right of primitive spatial and emotional functions.

Most of us are right handed (dextral) and left-hemisphere (LH) dominant for language (Bradshaw & Nettleton, 1983). The two sides of the face rarely are left-right symmetrical, as can be seen if we create photographic composites of the two left (L⅃) or right (RЯ) halves. Moreover the left side of the face may express emotions more strongly than the right, due probably to its more direct access to the right hemisphere (RH), known to be involved in the mediation of emotions (Borod & Koff, 1984). Conversely the right side of the mouth may produce earlier, and larger, articulatory movements during speech than the left (Wolf & Goodale, 1987) again due to its more direct access to the LH. If male, the left testicle usually depends lower, as Greek sculptors knew 2,500 years ago (McManus, 1976). However we now know that many nonhuman species are also laterally asymmetrical, due ultimately perhaps to the chirality (handed-

---

Address all correspondence to John L. Bradshaw at Department of Psychology, Monash University, Clayton, Victoria 3168, Australia.

ness) of organic sugars, amino acids, and even the asymmetrical arrangement of the four bonds of the carbon atom. Thus virtually all the amino acids which constitute proteins are left handed, while the progenitor nucleotides in nucleic acids are correspondingly right handed. Even the weak nuclear interaction in physics contains a chiral bias; thus electrons emitted during the β decay of cobalt-60 are predominantly left handed, in terms of the preferred alignment of the particle's spin with its direction of motion. Such physical forces, acting through biochemistry, may have determined cytoplasmic asymmetries in the cell in terms of an asymmetric arrangement of fibrils formed by structural proteins. These would determine the directional beat of cilia and ultimately perhaps even the structure and function of the nervous system (Geschwind & Galaburda, 1985).

According to Jeffries and Lewis (1978), the most primitive fossil chordates (calcichordates, occurring during the Cambrian epoch) were very asymmetric in the head region. More advanced mitrate calcichordates, foreshadowing vertebrates, became almost externally symmetrical, while retaining an internal asymmetry. Whether or not true vertebrates did arise from calcichordates, it is noteworthy that the habenular nuclei of the frog, newt and eel thalamus tend to be more "lobate" on the left (Braitenberg & Kemali, 1970), and the anatomically-connected parietal eye of the lizard exhibits similar asymmetries (Engbreston, Reiner & Brecha, 1981). In the domestic chick, at least in males, the medial habenular nucleus (which responds to testosterone) is larger on the right (Gurusinghe & Ehrlich, 1985). In rabbit, rat, mouse and cat the RH is larger (Kolb, Sutherland, Nonneman & Whishaw, 1982). Behavioral asymmetries may even occur as early as the Paleozoic. Thus healed scars on Paleozoic trilobites attributed to sublethal predation are found more frequently on the right side, suggesting that predators prefer to attack in a specific direction, or that the arthropod victims tended to face their attackers in a specific (i.e. asymmetric) orientation (Babcock & Robinson, 1989). So far this is the earliest evidence of behavioral asymmetry in the fossil record.

Until recently, only humans were thought to exhibit motor (handedness) or cognitive (e.g. language) asymmetries. Asymmetry was even thought to be disadvantageous, in that it might be more useful to be able to generalize between events occurring on either side of the body, rather than to distinguish between them. (We shall however shortly see that asymmetries may permit the development of spatial or directional maps where directional turns to left or right could be important.) While manipulative dexterity has reached an evolutionary peak in our own species, it is nevertheless well developed in rodents, racoons, cats, bears, monkeys and apes. Such animals have long been known to possess strong and stable hand or paw preferences, but were thought not to be biased at the population level. Innate individual differences seemed to be relatively resistant to imposed environmental biases; nor did selective breeding alter the $^{50}/_{50}$ distributions of right and left pawed mice in later generations (Collins, 1977). However we shall examine the very recent evidence that monkeys are biased with respect to handedness at a population level, that the brains of apes exhibit asymmetries similar to our own, and that a host of mammals and birds show striking sensory and motor asymmetries at the population level.

STUDIES WITH BIRDS

There is a striking functional asymmetry in the vocal control of song in various passerines (see e.g. Nottebohm, 1979). In adult male canaries, section of the right hypoglossal nerve (supplying the right side of the syrinx or vocal organ) has relatively little effect upon song, while section of the left side leads to elimination of most of the song's components. Within the brain itself, lesions of the caudal nucleus of the hyperstriatum ventrale on the left has a similarly detrimental effect (unlike the normal vertebrate pattern of limb control, but like the olfactory sense, the entire system is nondecussatory or uncrossed). Damage to the left side in young chaffinches, or in canaries early in the season before they commence their annual learning of a new repertoire, may release the right from left-side inhibition. Thus the right may be permitted to take over song function, just as in very young children the RH can take over speech functions from a damaged LH (Goodman & Whitaker, 1985). However McCasland (1987), employing both bilateral brain lesions and peripheral disruptions of the vocal apparatus, was unable to demonstrate any functional asymmetry, and concluded that both hemispheres and syringeal halves normally make similar contributions to song production.

In parrots there seems to be bilateral representation of the vocal apparatus, despite their ability to learn and reproduce complex sounds. However many species are left footed for food manipulation (Rogers, 1980), suggesting an analogy (but not a homology) with humans. (Indeed some Australian species are predominantly *right* footed.) Moreover as there is no evidence of a correlation between limb and vocal asymmetries, we should be wary of arguments that humans need unilateral control of a single set of articulators to avoid competition and e.g. stuttering (Corballis, 1981; Falk, 1987). Nevertheless it is intriguing (Walker, 1987) that the right branch of the recurrent laryngeal nerve which innervates the intrinsic muscles of the human larynx is the shorter. We might then require unilateral control (by the contralateral LH?) in the presence of two routes of different lengths which could otherwise lead to synchronization problems. (MacNeilage, Studdert-Kennedy & Lindblom, 1988, however, ask why an earlier-arriving subsystem should thereby acquire a processing advantage, and why differences in pathway lengths should lead to problems in coordination; they also note that length differences seem to be exactly compensated for by differences in diameter, thus negating any differences in arrival times.) Finally, to return to avian foot asymmetries, Güntürkün, Kesch and Delius (1988) report that, like parrots, goldfinches are asymmetrical in foot usage; however they exclusively use the *right* foot to release catches.

In the bird visual system, there is complete decussation, so that occlusion of one eye permits direct stimulation of the ipsilateral hemisphere via the opposite eye. Moreover injection of e.g. amnesic agents into one or the other side of the brain can unilaterally suppress memory formation. Rogers (1980) reviews the earlier evidence that learning which is lateralized to the left forebrain of domestic chicks includes imprinting, visual discrimination learning, auditory habituation and attention switching. The left forebrain is more likely to activate a pecking response, and also to inhibit it when no longer rewarded, while responses to attack, novelty and copulation tend to be activated by the RH and inhibited by the LH. However, the sexes differ in how brain lateralization is manifested, which itself is subject to further developmental changes. Thus only males, and only for the first two weeks after hatching, exhibit structural asymmetries in certain thalamofugal visual pathways (Adret & Rogers, 1989). In females, there is no such *structural* asymmetry, though there is some evidence of *functional* asymmetry in visual discrimination learning in female chicks during the first few days post-hatch. While both sexes exhibit similar asymmetries with respect to learning, attack, novelty and copulation (see above), they can only be demonstrated, in young males, by direct testing via one or other eye; in females, however, as in males, they can be demonstrated by chemical inactivation of one or other hemisphere. These asymmetries may be important for the early imprinting process, (and indeed Horn and Johnson, 1989, describe functional asymmetries between the left and right hyperstriatum ventrale in short and long term storage functions in the acquisition of visual imprinting). Moreover testosterone can even reverse asymmetries in male chicks, and light seems to play a crucial role. Thus, *in ovo*, just before hatching, the chick's head is turned up on its left shoulder, shielding the left eye and ear, and only the right eye and ear can receive sensory inputs to activate the LH. Indeed consistent lateralization at a population level may fail to appear if the eggs are protected from light and sound before hatching (Rogers, 1980, 1982), though at the level of the individual chick the brain remains (inconsistently) asymmetric. (A somewhat similar argument, position *in* *utero*, has been developed to explain head-turning reflexes in human neonates, which could possibly underlie subsequent hand preferences, Turkewitz, 1977.) Thus light determines the *direction*, not the *presence* of asymmetries, and indeed if light is shone prior to hatching into the normally occluded left eye, with occlusion now of the normally exposed right eye, the direction of asymmetries, structural and behavioural, reverses. Genes, hormones and environmental influences all therefore contribute to the manifestation of lateral asymmetries. The same is probably true with humans.

Andrew and colleagues (Andrew, 1983, 1988; Andrew, Mench & Rainey, 1982) extended Rogers' conclusions, though their conclusions were frequently modified by complex sex and developmental differences. They showed that untreated chicks learn simple visual discriminations faster via the right eye/LH system (and see also Zappia and Rogers, 1987); with left eye/RH input, fear responses increased. The right eye/LH system may habituate faster to novelty, and be better able to withold responses to irrelevant stimuli by controlling lower-level instinctive emotional responses, than the left eye/RH system. The latter, according to Andrew, may have a special interest in spatial positioning and emotional reactivity; it may act as a passive observer, while the right eye/LH system may actively catergorize and select important stimuli for sequential responding. Such a model, which can be extended to cover LH mediation of song control in passerines (above) has obvious affinities with the idea of an analytic/holistic processing dichotomy in humans (Bradshaw & Nettleton, 1981). Indeed Andrew and Brennan (1985) showed that while birds using the left-eye/RH system were less competent than those using the right eye/LH system at "analytic" tasks of discriminating between categories of peckable objects, they were much better at generalizing aversive training to ill-tasting beads of different colors. There may also be a similarity with Bianki's (1983) findings with the formation, generalization and specialization of conditioned reflexes in rats while one or other cerebral hemisphere was chemically inactivated; he claims that synthetic generalizations proceeds more strongly in the RH, while analytic specialization proceeds better in the LH. Stewart, Rose, King, Gabbott and Bourne (1984) used acquisition of a similar passive avoidance task (withholding pecking of bright beads with unpleasant taste) to study the effects upon synapses in the medial hyperstriatum ventrale. In terms of the number of vesicles per synapse, values on the left side of trained chicks massively exceeded those on the right. This structure may also be asymmetrically involved in imprinting (Bradley, Horn, & Bateson, 1981). Indeed just as in the chick, use of the right eye/LH system in pigeons may lead to better visual discriminations (Güntürkün & Kesch, 1987). Finally Vallortigara, Zanforlin and Caillotto (1988) showed that male chicks demonstrated faster discrimination learning when a critical box is placed to the right rather than the left in a T maze.

STUDIES WITH RODENTS

Studies with rats have recently demonstrated some of the most striking morphological, pharmacological and behavioural asymmetries. However mice, while possessing strong individual paw preferences, nevertheless split $^{50}/_{50}$ at the population level even after prolonged selective breeding (Collins, 1985). However, just as with humans (Bryden & Steenhuis, 1987), breeding may selectively alter *strength* of pawedness, and likewise female mice turn out to be the more lateralized in motor preferences. (In humans, at the *cognitive* as opposed to the *motor* level, e.g. with respect to language, females may be *less* lateralized, McGlone, 1980.) Mice bred for stronger behavioural asymmetries also possess more asymmetrical and heavier brains, and tend to be more reproductively successful and masculinized (Ward & Collins, 1985, and cf. the role of testosterone in human cerebral asymmetry, Geschwind & Galaburda, 1985). Furthermore, more lateralized rats may learn spatial responses faster (Zimmerberg, Strumpf, & Glick, 1978; Camp, Therrien, & Robinson, 1981).

The neocortex of the RH of New Zealand black mice is larger than the left (Rosen, Sherman, Mehler, Emsbo, & Galaburda, 1989), and the rat likewise exhibits pronounced brain asymmetries (Heine & Galaburda, 1986), though there are considerable sex differences (Diamond, 1984, 1985). Lesions to the RH, rather than the LH, may cause (transient) changes in catecholamine levels and emotional behaviour (Dewberry, Lipsey, Sood, Moran & Robinson, 1986). Indeed RH ablations may even lead to immune suppression in female rats, apparently mediated via prolactin (LaHoste, Neveu, Morméde & Le Moal, 1989).

Denenberg and Yutzey (1985) review Denenberg's complex studies on the effects of (preweaning) handling and (postweaning) environmental enrichment upon subsequent behavioural asymmetries in the unilaterally lesioned rat. The RH may be preferentially involved in emotional behaviour and the ability to perform left-right spatial discriminations, and early handling may initiate or augment brain and behavioural asymmetries. Damage to the RH may increase spontaneous activity, though sex and strain differences complicate the picture, while the LH again tends to inhibit emotional reactivity in the RH, probably via the interconnecting corpus callosum. Indeed according to Denenberg, Berrebi and Fitch (in press) male rats possess wider callosa than females, especially in the genu and the most posterior portion of the splenium, these differences being greatest among those handled in infancy. Sex differences in the thickness of the human corpus callosum have also been reported (Witelson & Kigar, 1988), though the findings are subject to dispute (Byne, Bleier & Houston, 1988).

Glick and Shapiro (1985) review Glick's work with mostly female rats, which were found generally to be more lateralized than males, just as Collins (1985, above) found with mice, and as occurs in humans with respect to motor (but not cognitive) asymmetries. Normal rats tend to turn or rotate, either spontaneously at night or after drug treatment in the daytime, and for any individual the preferred or dominant direction is consistent. Neonatal asymmetries in tail posture may even predict adult turning preferences (cf. the possibility that human head-posture asymmetries in the neonate may predict subsequent hand preferences, Michel, 1981). Unilateral damage to the subcortical nigrostriatal motor system, which contains the neurotransmitter dopamine (DA), causes ipsiversive turning towards the side of the lesion, and this effect can be further potentiated by dopaminergic drugs. In normal rats, too, there are left-right asymmetries in DA concentrations in the two striata, and high doses of d-amphetamine (d-AMPH) increase this DA asymmetry, inducing daytime rotation in the direction contralateral to the side with the higher DA levels. Normal left-right operant preferences also correlate with the direction of d-AMPH induced rotation, and DA levels are normally higher in the striatum contralateral to the rat's side preferences. Moreover rats lacking clear spatial biases may be hyperactive and have learning difficulties in spatial tasks, and may be unable to learn to discriminate left from right (cf. similar claims about dyslexic children, see Bradshaw & Nettleton, 1983); interestingly amphetamine seems to help both children and rats develop a sense of left-right, and, paradoxically, may also reduce childhood hyperactivity (paradoxically, because amphetamine is normally a stimulant). The deoxyglucose (dGlc) technique indicates that the left frontal cortex is normally the more active, and this in turn modulates pre-existing nigrostriatal asymmetries such that measured over a sufficiently large sample, more rats naturally turn right than left. (Indeed Castellano, Diaz-Palarea, Rodriguez and Barroso, 1987, find that in a T maze a majority of rats turn right.) Cocaine inhibits re-uptake of the neurotransmitter dopamine (DA) into the striatum, and enhances rotation, but interacts with sex: after cocaine, naturally right-biased females rotate more than naturally left-biased females, while the reverse occurs for males, though again females are more lateralized, generally, than males. These behavioural sex differences may relate to sex differences in anatomical asymmetries in the cortex and hippocampus, whereby the left side is thicker than the right in females and vice versa in males (Diamond, Murphy, Akiyama & Johnson, 1982). Note however that according to Drew, Lyon, Titeler & Glick (1986), asymmetries in the DA receptor densities in the striata, while favoring the right side in females and left in males, are independent of directional preferences exhibited during normal nocturnal circling.

One wonders, though curiously this question seems not to have been addressed until 1987, whether humans might also show natural or drug-induced turning biases. Bracha, Seitz, Otemaa & Glick (1987) measured people's clockwise or anticlockwise turning tendencies, without their awareness, during a routine working day. They found that females have a higher average rate of rotation than males (again indicating that females may be more asymmetric than males in motor behaviour); consistently right-sided males (in terms of hand, foot and eye dominance) showed a rightwards (clockwise) rotational preference, while right-sided females and mixed dominance males showed leftwards (counterclockwise) preferences. On the other hand, Bradshaw and Bradshaw (1988) found that when required to rotate through exactly twice 360° clockwise (rightwards) or counterclockwise (leftwards), blindfolded dextrals, especially females, showed a rightwards bias and sinistrals a leftwards tendency. When however attempting to walk in a straight line all four groups of subjects deviated to the right, especially females and dextrals. Moreover two studies with schizophrenics (Corbin, Williams, & White, 1987, and Reynolds, Czudek, Bzowej, & Seeman, 1987) showed strong clockwise turning tendencies, which both groups of authors believe to be related to increased DA asymmetries, in schizophrenics, in the amygdala or putamen. Further it must not be forgotten that in humans, psychoactive drugs affect emotional and cognitive functioning, which itself is lateralized; so do psychoactive drugs therefore affect lateralized behaviour? Frumkin and Grim (1981) claim that barbiturates, via the action of the inhibitory neurotransmitter GABA, may shift hemispheric lateralization in favour of LH dominance, leading to an increase in loquacity (LH) and a decrease in emotionality (RH).

Before leaving the rodents, we should note (Ehret, 1987) that in the house mouse the ultrasonic calls emitted by the young pups to evoke maternal attention, and which are perceived categorically in the frequency domain, are preferentially recognized by the right ear/LH. Moreover in females without experience of pups, which have been trained to respond to the same signals by conditioning, no asymetries appear. As Ehret observes, mice must have an innate predisposition for attending to and perceiving communication sounds via the LH, even though the mothers must learn to identify them through actual interaction with young. Thus the LH involvement depends upon the *biological significance* of the sounds, just as is the case (see below) with the LH processing of species-specific communicatory sounds by monkeys.

Finally, there are reports of behavioural asymmetries in impala, cats and dogs. There are many more scars on the right sides of male impala, the result of inter-male contests, indicating that the contestants may turn to the left when facing an adversary, which is again compatible with RH mediation of such emotional, agonistic, precopulatory activity (Jarman, 1972). Cole (1955) found that of 60 cats reaching for food in a tube, 20 percent were classifiable as right paw preferring and 38 percent as left; the rest were ambidextrous (defined as less than 75 percent consistent in reaching). Again females were more lateralized. He suggested that a variation in the number of fibres crossing to form the pyramidal tract determines limb preference, but sex differences may be hard to explain thus, and a left paw preference for visually guided reaching is very reminiscent of similar claims (below) with monkeys (MacNeilage, Studdert-Kennedy & Lindblom, 1987). According to Tan & Caliskan (1987a, b), dogs prefer to wipe adhesive tape from the face with their right paws. Moreover while there appeared to be no correlation with paw preferences, Tan and Caliskan (1987a) found asymmetries in the cerebral dimensions and fissures; thus the RH may be longer and higher, but not wider, and the Sylvian fissure on the right side may be lower. Indeed in a later study, Tan and Caliskan (1987b) found that the RH is heavier regardless of paw preference.

MORPHOLOGICAL ASYMMETRIES IN THE PRIMATE BRAIN

Left-right asymmetries in the human peri-Sylvian (speech related) cortex, especially in the region of the temporal planum, have been known for over a century. The Sylvian fissure is generally longer on the left, and continues further horizontally before bending upwards. Its posterior end (the Sylvian point) is usually higher on the right, even as early as the 16th week of gestation, and has been observed in at least two species of fossil humans (LeMay, 1976), *H. sapiens neanderthalensis* and *H. erectus* (Peking Man). The temporal planum, especially the superior portion of the temporal gyrus, an important language area through which the Sylvian fissure passes, is generally larger on the left, even in the fetus; the same holds for another speech area, the parietal operculum (see e.g. Wada, Clarke & Hamm, 1975; Witelson & Pallie, 1973). The left occipital pole is wider and protrudes more posteriorly than the right; anteroparietal and posteroccipital regions are generally larger on the left. The right frontal pole extends beyond the left, and together with the prefrontal portion of the right hemisphere, is wider (LeMay, 1976; Chui & Damasio, 1980), giving the brain an overall counterclockwise torque. The LH has a higher ratio of grey to white matter (Gur et al., 1980); the right has more tissue and is heavier (LeMay, 1976; Whitaker & Ojemann, 1977).

In the chimpanzee, the Sylvian fissure is also longer on the left (Yeni-Komshian & Benson, 1976), and the Sylvian point is lower on the left in chimpanzees and orangs (LeMay & Geschwind, 1975), due to expansion of the left posterior parietal cortex. Moreover, Falk (1978) studied 88 brain endocasts representing 8 genera of Old World monkeys, and found cortical asymmetries in the lengths of the Sylvian fissure, the superior temporal sulcus, the lateral edge of the orbit and the distance separating the rectus and arcuate sulci. While not all asymmetries matched those found in humans (though in a later study by Falk, Cheverud, Vannier & Conroy, 1986, the length of the left Sylvian fissure of rhesus monkeys was found to be longer, as in chimpanzees and humans), she suggested that a hypothetical expansion of left prefrontal and parietal integration cortices was sufficient to explain these asymmetries, and concluded that the ancestor common to monkeys and humans possessed them. Likewise Sherman, Galaburda, & Geschwind (1982) conclude that during primate evolution the Sylvian fissure has migrated from a nearly vertical to a horizontal posture, due to increasing development of the inferior parietal region which has come, perhaps by a process of preadaptation, to subserve human speech. Again, just as with ourselves, in New and Old World monkeys and baboons the RH frontal and LH occipital regions are wider and protrude further (LeMay, 1985). Indeed Heilbronner and Holloway (1988) report greater Sylvian fissure length in the LH even in *New* World species of monkeys, and de la Coste, Haworth and Woodward (1988) find striate cortex asymmetries even in *lemuridae*, though now it is the right side which is larger, possibly reflecting specializations in visuospatial processing. Finally, Holloway and de la Coste-Lareymondie (1982) studied the petalial asymmetries (projections of the frontal and occipital poles) for 190 hominoid endocasts. They found that all fossil hominids (*Australopithecus*, *H. erectus*, *H. sapiens neanderthalensis*, *H. sapiens sapiens*) showed the same pattern of left occipital and right frontal petalias, while gorilla showed left occipital petalia only. Left occipital width was greatest in all species of *Homo*, *Australopithecus*, possibly gorilla, but not in chimpanzee, leading to the conclusion that ‘human’ brains are more asymmetrical than those of the pongids, and have been so for 3 million years.

PERCEPTUAL AND MOTOR ASYMMETRIES IN THE NONHUMAN PRIMATE

Horster and Ettlinger (1985) observed that 78 rhesus monkeys spontaneously using the left hand, learnt a tactile discrimination task significantly quicker than 77 spontaneously using the right hand. In humans, the left hand (RH) also tends to be slightly superior at performing tactile discriminations (Bradshaw & Nettleton, 1983). In the visual modality, Jason, Cowey and Weiskrantz (1984) required monkeys to discriminate between squares with a central dot or one displaced slightly upward, before and after a LH or RH occipital lobectomy. In this spatial task for which humans have a RH superiority, animals with a LH lesion (4) all performed worse than those with a RH lesion (5). Likewise Hamilton (1983) found that split brain monkeys learned to discriminate lines differing in slope by 15° much better with the LH. Similarly, Hamilton and Vermeire (1983) tested the ability of each hemisphere of 18 split brain monkeys to learn to discriminate the photographs of faces of other monkeys. Only females (9) showed an asymmetry, a LH advantage, especially animals which were older at surgery. (Perrett, et al., 1988, using single unit recording techniques, claim to have identified the LH regions in the superior temporal sulcus, perhaps responsible for such face processing.) However, later, Hamilton and Vermeire (1985) report a RH superiority as with humans, for face processing by monkeys of both sexes, while confirming their earlier findings of a LH involvement in judgements of line slope. (In a subsequent, 1988, report they confirm and extend these findings of a double dissociation, observing that complementary hemispheric specialization characterized most of their subjects; they also note that, just as with humans, inversion of the facial stimuli eliminates the RH advantage). Ifune, Vermeire and Hamilton (1984) also found that the number of facial expressions elicited from the RHs of split brain monkeys viewing faces was greater than that made by the LH system. For further evidence in chimpanzees of a RH contribution to the perception of (human) faces, chimerically presented (i.e. with left and right halves from differented originals abutted at the midline), see Morris and Hopkins (1989). However we should nevertheless be wary of assuming that asymmetries in other species are necessarily homologous (i.e. of common evolutionary origin) to our own; common evolutionary pressures may bring about similar though otherwise independent (i.e. analogous) patterns of form or function in different species.

It is perhaps in the auditory modality that asymmetries most similar (and perhaps homologous) to our own emerge in the monkey, though as discussed above (Ehret, 1987), a LH specialization for recognizing pup calls appears in the mouse. Petersen, Beecher, Zoloth, Moody and Stebbins (1978) found evidence of a right ear advantage (REA) in Japanese macaques' abilities to perform discriminations between calls specific to their own species, exactly analogous to our own REA/LH superiority for verbal material. Subsequently Petersen et al, (1984) replicated the above findings, and showed that monkeys of a slightly different species (to whom the taped calls were not species-specific) showed no ear advantage; moreover they demonstrated that both species were attending to the same features, as generalization gradients were highly similar. Heffner and Heffner (1984) trained Japanese macaques to discriminate between two forms of their "coo" vocalization before and after unilateral and bilateral ablation of the temporal cortex. Performance was affected by unilateral ablation of the left (not right) superior temporal gyrus (the analog of our Wernicke's area for speech perception); ablations dorsal to and sparing the auditory cortex had no effect upon discriminations. We must conclude that just as in humans, the temporal cortex of the LH plays a major role in mediating the perception of species-specific vocalizations. Moreover, in an earlier study, we may note that Dewson (1977) trained crab-eating macaques to execute a delayed conditional discrimination between auditory and visual stimuli; lesions in the left superior temporal gyrus again led to more severe performance deficits than damage to the corresponding area of the RH. Finally, Pohl (1983) studied monaural ear advantages for discriminating between members of various acoustic classes in four baboons. Left ear advantages (LEAs) appeared for pure tones in all four subjects, and for three-tone chords in three, for vowel sounds in three, and consonant-vowel sounds (CVs,/pa/vs/ba/) in three. In a subsequent (1984) study he used a gap-detection task requiring resolution of brief silent intervals in noise bursts, and got exactly the same findings as in the previous CV task. Such a RH superiority, in this case indexed by evoked potentials, for humanlike discrimination in a categorical fashion of voice onset time (VOT), was shown by Morse, Molfese, Laughlin, Linnville and Wetzel (1987), working with rhesus monkeys. Humans also evince RH superiorities in discriminating between tokens differing along the voicing dimension, despite the fact that such stimuli are perhaps rather distantly language related.

Turning to motor or response asymmetries, Kuhl (1988) found that all 30 macaques (of 3 species) favored the right hand when making complex, highly-stereotypic manipulative responses, despite often using the other hand in simpler situations. Preilowski, Reger and Engele (1986) required rhesus monkeys to produce specific pressures for specific times with the fingertips; while individuals showed extreme degrees of hand preference which were nevertheless independent of hand performance, when difficulty levels were adjusted to the performance of each hand, the *right* (but not necessarily the *preferred*) hand proved superior. Indeed Falk, Pyne, Helmkamp and DeRousseau (1988) report that out of 150 rhesus monkeys, 7 out of 10 forelimb dimensions are larger on the right, especially those relating to the ulna and humerus. The authors speculate that such hypertrophy reflects greater use, as similar relationships are found in humans. In the baboon, Vauclair and Fagot (1987) report that of a troop of 18, 5 showed a right hand preference for spontaneous activities and 2 a left hand preference—hardly a major asymmetry when 11 were ambilateral—though a developmental increase was apparent. However in a companion paper (Fagot & Vauclair, 1988a) they found a *left* hand preference in the baboon for complex novel manipulations requiring fine visuospatial discrimination—an issue to which we shall return shortly. In the lowland gorilla these authors (Fagot & Vauclair, 1988b) also obtained a left-hand preference (7 out of 8 animals) in a precise manipulospatial task similar to that employed above with the baboons, while hand differences were absent when the animals simply reached for objects. (They also reviewed a number of earlier minor and largely observational studies employing between one and 8 animals: out of 18 gorillas, 15 were reported as preferring the right hand and 1 the left in relatively stereotyped situations.) A possible resolution of these conflicting data is indicated by the findings of Sanford, Guin and Ward (1984). They studied 25 bushbabies for hand preferences for reaching for and grasping objects; only under conditions of an obligatory bipedal stance did a left hand preference emerge. (Ward, 1988, later noted that a left hand bias in food reaching is a salient characteristic that extends across several species in prosimians). These findings were taken up by MacNeilage, et al. (1987) in their review and re-analysis of old data. They argue for a *left* hand superiority for visually guided reaching, and a *right* hand preference for manipulation and practiced performance in stereotyped situations, though they have been criticized for inappropriate statistics and for ignoring many null findings. They claim that earlier negative conclusions arose from use of juvenile animals, or tasks which did not adequately call upon such preferences. They suggest that primate handedness patterns are structural, and a functional adaption to feeding, and are precursors to aspects of human LH and RH specializations. Specifically, they suggest that a left-hand RH specialization for visually guided reaching occurred in early prosimians, which were vertical clingers and leapers. This led to two complementary specializations, a left-hand, RH perceptuomotor specialization for unimanual predation, perhaps with visuospatial components, and a LH (right-limb) specialization for whole-body postural organization, again perhaps associated with a pre-existing LH mediation of communication. With the advent of quadrupedalism, from a vertical leaping and clinging posture, the right forelimb undertook manipulation, and now the left side of the body reversed roles to undertake postural support. Consequently, they emphasize the important predictive role of footedness in humans, claiming that a right foot dominance is more strongly linked with language lateralization than is handedness (MacNeilage et al., 1988), though see Peters (1988) for problems in dissociating the postural and the active aspects of foot asymmetry. Such an account, however, only accommodates with some difficulty the findings of asymmetries among birds and rats, and there is much evidence that speech and other cognitive specializations in the LH precede manual asymmetries, both phylogenetically and ontogenetically. Thus far more of us have some left hand preferences (the writing hand not always being the preferred hand for all other tasks) than have RH language, manual skills being more flexible with respect to hemispheric specialization than language skills, as evidenced both by the clinical and the learning literature. Moreover, as Michel and Harkins (1987) observe, it seems maladaptive for humans to have now lost a left-hand bias in reaching (the LH/right hand system presumably having taken over *both* functions) as an object would have to be transferred from right to left hand if it is to be bimanually manipulated or worked on by the right hand. Michel and Harkins also note that during infancy a right hand bias for reaching *precedes* the appearance of bimanual manipulation. When the latter appears, infants often switch reaching preference to the formerly nonpreferred hand, to facilitate using the preferred hand for more active manipulation, and only later revert to using the right hand for both reaching and manipulation, necessitating a fumbling intermanual transfer. For these reasons, bimanual manipulation seems to be an unlikely source of a right-hand bias in reaching. Our use of the right hand both for reaching and manipulation may reflect the emphasis in our manual behaviors of rapid, accurate, sequential activities of a temporal rather than a purely spatial (RH) nature; thus the precise temporal integration of a number of sequential movements (as in reaching, grasping and then manipulating an object) may outweigh the purely spatial components, which could nevertheless continue to feed, albeit indirectly via ipsilateral pathways, to the right limb. Indeed under certain conditions emphasizing the more spatial aspects of reaching, a left-hand superiority and/or a RH contribution may appear (for review, see Goodale, in press).

HOMINID ORIGINS AND POSSIBLE EARLY DEXTRALITY

There is substantial current disagreement concerning the details and chronology of hominid lineage (Andrews, 1986; Lovejoy, 1981;

Stringer & Andrews, 1988). Hominids and African apes probably split between 9 and 5 million years ago, due perhaps to major environmental changes, though the hominid-chimpanzee split would be closer to the lower figure. Indeed in terms of genetics (DNA sequencing and hybridization techniques) and evolutionary time, we are probably closer to chimpanzees than the latter are to gorillas (Lowenstein & Zihlman, 1988), despite the fact that chimpanzees and gorillas look more alike; both are hairy, walk on all fours, knuckle walk, have short legs and long arms, brachiate, are less dextrous manually than ourselves, have smaller brains and larger canine teeth with thin enamel. Thus apparent chimpanzee-gorilla similarities do not necessarily reflect closeness of kinship, or convergent evolution, so much perhaps as retention of ancestral traits which we have lost. Our own physical differences from chimpanzees, despite the close genetic similarity, probably stem from the fact that much of our joint genetic make-up is in fact largely nonfunctional in both species without an impact upon morphology, thus even permitting it to be used as a clock for genetic change or drift uninfluenced by selective pressures.

By 4 million years ago, species of the hominid *Australopithecus* had emerged. Our possible ancestor *A. afarensis* may have produced the dramatic and seemingly-fully-bipedal footprints preserved at Laetoli 3.5 million years ago (Leakey & Hay, 1979): even if posture was not fully modern (though see Lovejoy, 1988), bipedalism seems to have greatly antedated brain enlargement and the emergence of tools. The African hominids split into the gracile (*A. africanus*) and robust (*A. boesei*) australopithecines, and our first probable ancestor *H. habilis*, before 2 million years ago; the human fossil record is limited to Africa for the first 3 million years. (It is possible that more than one species may currently be "lumped" into *H. habilis*, and certain that this—or these—species co-existed with other australopithecines.) The first undisputed stone cultural remains (*H. habilis*, Oldowan culture) appear 2.5 to 2 million years ago. Indeed, according to Toth (1985), *H. habilis* was habitually dextral, to judge from an analysis of the pattern of successive flaking from stone cores: thus dextrals typically hold the core in the more passive left hand and rotate it clockwise. The resulting sequence leaves its trace of superimposed scars on the flakes; these Toth believes were used as tools, rather than the residual cores. Whether or not these conclusions are upheld, it is interesting to note that there is quite separate evidence in that species (Bahn, 1989) from the presence of characteristic grooves, together with reactive ridges, along the junction between cementum and enamel, of the use of toothpicks at Omo (Ethiopia) by 1.84 million years ago. These patterns, not otherwise accountable for by e.g. root caries, gritty saliva or fibre processing, are similarly found in all later species including ourselves, and are indicative of prolonged repetitive action. Yellen (1986) observes that *H. habilis* was the first hominid with an enlarged cranium (600 to 800 cm^3).

The transition from *H. habilis* to *H. erectus* (Java, Peking Man, the Acheulian stone tool culture) probably occurred at about 1.5 to 2 million years ago; the latter had a still larger brain (800 to 1200 cm^3) and more advanced tools (bifacials) and possibly fire. (Brain & Sillen, 1988, report burnt bones heated to a range consistent with campfires in the Swartkrans cave Member 3 layers, dated to between 1.0 and 1.5 million years ago; only the remains of *A. robustus* were found associated, though *H. erectus* was presumably also present. Thus there is the possibility even of australopithecine use of fire.) *H. erectus* at 1.5 million years ago constructed flint axes *around*, and thereby preserving spectacular fossils in a prominent central locus, perhaps to serve as a "personal blazon" (Oakley, 1981). (It could be argued that the concretionary nature of the flint nodules around fossil nuclei was such as to inhibit flaking in the immediate vicinity of the core fossil, thereby artifactually leaving the fossil in a prominent central position). Shortly after, the australopithecines which had hitherto coexisted with *Homo* became extinct (1.3 to 1 million years ago). De Castro, Bromage, and Jalvo (1988) analyzed the orientation and location of striations on the anterior teeth of anteneanderthal hominids from the Spanish Middle and early Upper Pleistocene. They concluded that the patterns were indicative of antemortem stone tool use to cut meat held between the teeth, preferentially by the right hand (and see also Bromage & Boyde, 1984). While archaic *H. sapiens* at 0.5 million years ago was African (Andrews, 1986), and the same was perhaps true of modern *H. sapiens* (which much later developed the European Cro-Magnon culture) at about 100,000 years ago, nevertheless the latter date has now been proposed for its arrival in the Levant (Valladas et al. 1988). Neanderthals (with their Mousterian stone tool culture) were probably not closely related phylogenetically, and may have subsequently arrived there at a relatively late date from Europe, where they might have emerged 300,000 years ago. They became extinct around 35,000 years ago, perhaps in competition with modern *H. sapiens*.

BIPEDALISM, TOOL USE AND THE ORIGINS OF LANGUAGE

While the use of language, tools and an upright bipedal posture and locomotion are characteristics not totally unique to humans, all three only appear consistently in our own species. Thus, depending upon the definition of language, and resolution of arguments concerning whether or not apes taught (painfully) to communicate with us are capable of deliberate deception and formulation of totally novel sequences etc. (Premack, 1986), apes may or may not be said to employ language. Moreover other species may occasionally move bipedally, and use tools (Beck, 1980), and maybe even partake of some form of consciousness (Griffin, 1984). Whatever may be the case with *A. afarensis*, *H. habilis* undoubtedly possessed an upright bipedal posture, though debate continues whether this posture was acquired early (Lovejoy, 1988), or gradually (Jungers, 1988), within the latter instance individuals dividing their time between trees and ground. Thus Lovejoy (1988) argues that the 3,000,000 year old australopithecine female “Lucy” was even *better* designed for bipedalism than we are, to judge from the shape of her pelvic ilium and femoral neck; this was so only because the resultant constriction (relative to that of a modern woman) in her birth canal was tolerable because her species predated the dramatic expansion (see below) in fetal head size at birth. Lovejoy goes on to claim that her bipedal progression was truly habitual, all other kinds of locomotion having been foresaken, as the particular muscular rearrangements enabling her to walk upright would not have permitted efficient quadrupedal locomotion on the ground. He does at one point allow that she might often have taken to the trees and climbed, as most primates do, using all four limbs. Later, however, in the same article, he appears to explicitly disallow even this possibility. Indeed, according to Latimer and Lovejoy (1989), the calcaneus in the foot of *A. afarensis* had already undergone the primary adaptive alterations to bipedality seen in *H. sapiens*, indicating that a completely terrestrial life-style was responsible; these authors conclude that it is highly unlikely that significant climbing behaviours were included in the locomotor repertoire of that species. On the other hand, according to Jungers (1988), compared to ourselves, apes have curved hand and foot bones, small hindlimbs and a rather different lumbo-sacral structure, with *fully* modern morphology in every respect possibly not appearing until *H. erectus*, which might have been the first to habitually employ a true striding gait. (Susman and Brain, 1988, report finding a hallucal metatarsal bone from the Swartkrans cave, dated to ca. 1.8 million years ago, and attributed to *Paranthropus (= Australopithecus) robustus*; closely resembling that of humans, it suggests a human like posture and range of foot movements, though the human “toe-off” in walking may have been absent. Thus *H. habilis* and surviving austalopithecines may have attained a similar grade of bipedality at that date.) While *H. habilis* may therefore have possibly retained a mosaic of primitive and derived features (and see Susman & Stern, 1982), it could nevertheless also fabricate simple cobble tools, the first undisputed stone tools in the archaeological record. Whether or not climatic changes occasioned its ancestors' move to the open savannah (other lineages of course successfully remained in a forest environment), its upright posture may have been pre-adapted for by retained habits of brachiation while seeking opportunistic or nocturnal arboreal refuge: similar musculature to upright walking is employed in tree climbing.

Hardy (1960, and see also Morgan, 1984, 1986) instead proposed an aquatic phase in hominid evolution, leading to loss of body hair, the presence of subcutaneous fat, face to face copulation (as in all aquatic animals), the presence and distribution of fetal hair, weeping (salt excretion), the diving reflex (apnea, bradycardia) and of course bipedalism, as swimming is said again to employ similar musculature. However there is no paleoclimatic evidence for the proposed widespread flooding; moreover other explanations can account for our nude skin, e.g. the dissipation of excess metabolic heat during temporary exertion, such as fleeing predators, or opportunistically pursuing small savannah prey. Indeed a new ecological niche would be opened for hominids were they to do the latter during noonday heat. Furthermore, bipedalism is itself a thermoregulatory advance, removing much of the body from close proximity to the heated ground, and exposing less skin to the sun's rays. Such a thermoregulatory advance (Ebling, 1985; Wheeler, 1984), together with a massive increase in sweat glands (themselves of course useless in water) would remove a barrier to further brain growth. A large brain is itself also a considerable source of metabolic heat. However, even these factors on their own may have been insufficient to account for the adoption of a posture which is so unfavorable for speed and agility.

Other factors which favor bipedalism and ultimately dextrality include missile throwing (Calvin, 1983) and tool use (Frost, 1980). The latter factor really subsumes the former. Thus manual specialization would result in one hand holding a store of missiles, and the other throwing, or one hand holding and steadying an object, while the other hand sequentially operates upon it, with consequent economies of brain processing space. Indeed Frost emphasises the sequential syntactic character of both tool operations and language, and suggests that this may be why both functions are co-lateralized to closely adjacent regions of the LH. These peri-Sylvian regions seem from electrostimulation studies (Ojemann, 1983) to be essentially motor, whether for sequencing, temporal ordering or precise perceptual timing. Such *perceptual* aspects, as in discrimination between heard phonemes during speech perception, suggest that speech perception itself may depend upon the mechanisms otherwise used for speech *production* (Liberman, Cooper, Shankweiler & Studdert-Kennedy, 1967), and that there are close anatomical and functional links between manual and oral movement control, speech production and perception (and see Kimura & Harshman, 1984). Such considerations, however, do not necessarily imply that gesture must have preceded language (see below), or that tool making or tool using behaviors *presuppose* some form of syntactic language (Holloway, 1981), since even the simplest of such behaviors are notoriously difficult to describe and are far more easily transmitted by example or imitation. Imitative learning in fact is an additional factor which we can invoke to account for asymmetries at the *population* level, the fact that most individuals in a population are lateralized in the same direction. Thus two dextrals (or two sinistrals, i.e. two individuals of the *same* handedness) learn more efficiently from each other how to tie knots (Michel & Harkins, 1985), a possible paradigm of tool use acquisition. However as discussed above, *H. habilis* may already have been dextral, and anyway tools, until maybe *H. erectus*, were hardly of the complexity that interactive or imitative learning would benefit from homogeneity of handedness. (Indeed the techniques available to *H. habilis* of essentially clumsy rock-bashing probably only permitted a limited range of possible artifact shapes, thus obviating the need for either language or careful imitation.) We must therefore conclude that dextrality appeared either much earlier, for other reasons, or much later. In any case while evolutionary pressures may have favored either uniformity of handedness, for whatever reasons, or outright dextrality (which of course is not *itself* presupposed by uniformity of handedness), we should note that there may be certain residual advantages in sinistrality; such individuals can often use their nonpreferred hands more efficiently than dextrals (Kilshaw & Annett, 1983), and may under certain circumstances even be superior in spatial skills (Benbow, 1988; Geschwind & Galaburda, 1985).

Parker and Gibson (1979) propose their own version of the tool use hypothesis in the context of a general theory of the evolution of language and intelligent behavior. They suggest that expanded tool use developed as an aid for extractive foraging. The latter, rather than hunting, differentiated hominids from the apes, and involved hammering, digging, stabbing, probing, hitting, cutting and ultimately throwing; it led to food sharing and on to language, via gesture. However, their particular argument relies heavily upon ontogeny recapitulating phylogeny, at the levels both of brain and of behaviour, and upon Piagetian stages of intellectual development in children and other species, two areas currently of some controversy. Nevertheless, the general scenario of an upright posture leading to tool use, gesture and on to language (Hewes, 1976) is a popular one: we readily fall back upon gesture; retardates may rely upon it, and we can teach chimpanzees a gestural channel of communication with us; among primates only humans possess unpigmented (i.e. clearly visible) palms; gesture is superior to speech in showing how to do things; there may be syntactic commonalities between gesture, tool use and butchery; gestures precede or are synchronous with speech;

an intervening gestural stage would separate the supposedly involuntary subcortical calls of other primates from the voluntary, cortical and propositional language of humans. As we shall see, this last distinction may well be invalid, and in any case there is a major problem with the late location of gesture in the sequence. Thus chimpanzees (and therefore presumably a common ancestor of chimpanzees and of our own species) share many of our gestures (Harré & Reynolds, 1984), despite not being habitual tool users. Indeed increasing tool use might well have *hampered* gesture and instead favoured a vocal/auditory channel of communication, as also would have the need to communicate at a distance, in the dark or among vegetation (Hewes, 1973, 1977), though problems associated with vocal rather than gestural communication include, e.g., interference with breathing and swallowing, and arousal of predators and prey. Moreover, the fact that chimpanzees can be taught to sign, but not to speak, with cognitive powers probably similar to those of the early hominids, does not prove the priority of gesture over vocal language, whether or not we can decode "gesturelike" written characters faster than speech. Thus some would argue (e.g., Count, 1974) that human infants learn vocal speech *before* gesture.

A general problem with the tool-use scenario is that it seems to have progressed and developed extremely slowly; it first appeared 2.5 to 2 million years ago, a standard "tool kit" emerging 1.5 million years ago, with no other major advances until 300,000 years ago, despite enormous increases in brain size (Calvin, 1987). Toolmaking would not therefore seem to be a major evolutionary force behind increases in brain size, or other evolving behaviours, e.g., language. Indeed Susman (1988) reports that small-brained *A. robustus* (a descendent of earlier australopithecines) at 1.8 million years ago possessed a hand adapted for precision grasping and may have used tools (though tools associated with the remains could instead have come from *H. erectus*). While he concludes that tool acquisition might not therefore account for the emergence and success of early *Homo*, and the absence of tool behavior would not have been responsible for the (competitive) demise of *A. robustus*, it should be noted that the tool kit of the putative competitor, *H. erectus*, was considerably more advanced than any others present or before.

It is possible that several factors (e.g. food carrying, family bonding and an altricial juvenile phase) co-evolved in a mutually synergistic or facilitatory way, rather than occurring, as traditionally conceived, in a linear sequence. While it is certainly easy to invoke complex interactions between a number of factors, medical pathology often requires the interactive co-occurrence of several (not always the same) factors from among a larger subset. Multifactorial interactions are also evident in ecological equilibria. Language (and specialized modes of cognition, thought and conscious awareness, cf. Jaynes 1977) may be seen as developing as an inevitable concomitant of increasing cortical development. The latter was perhaps demanded by survival needs in the new ecological niche created by climatic deterioration. This would have required a change in habits of acquiring and sharing food, e.g., socially cooperative foraging, hunting and butchering (see e.g. Isaac, 1983; Parker & Gibson, 1979). In addition to the other advantages conveyed by bipedalism (thermoregulation, improved vision, hands free for carrying and using tools and weapons) and in addition to its possible arboreal origins thereby favoring gripping, releasing, pulling, poking, picking, waving, hitting, throwing etc. (Richards, 1987), it would have been an essential adaptation for cooperative foraging. While a substantial increase in brain size (which cannot simply be explained as an allometric effect of a concomitant but much smaller increase in body weight) and the use of tools both undoubtedly long postdated bipedalism, nevertheless with an increase in the size of fetal heads, mothers had as it were to compromise between a walking pelvis and one which could accommodate the fetus at birth. A solution (and see Lovejoy, 1981) was perhaps a prolonged postnatal development, with a shift to learning, socialization, parenting, family bonding, a home base controlled by the mother, and foraging activity. The latter could have been accomplished by the father, perhaps more as a scavenger than as a hunter, and of meat rather than of vegetable products, to transport and furnish sufficient protein for a family of three, and to provide the structural fats required for the development of a large brain (Crawford & Sinclair, 1971, cited in Ebling, 1985). While early hominid teeth seem in terms of morphology and wear patterns to be characteristic more of plant than of meat eaters (Lewin, 1987), and modern hunter-gatherers may rely more upon the vegetable products of female foraging than the animal products of male hunting, the opportunistic carnivory of the predominantly vegetarian chimpanzee might provide an appropriate model. The multifactorial-interactive account (Holloway, 1981; Wind, 1983; see also Commentary to Parker & Gibson, 1979, especially Gould, Gruber, Isaac, Jolly and Lamendella), therefore invokes an enlarging neocortex, bipedalism, a characteristic dentition (reduced anterior, with molar dominance), an increasingly material culture, and unique social (Byrne & Whiten, 1988), sexual and reproductive behavior (Lovejoy, 1981), rather than the evolution of intelligence simply to solve ecological problems or to manufacture and use tools. Thus intense social pressure (the need to deal adequately with fellow group members, to obtain and provide social favors, to participate in alliances, to deceive and to dominate) and the needs of parenting (which are still evident today) would provide the evolutionary driving force for an enlarging brain and, ultimately, tool use, a material culture, and advanced communicatory skills. With the development of language, genetically programmed behavior could now be subordinated to learnt cultural programs. The recurring suggestions of a division of labor between the sexes (spatially-oriented hunting and foraging by the male parent, the development of the offsprings' social and communicatory skills by the female) are reminiscent of two claims; on the one side that males may be slightly superior to females with respect to spatial abilities and correspondingly inferior verbally (Halpern, 1986; McGlone, 1986), and on the other that in females there is a more focal and anterior representation of speech and manual praxis (Kimura & Harshman, 1984). Kimura (1983) speculates that this situation might improve the precision and speed of fine motor skills and speech control, important aspects for a home-based parent, while the father would have benefited from a more diffusely represented posterior (i.e. *perceptual*) mediation of spatial skills for foraging and hunting, where fine manual dexterity and fluent speech is less important.

Despite the comparatively primitive nature of the tools of *H. habilis*, and the fact that upright walking and tool use might have been possessed by contemporaneous australopithecines (see above), new studies of brain endocasts of Olduvai specimens of *H. habilis* (Tobias, 1987) indicate that that species was closer to *H. erectus* than to the australopithecines. Thus *H. habilis* possessed a disproportionate expansion of frontal and parieto-occipital regions, especially in the two areas governing speech in modern humans, so much so that Tobias concludes that it possessed the structural markers of the neurological basis of spoken language.

Jerison (1982) also believes that language evolved in response to an environmental demand for additional cognitive capacity, rather than specifically for new and better communicatory skills. As he observes, had its evolution been driven solely by the need to communicate the sorts of things that *other* predator and prey species are vitally interested in, the resultant system would probably have been far simpler, less flexible, less ambiguous, and less demanding of processing capacity. However, his conclusion (shared with Chomsky, 1980, see below), that human language could not at the same time have evolved from earlier primate call systems, may be less secure.

IS LANGUAGE "SPECIAL" OR CONTINUOUS WITH PRIMATE VOCALIZATIONS?

According to Chomsky's nativist account, our language ability derives from an innate language-specific neural mechanism, with no prior evolutionary history, no prior preadapting counterparts in earlier species, and no biological precedent. (Compared to this "creationist" viewpoint, more extreme even than one which could be accommodated in terms of a punctate evolutionary process, the corollary idea, that there is a common deep structure to all languages and grammars which is independent of meaning, is less controversial.) However, there is abundant evidence for the evolutionary utilization and adaptation of pre-existing structures for new functions; the swim bladders of lung fish became lungs, the airway between lungs and mouth was adapted for phonation, and many other peripheral and central structures have been adapted in our species for speech, the most complex motor activity of which mammals are capable. Thus Lieberman (1985) agrees with Chomsky only to the extent that the sounds of speech are special, permitting data transmission 10 times faster than what is attainable by any other signals in the auditory domain. Like other complex yet automatic human and primate motor skills, it involves rapid goal-directed responses *towards* target loci, in the absence of innate control mechanisms to cope with every possible starting point. It involves reflex-like motor control mechanisms which can compensate (within 40 msec) for any unexpected imposed environmental perturbation. Nevertheless nonhuman primates seem to have neither the oral nor the neural capabilities of producing the full range of human speech sounds that are acoustically distinct and resistant to articulatory perturbation. The descent during evolution of the supralaryngeal tract, perhaps partly as a consequence of the adoption of an upright posture, and an adaptation permitting the development of a wide range of articulatory gestures, has however been at the expense of efficient respiration, swallowing and chewing. In addition, the tongue has been recessed, and the jaw shortened with a reduction in the number of teeth, adaptations which facilitate speech at the expense of eating. Other species (including the human neonate, thereby disproving claims of human neoteny) can breathe while drinking; they do not choke since the epiglottis can connect the larynx directly to the nasal cavity, sealing it off while swallowing. (Wind, personal communication, 1989, March 8, nevertheless observes that with a population of 5 billion our throats must nevertheless function reasonably efficiently.) Lieberman believes that neanderthals lacked the supralaryngeal tract characteristic of modern adult *H. sapiens sapiens*, based on his soft-tissue reconstruction from fossil skull-base anatomy; the neanderthals would therefore have lacked the requisite articulatory control mechanisms, and would have been capable of greatly reduced communicative abilities. However, Wind (1978) queries the accuracy of the vocal tract reconstructions, and observes that even if they are accurate they may not be relevant for assessing ancestral speech capacities, given the enormous redundancy of the human tract (as evident from pathology, e.g. intelligible speech being possible even with partial laryngectomy). Indeed other species (e.g. parrots) can give very passable imitations of human speech. Thus if a modern human possessed Lieberman's reconstruction of a neanderthal vocal tract, his speech might be only slightly depauperate. In fact the discovery (Arensburg et al., 1989) of a well-preserved neanderthal hyoid bone, dating from about 60,000 years ago, which is almost identical to those of present day populations, suggests that there has been little or no change to laryngeal structures, and that neanderthals possessed the morphological basis for modern speech capability.

What can we say about the possible evolution of the *neural* mechanisms to drive our articulatory, phonological and syntactic capacities? Lieberman again rejects the Chomskian viewpoint, in favor of an evolutionary continuum from neural mechanisms which facilitated complex, skilled automatized motor behavior in earlier species during the previous 0.25 million years. He believes that speech evolved in two stages: what is now Broca's motor speech area initially came to control *noncommunicative* aspects of the orofacial musculature, and later was modified for the automatization of the complex articulatory manoeuvres necessary to produce rapid encoded speech and rule-governed phonology and syntax. He appeals to preadaptation acting upon the neural substrate governing complex orofacial movements in these earlier primates, and argues that our species-specific speech areas in the brain, required both to produce an acoustically complex signal and to unscramble what is heard, evolved in synchrony with the human supralaryngeal tract. Of course it could be argued (cf. Count, 1974, and Wind, 1978) that our information processing capacity evolved *before* a modern vocal-tract morphology, as our symbol decoding capacity, as in reading, is far faster than the speeds achievable with articulatory speech.

Could the evolution of human speech therefore have been built upon and been continuous with earlier primate vocalizations and vocal-auditory signalling? Traditionally (see e.g., Malmi, 1976) monkey calls convey information only on the signaller's location and motivational state, being involuntary, nonpropositional, nonreferential, nonsymbolic, and controlled by subcortical centres of limbic affect. Thus Dingwall (1988) reviews evidence that the control of nonhuman primate *vocalization* (as distinct from *reception*) terminates at the supplementary motor area, which in humans is thought to mediate the planning of complex volitional motor sequences. While ablation in monkeys of homologs of human language areas has little appreciable effect upon vocalization, the same may not of course be true with respect to reception. Our speech, on the other hand, consists of voluntary propositional communication, which involves cortical mediation and learning. However monkey vocalization both in the wild and in the laboratory has recently been found to be far richer and more flexible than previously thought (see e.g. Steklis, 1985), conveying information on sex, personal identity, group membership, social relationships and at least three different kinds of predator; thus a particular alarm call will evoke the appropriate kind of looking behaviour in listeners. Indeed, while our *own* speech *also* depends heavily upon subcortical (thalamic, basal ganglia) mechanisms (Crosson, 1985), as we saw earlier (Heffner & Heffner, 1984) monkeys may employ cortical areas in the LH homologous to our own speech centers, at least at the level of reception. This all suggests a direct continuum from the common ancestor of monkey and humans (maybe even down to the level of the rodents, see Ehret, 1987, above) for a LH mediation of auditory communication.

Falk (1980, 1987) also believes that our vocal language has a long evolutionary history, continuous with an early primate call system in an arboreal habitat; that *some* form of language was selected for *before* bipedalism, tool use and gesture; and that developed tool use presupposes language. (Jaynes, 1977, disagrees; as he observes, even our *modern* language can no more describe how to make or use a tool than it can instruct one how to learn to ride a bicycle). While language may not have been useful in instruction in this respect, it could be argued (again cf. Jaynes, 1977) that language potentiated the cognitive strategies for successful tool manufacture and use. Again, it may be objected that, until perhaps 50,000 years ago, tool deployment was at a comparatively simple level. Holloway (1976) believes that the australopithecine brain was large enough to accommodate some form of language; certainly modern microcephalics with a brain ($300cm^3$) in the chimpanzee range, though severely retarded, possess some speech and reasonable sensorimotor abilities (Jensen-Jazbutis, 1970, cited in Jerison, 1982). Why then do chimpanzees not learn to speak? They can of course be taught to communicate after a fashion, but dogs can be taught to walk on their hind legs for short distances without showing any natural innate predisposition to be bipedal. On the other hand Man may acquire some degree of language even against enormous odds (e.g. deafness or partial isolation). Some form of communication *can* be taught to the great apes. However debate continues (Premack, 1986) about the true status of chimpanzee and gorilla nonverbal language capacities (e.g. is it true language, can and do chimpanzees prevaricate, can they invent new strings in new and appropriate syntactic order, is it just a "clever Hans" phenomenon, is it smart problem-solving but nonlinguistic behaviour, how should we *define* language . . . ?). While we should perhaps reject the Chomskian view of the absolute uniqueness of language to *H. sapiens*, nevertheless certain conclusions (see Lenneberg, 1967) should be born in mind: we do have anatomical specializations (neurally, and peripherally) for language, even though they may be directly evolved from nonhuman primate structures; critical periods for language acquisition in the developing child are universal in all races everywhere; language cannot easily be suppressed by isolation, even though it cannot be acquired if the individual is isolated beyond certain critical periods (Fromkin, Krashen, Curtiss, Rigler, & Rigler, 1974); it can only be taught, in highly modified form, with great difficulty or not at all to other species; linguistic universals appear to exist; certain language dysfunctions are heritable; all cultures possess language; the laboured artificial process of learning a second language in adulthood is quite different from the ready natural acquisition of the first language; even neonates exhibit language lateralization, and move in synchrony to the rhythms of speech (see e.g. Leahey & Harris, 1985, Ch. 11). While therefore language may not be totally unique to our species, and may have evolved from earlier forms of communication, in its present form it is very substantially different to anything which might have preceded it.

The viewpoint most directly opposed to the one that language has a long evolutionary history argues that around 50,000 years ago an innovation occurred in how we communicate (Davidson & Noble, 1989; Jaynes, 1977; McHenry, 1982). At that time artifacts and art dramatically increased in complexity. Jaynes believes that this reflects the sudden appearance of language. This eventually permitted humans to achieve (self)consciousness, the latter (and language in its "modern" guise) not emerging until literally the last few thousand years, according to Jaynes, in the vicinity of the Mediterranean and the Near East. (Such a late date ignores the much longer independence and isolation of e.g. the Australian aborigines.) In any case as Jerison (1982) observes, and comparative psychologists are increasingly assuming (see e.g. Griffin, 1984), some form of consciousness is probably not restricted even to the primates; the same of course is true of tool use (Beck, 1980), where one detached object separate from the user's anatomy is used to change the state of another. This is not to deny that a great change occurred in the archaeological record after 50,000 years ago, and even glottochronological studies based on the rates of "modern" language change converge upon a figure of around 40,000 years for a putative ancestor of most extant tongues (Miller, 1981; Ruhlen, 1987). However this change could simply reflect the reaching of a "critical state" in technology, society and communication, a flowering of potentialities and precursors with a long evolutionary history, rather than a wholly new innovation. It is interesting to note that in a detailed analysis of modern gene distributions to reconstruct the phylogeny of extant human populations, Cavalli-Sforza, Piazza, Menozzi and Mountain (1988) recognize six main population clusters, the oldest split being between African and the remaining clusters, which then progressively fractionated further. For each of Ruhlen's (1987) 17 language phyla, aboriginal speakers of all the languages in that phylum belonged to the same genetic cluster proposed by Cavalli-Sforza et al. (1988). Thus at long last there arises the possibility of bringing together genetic, archaeological and linguistic data, as Cavalli-Sforza et al., observe in the very title of their article.

CONCLUSIONS

There may be a continuity with earlier species of our two most obvious asymmetries, language lateralization, and movement control and sequencing by either hand. Indeed there may be an ancestral LH specialization for sensory and motor discrimination learning. Perhaps by default (Corballis & Morgan, 1978) more primitive spatial and emotional functions were relegated to the RH, though we cannot exclude the possibility that the latter hemispheric specializations instead were in fact the prior ones. However in all species, asymmetries tend to be quantitative rather than all-or-nothing, and subject to effects from sex and development. The (disputed) left-hand preference in primates for visually guided reaching may reflect the contribution from the RH of (visuo)spatial control, rather than simply being a consequence of the right hand pre-empting a postural role. Inhibitory control processes involving higher learning in the LH might have subsumed the development of communicatory processes, together with practised manual responses; hence the close cortical proximity of our centers for speech and manipulation. Our two basic LH functions, communication and manipulation, are however only loosely linked to each other, each being independently associated with that hemisphere's original specialization for higher sensory and motor discrimination learning; hence dextrality, and LH mediation of communication and manipulation, often dissociate. Finally, if modern language first appeared around 50,000 years ago, it was probably not a sudden evolutionary innovation so much as the attainment then of some kind of "critical mass" in the make-up of society.

ACKNOWLEDGEMENT

The helpful comments of Lesley Rogers are gratefully acknowledged.

REFERENCES

Adret, P., & Rogers, L.J. (1989). Sex differences in the visual projections of young chicks: A quantitative study of the thalamofugal pathway. *Brain Research, 478*, 59-73.

Andrew, R. J. (1983). Lateralization of emotional and cognitive function in higher vertebrates, with special reference to the domestic chick. In J. R. Ewert & D. Ingle (Eds.), *Advances in vertebrate neuroethology* (pp. 477-510) New York: Plenum.

Andrew, R.J. (1988). The development of visual lateralization in the domestic chick. *Behavioral Brain Research, 29*, 201-209.

Andrew, R. J., & Brennan, A. (1985). Sharply timed and lateralized events at time of establishment of long term memory. *Physiology and Behavior, 34*, 547-556.

Andrew, R. J., Mench, J., & Rainey, C. (1982). Right-left asymmetry of response to visual stimuli in the domestic chick. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 197-209) Cambridge, MA: MIT Press.

Andrews, P. (1986). Fossil evidence on human origins and dispersal. *Cold Spring Harbor Symposia on Quantitative Biology, 51*, 419-428.

Arensburg, B., Tillier, A.M., Vandermeersch, B., Dudey, H., Schepartz, L.A. & Rak, Y. (1989). A Middle Paleolithic human hyoid bone. *Nature, 338*, 758-760.

Babcock, L.E. & Robinson, R.A. (1989). Preferences of Paleozoic predators. *Nature, 337*, 695-696.

Bahn, P.G. (1989). Early teething troubles. *Nature, 337*, 693.

Beck, B. B. (1980). *Animal tool behavior*. New York: Gordon.

Benbow, C. B. (1988). Sex differences in mathematical reasoning ability in intellectually talented pre-adolescents: Their nature, effects and possible causes. *The Behavioral and Brain Sciences, 11*, 169-232.

Bianki, V. L. (1983). Hemisphere lateralisation of inductive and deductive processes. *International Journal of Neuroscience, 20*, 59-74.

Borod, J. C. & Koff, E. (1984). Asymmetries in affective facial expression: Behavior and anatomy. In N. A. Fox & R. J. Davidson (Eds.) *The psychobiology of affective development*. (pp. 293-323). Hillsdale, NJ: Erlbaum.

Bracha, H. S., Seitz, D. J., Otemaa, J., & Glick, S. D. (1987). Rotational movement (circling) in normal humans: Sex difference and relationship to hand, foot and eye preference. *Brain Research, 411*, 231-235.

Bradley, P., Horn, G., & Bateson, P. (1981). Imprinting: An electron microscopic study of chick hyperstriatum ventrale. *Experimental Brain Research, 41*, 115-120.

Bradshaw, J. L., & Bradshaw, J. A. (1988). Rotational and turning tendencies in humans: An analog of lateral biases in rats? *International Journal of Neuroscience, 39*, 229-232.

Bradshaw, J. L., & Nettleton, N. C. (1981). The nature of hemispheric specialization in man. *Behavioral and Brain Sciences, 4*, 51-63.

Bradshaw, J. L. & Nettleton, N. C. (1983). *Human cerebral asymmetry*. Englewood Cliffs, NJ: Prentice-Hall.

Brain, C. K., & Sillen, A. (1988). Evidence from the Swartkrans cave for the earliest use of fire. *Nature, 336*, 464-466.

Braitenberg, V., & Kemali, M. (1970). Exceptions to bilateral symmetry in the epithalamus of lower vertebrates. *Journal of Comparative Neurology, 38*, 137-146.

Bromage, T. G., & Boyd, A. (1984). Microscopic criteria for the determination of directionality of cutmarks on bone. *American Journal of Physical Anthropology, 65*, 359-366.

Bryden, M. P., & Steenhuis, R. F. (1987). Handedness is a matter of degree. *Behavioral and Brain Sciences, 10*, 266-267.

Byne, W., Bleier, R., & Houston, L. (1988). Variations in human corpus callosum do not predict gender: A study using MRI. *Behavioral Neuroscience, 102*, 222-227.

Byrne, R., & Whiten, A. (eds.) (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford: Clarendon Press.

Calvin, W. H. (1983). *The throwing madonna: From nervous cells to hominid brains*. New York: McGraw-Hill.

Calvin, W. H. (1987). On evolutionary expectations of symmetry in tool making. *Behavioral and Brain Sciences, 10*, 267-268.

Camp, D. M., Therrien, B. A., & Robinson, T. E. (1981). Spatial learing ability is related to an endogenous asymmetry in the nigrostriatal dopamine system in rats. *Society for Neuroscience Abstracts, 7*, 455.

Castellano, M. A., Diaz-Palarea, M. D., Rodriguez, M., & Barroso, A.J. (1987). Lateralization in male rats and dopaminergic system: Evidence of right-side population bias. *Physiology and Behavior, 40*, 607-612.

Cavalli-Sforza, L.L., Piazza, A., Menozzi, P., & Mountain, J. (1988). Reconstruction of human evolution: Bringing together genetic, archaeological and linguistic data. *Proceedings of the National Academy of Sciences, 85*, 6002-6006.

Chomsky, N. (1980). Rules and representations. *The Behavioral and Brain Sciences, 3*, 1-61.

Chui, H. C., & Damasio, A. R. (1980). Human Cerebral asymmetries evaluated by computed tomography. *Journal of Neurology, Neurosurgery, and Psychiatry, 43*, 873-878.

Cole, J. (1955). Paw preferences in cats related to hand preferences in animals and Man. *Journal of Comparative and Physiological Psychology, 48*, 137-140.

Collins, R. L. (1977). Toward an admissible genetic model for the inheritance of the degree and direction of asymmetry. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 137-150). New York: Academic Press.

Collins, R. L. (1985). On the inheritance of direction and degree of asymmetry. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 41-72). New York: Academic Press.

Corballis, M. C. (1981). Toward and evolutionary perspective on hemispheric specialization. *The Behavioral and Brain Sciences, 4*, 69-70.

Corballis, M. C., & Morgan, M. J. (1978). On the biological basis of human laterality: 1. Evidence for a maturational left-right gradient. *The Behavioral and Brain Sciences, 2*, 261-336.

Corbin, D. O. C., Williams, A. C., & White, A. C. (1987). Tardive dystonia: Which way do schizophrenics twist? *The Lancet*, January 31, 268-269.

Count, E. W. (1974). On the phylogenesis of the speech function. *Current Anthropology, 15*, 81-88.

Crosson, B. (1985). Subcortical functions in language: A working model. *Brain and Language, 25*, 257-292.

Davidson, I., & Noble, W. (1989). The archaeology of perception: Traces of depiction and language. *Current Anthropology, 30*, 125-137.

de Castro, J.M., Bromage, T. G., & Jalvo, Y. F. (1988). Buccal striations on fossil human anterior teeth: Evidence of handedness in the middle and early upper Pleistocene. *Journal of Human Evolution, 17*, 403-412.

de la Coste, M.C., Haworth, D.S., & Woodward, D.J. (1988). Prosencephalic asymmetries in *lemuridae. Brain, Behaviour and Evolution, 31*, 296-311.

Denenberg, V.H., Berrebi, A.S., & Fitch, R.H. (In Press). A factor analysis of the rat's corpus callosum. *Brain Research.*

Denenberg, V. H., & Yutzey, D. A. (1985). Hemispheric laterality, behavioral asymmetry, and the effects of early experience in rats. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 110-135). New York: Academic Press.

Dewberry, R. G., Lipsey, J. R., Sood, K., Moran, T. H., & Robinson, R. B. (1986). Lateralized response to cortical injury in the rat: Interhemispheric interaction. *Behavioral Neuroscience, 100*, 556-562.

Dewson, J.H. (1977). Preliminary evidence of hemispheric asymmetry of auditory function in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 63-71). New York: Academic Press.

Diamond, M. C. (1984). Age, sex and environmental influences. In N. Geschwind & A. M. Galaburda (Eds.), *Cerebral dominance: The biological foundations* (pp. 134-146). Cambridge, MA: Harvard University Press.

Diamond, M. C. (1985). Rat forebrain morphology: Right-left; male-female; young-old; enriched-impoverished. In S. D. Glick (Ed.), *Cerebral lateralisation in nonhuman species* (pp. 73-88). New York: Academic Press.

Diamond, M. C., Murphy, G. M., Akiyama, K., & Johnson, R. E. (1982). Morphologic hippocampal asymmetry in male and female rats. *Experimental Neurology, 76*, 553-566.

Dingwall, W. O. (1988). The evolution of human communicative behavior. In F. J. Newmeyer (Ed.), *Linguistics: The Cambridge survey Vol. III: Language, psychological and biological aspects* (pp. 271-313). Cambridge: Cambridge University Press.

Drew, K. L., Lyon, R. A., Titeler, M., & Glick, S. D. (1986). Asymmetry in D-2 binding in female rat striata. *Brain Research, 363*, 192-195.

Ebling, J. (1985). The mythological evolution of nudity. *Journal of Human Evolution, 14*, 33-41.

Ehret, G. (1987). Left hemisphere advantage in the mouse brain for recognizing ultrasonic communication calls. *Nature, 325*, 249-251.

Engbreston, G. A., Reiner, A., & Brecha, N. (1981). Habenular asymmetry and the central connections of the parietal eye of the lizard. *Journal of Comparative Neurology, 198*, 155-165.

Fagot, J., & Vauclair, J. (1988a). Handedness and manual specialization in the baboon. *Neuropsychologia, 26*, 795-804.

Fagot, J., & Vauclair, J. (1988b). Handedness and bimanual coordination in the lowland gorilla. *Brain, Behavior and Evolution, 32*, 89-95.

Falk, D. (1978). Cerebral asymmetry in Old World monkeys. *Acta Anatomica, 101*, 334-339.

Falk, D. (1980). Language, handedness and primitive brains. Did the australopithecines sign? *American Anthropologist, 82*, 72-78.

Falk, D. (1987). Hominid paleoneurology. *Annual Review of Anthropology, 16*, 13-30.

Falk, D., Cheverud, J., Vannier, M. W., & Conroy, G. C. (1986). Advanced computer graphics technology reveals cortical asymmetry in endocasts of rhesus monkeys. *Folia Primatologica, 46*, 98-103.

Falk, D., Pyne, L., Helmkamp, R. C., & DeRousseau, C. J. (1988). Directional asymmetry in the forebrain of *Macaca mulatta*. *American Journal of Physical Anthropology, 77*, 1-6.

Fromkin, V., Krashen, S., Curtiss, S., Rigler, D., & Rigler, M. (1974). The development of language in Genie: A case of language acquisition beyond the "critical period". *Brain and Language, 1*, 81-107.

Frost, G. T. (1980). Tool behavior and the origins of laterality. *Journal of Human Evolution, 9*, 447-459.

Frumkin, L. R., & Grim, P. (1981). Is there pharmacological asymmetry in the human brain? An hypothesis for the differential hemispheric action of barbiturates. *International Journal of Neuroscience, 13*, 187-197.

Geschwind, N., & Galaburda, A. M. (1985). Cerebral lateralization: Biological mechanisms, associations and pathology. *Archives of Neurology, 42*, 428-459.

Glick, S. D., & Shapiro, R. M. (1985). Functional and neurochemical mechanisms of cerebral lateralization in rats. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 158-184). New York: Academic Press.

Goodale, M.A. (In Press). Brain asymmetries in the control of reaching. In M.A. Goodale (ed.), *Vision and action: the control of grasping*. Ablex: Norwood.

Goodman, R. A., & Whitaker, H. A. (1985). Hemispherectomy (1928-1981) with special reference to the linguistic abilities and disabilities of the residual right hemisphere. In C. T. Best (Ed.), *Hemispheric function and collaboration in the child* (pp. 121-155). New York: Academic Press.

Griffin, D. R. (1984). *Animal thinking*. Cambridge, MA.: Harvard University Press.

Güntürkün, O., & Kesch, S. (1987). Visual lateralization during feeding in pigeons. *Behavioral Neuroscience, 10*, 453-455.

Güntürkün, O., Kesch, S., & Delius, J.D. (1988). Absence of footedness in domestic pigeons. *Animal Behavior, 36*, 602-623.

Gur, R. C., Packer, I. K., Hungerbuhler, J. P., Reivich, M., Obrist, W. D., Amarnek, W. S., & Sackeim, H. A. (1980). Differences in the distribution of gray and white matter in human cerebral hemispheres. *Science, 207*, 1226-1228.

Gurusinghe, C. J., & Ehrlich, D. (1985). Sex dependent structural asymmetry of the medial habenular nucleus of the chicken brain. *Cell Tissue Research, 240*, 149-152.

Halpern, D. F. (1986). *Sex differences in cognitive abilities.* Hillside, NJ: Erlbaum.

Hamilton, C. R. (1983). Lateralization for orientation in split brain monkeys. *Behavioral Brain Research, 10*, 399-403.

Hamilton, C. R., & Vermeire, B. A. (1983). Discrimination of monkey faces by split brain monkeys. *Behavioral Brain Research, 9*, 263-275.

Hamilton, C. R., & Vermeire, B. A. (1985). Complementary hemispheric specialization in monkeys. *Society for Neuroscience Abstracts, 11*, 869.

Hamilton, C.R., & Vermeire, B.A. (1988). Complementary hemispheric specialization in monkeys. *Science, 242*, 1691-1694.

Hardy, A. (1960). Was Man more aquatic in the past? *New Scientist, 7*, 642-645.

Harré, R., & Reynolds, V. (Eds.), (1984). *The meaning of primate signals*, Cambridge: Cambridge University Press.

Heffner, H. E., & Heffner, R. S. (1984). Temporal lobe lesions and perception of species-specific vocalizations by macaques. *Science, 226*, 75-76.

Heilbronner, P.L., & Holloway, R.L. (1988). Anatomical brain asymmetries in New and Old World monkeys: Stages of temporal lobe development in primate evolution. *American Journal of Physical Anthropology, 76*, 39-48.

Heine, O., & Galaburda, A. M. (1986). Olfactory asymmetry in the rat brain. *Experimental Neurology, 91*, 392-398.

Hewes, G.W. (1973). Primate communication and the gestural origin of language. *Current Anthropology, 14*, 5-24.

Hewes, G. W. (1976). The current status of the gestural theory of language origin. *Annals of the New York Academy of Sciences, 280*, 482-504.

Hewes, G.W. (1977). Language origin theories. In D. M. Rumbaugh (ed.), *Language learning by a chimpanzee: The Lana Project* (pp. 3-53). New York: Academic Press.

Holloway, R. L. (1976). Paleoneurological evidence for language origins. *Annals of the New York Academy of Sciences, 280*, 330-348.

Holloway, R. L. (1981). Culture, symbols and human brain evolution: A synthesis. *Dialectical Anthropology, 5*, 287-303.

Holloway, R. L., & de la Coste-Lareymondie, M. C. (1982). Brain endocast asymmetry in pongids and hominids: Some preliminary findings on the paleontology of cerebral dominance. *American Journal of Physical Anthropology, 58*, 101-110.

Horn, G., & Johnson, M.H. (1989). Memory systems in the chick: Dissociations and neuronal analysis. *Neuropsychologia, 27*, 1-27.

Horster, W., & Ettlinger, G. (1985). An association between hand preference and tactile discrimination performance in the Rhesus monkey. *Neuropsychologia, 23*, 411-413.

Ifune, C.K., Vermeire, B. A., & Hamilton, C. R. (1984). Hemispheric differences in split brain monkeys viewing and responding to videotape recordings. *Behavioral and Neural Biology, 41*, 231-235.

Isaac, G. L. (1983). Aspects of human evolution. In D. S. Bendall (Ed.), *Evolution from molecules to men* (pp. 509-545). Cambridge: Cambridge University Press.

Jarman, P.J. (1972). The development of a dermal shield in impala. *Journal of Zoology (London), 166*, 349-356.

Jason, G. W., Cowey, A., & Weiskrantz, L. (1984). Hemispheric asymmetry for a visuospatial task in monkeys. *Neuropsychologia, 22*, 777-784.

Jaynes, J. (1977). *The origin of consciousness in the breakdown of the bicameral mind.* Boston: Houghton Mifflin.

Jeffries, R. P. S., & Lewis, D. N. (1978). The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. *Philosophical Transactions of the Royal Society of London B, 282*, 205-323.

Jerison, H.J. (1982). The evolution of biological intelligence. In R. Sternberg (Ed.), *Handbook of intelligence* (pp. 723-791). Cambridge: Cambridge University Press.

Jungers, W. (1988). Relative joint size and hominid locomotor adaptations. *Journal of Human Evolution, 17*, 247-270.

Kilshaw, D., & Annett, M. (1983). Right and left-hand skill 1: Effects of age, sex and hand preference showing superior skill in left-handers. *British Journal of Psychology, 74*, 253-268.

Kimura, D. (1983). Sex differences in cerebral organization for speech and praxic functions. *Canadian Journal of Psychology, 37*, 19-35.

Kimura, D. & Harshman, R. A. (1984). Sex differences in brain organization for verbal and nonverbal functions. *Progress in Brain Research, 61*, 423-444.

Kolb, B., Sutherland, R. J., Nonneman, A. J., & Whishaw, I. Q. (1982). Asymmetry in the cerebral hemispheres of the rat, mouse, rabbit and cat: The right hemisphere is larger. *Experimental Neurology, 78*, 348-359.

Kuhl, P. (1988). On handedness in primate and human infants. *Behavioral and Brain Sciences, 11*, 727-729.

LaHoste, G.J., Neveu, P.J., Morméde, P., & Le Moal, M. (1989). Hemispheric asymmetry in the effects of cerebral cortical ablations on mitogen-induced lymphoproliferation and plasma prolactin levels in female rats. *Brain Research, 483*, 123-129.

Latimer, B., & Lovejoy, C.O. (1989). The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *American Journal of Physical Anthropology, 78*, 369-386.

Leahey, T. H., & Harris, R. J. (1985). *Human learning*. Englewood Cliffs, N. J.: Prentice Hall.

Leakey, M. D., & Hay, R. C. (1979). Pliocene footprints in the Laetolil beds at Laetoli, Northern Tanzania. *Nature, 278*, 317-323.

LeMay, M. (1976). Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primate. *Annals of the New York Academy of Sciences, 280*, 349-366.

LeMay, M. (1985). Asymmetries of the brains and skulls of nonhuman primates. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 234-246). New York: Academic Press.

LeMay, M., & Geschwind, N. (1975). Hemispheric differences in the brain of Great Apes. *Brain, Behavior and Evolution, 11*, 48-52.

Lenneberg, E. H. (1967). *Biological foundations of language*. New York: Wiley.

Lewin, R. (1987). Four legs bad, two legs good. *Science, 235*, 969-971.

Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review, 74*, 431-461.

Lieberman, P. (1985). On the evolution of human syntactic ability. Its pre-adaptive bases—Motor control and speech. *Journal of Human Evolution, 14*, 657-668.

Lovejoy, C. O. (1981). The origin of Man. *Science, 211*, 341-350.

Lovejoy, C.O. (1988). Evolution of human walking. *Scientific American*, November, 82-89.

Lowenstein, J., & Zihlman, A. (1988). The invisible ape. *New Scientist*, December 3 (1641), 56-59.

McCasland, J.S. (1987). Neuronal control of bird song production. *The Journal of Neuroscience, 7*, 23-39.

McGlone, J. (1980). Sex differences in human brain asymmetry: A critical survey. *The Behavioral and Brain Sciences, 3*, 215-263.

McGlone, J. (1986). The neuropsychology of sex differences in human brain organization. In G. Goldstein & R. E. Tarter (Eds.), *Advances in Clinical Neuropsychology, Vol 3* (pp. 1-30). New York: Plenum Press.

McHenry, H. M. (1982). The pattern of human evolution: Studies on bipedalism, mastication and encephalization. *Annual Review of Anthropology, 11*, 151-173.

McManus, I. C. (1976). Scrotal asymmetry in Man and ancient sculpture. *Nature, 259*, 426.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences, 10*, 247-303.

MacNeilage, P.F., Studdert-Kennedy, M.G., & Lindblom, B. (1988). Primate handedness: A foot in the door. *Behavioral and Brain Sciences, 11*, 737-744.

Malmi, W. A. (1976). Chimpanzees and language evolution. *Annals of the New York Academy of Sciences, 280*, 598-602.

Michel, G. F. (1981). Right handedness: A consequence of infant supine head-orientation preference. *Science, 212*, 685-687.

Michel, G. F. and Harkins, D. A. (1985). Concordance of handedness between teacher and student facilitates learning manual skills. *Journal of Human Evolution, 4*, 597-601.

Michel G. F. and Harkins, D. A. (1987). Ontogenetic considerations in the phylogenetic history and adaptive significance of the bias in human handedness. *Behavioral and Brain Sciences, 10*, 283-284.

Miller, G. (1981). *Language and speech*. San Francisco: Freeman.

Morgan, E. (1984). The aquatic hypothesis. *New Scientist*, April 12, 11-13.

Morgan, E. (1986). Lucy's child. *New Scientist*, December 25, 13-16.

Morris, R.D., & Hopkins, W.D. (1989). Perception of human chimeric faces by chimpanzees: Evidence for a right hemisphere asymmetry. Manuscript submitted for publication.

Morse, P. A., Molfese, D., Laughlin, N. K., Linnville, S., Wetzel, F. (1987). Categorical perception for voicing contrasts in normal and lead-treated rhesus monkeys: Electrophysiological indices. *Brain and Language, 30*, 63-80.

Nottebohm, F. (1979). Origins and mechanisms in the establishment of cerebral dominance. In M. S. Gazzaniga (Ed.), *Handbook of behavioral neurobiology, Vol 2, Neuropsychology* (pp. 295-344). New York: Plenum.

Oakley, K. P. (1981) Emergence of higher thought 3.0–0.2 Ma B.P. *Philosophical Transactions of the Royal Society of London B, 292*, 205-211.

Ojemann, G. A. (1983). Brain organization for language from the perspective of electrical stimulation mapping. *The Behavioral and Brain Sciences*, 6, 189-230.

Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences, 2*, 367-381.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A., Potter, D.D., Broennimann, R., & Harries, M. (1988). Specialized face processing and hemispheric asymmetry in man and monkeys. Evidence from single unit and reaction time. *Behavioral Brain Research, 29*, 245-250.

Peters, M. (1988). Footedness: Asymmetries in foot performance and skill, and neuropsychological assessment of foot movement. *Psychological Bulletin, 103*, 179-192.

Petersen, M. R., Beecher, M. D., Zoloth, S. R., Green, S., Marler, P. R., Moody, D. B., & Stebbins, W. C. (1984). Neural lateralization of vocalization by Japanese macaques: Communicative significance is more important than acoustic structure. *Behavioral Neuroscience, 98*, 779-790.

Peterson, M. R., Beecher, M. D., Zoloth, S. R., Moody, D. B., & Stebbins, W. C. (1978). Neural lateralization of species-specific vocalization by Japanese macaques (*Macaca fuscata*). *Science, 202*, 324-327.

Pohl, P. (1983). Central auditory processing V: Ear advantages for acoustic stimuli in baboons. *Brain and Language, 20*, 44-53.

Pohl, P. (1984). Ear advantages for temporal resolution in baboons. *Brain and Cognition, 3*, 438-444.

Preilowski, B., Reger, M., & Engele, H. C. (1986). Handedness and cerebral asymmetry in nonhuman primates. In D. M. Taub & F. A. King (Eds.), *Current Perspectives in primate biology* (pp. 270-282). New York: Van Nostrand and Reinhold.

Premack, D. (1986). *Gavagai or the future history of the animal language controversy*. Cambridge, MA: M.I.T. Press.

Reynolds, G. P., Czudek, C., Bzowej, N., & Seeman, P. (1987). Dopamine receptor asymmetry in schizophrenia. *The Lancet*, April 25, 972.

Richards, G. (1987). *Human Evolution: An introduction for the behavioural sciences*. London: Routledge Kegan Paul.

Rogers, L. J. (1980). Lateralisation in the avian brain. *Bird Behaviour, 2*, 1-12.

Rogers, L. J. (1982). Light experience and asymmetry of brain function in chickens. *Nature, 297*, 223-225.

Rosen, G.D., Sherman, G.F., Mehler, C., Emsbo, K., & Galaburda, A.M. (1989). The effect of developmental neuropathology on neocortical asymmetry in New Zealand black mice. *International Journal of Neuroscience, 45*, 247-254.

Ruhlen, M. (1987). *A guide to the world's languages*. Stanford: Stanford University Press.

Sanford, C., Guin, K., & Ward, J. P. (1984). Posture and laterality in the bushbaby (*Galago senegalensis*). *Brain, Behavior and Evolution, 25*, 217-224.

Sherman, G. F., Galaburda, A. M., & Geschwind, N. (1982). Neuroanatomical asymmetries in nonhuman species. *Trends in the Neurosciences, 12*, 429-431.

Steklis, H. (1985). Primate communication, comparative neurology, and the origin of language re-examined. *Journal of Human Evolution, 14*, 157-173.

Stewart, M. G., Rose, S. P. R., King, T. S., Gabbott, P. L. A., & Bourne, R. (1984). Hemispheric asymmetry of synapses in chick medial hyperstriatum ventrale following passive avoidance training: A stereological investigation. *Developmental Brain Research, 12*, 261-269.

Stringer, C. B., & Andrews, P. (1988). Genetic and fossil evidence for the origin of modern humans. *Science, 239*, 1263-1268.

Susman, R.L. (1988). Hand of *Paranthropus robustus*: Fossil evidence for tool behavior. *Science, 240*, 781-784.

Susman, R.L., & Brain, T.M. (1988). New first metatarsal (SKX5017) from Swartkrans and the gait of *Paranthropus robustus. American Journal of Physical Anthropology, 77*, 7-15.

Susman, R. L., & Stern, J. T. (1982). Functional morphology of *Homo habilis. Science, 217*, 931-934.

Tan, U. (1987). Paw preference in dogs. *International Journal of Neuroscience, 32*, 825-829.

Tan, U., & Caliskan, S. (1987a). Asymmetries in the cerebral dimensions and fissures of the dog. *International Journal of Neuroscience, 32*, 943-952.

Tan, U., & Caliskan, S. (1987b). Allometry and asymmetry in the dog brain: Right hemisphere is heavier regardless of paw preference. *International Journal of Neuroscience, 35*, 189-194.

Tobias, P.V. (1987). The brain of *Homo habilis*: A new level of organization in cerebral evolution. *Journal of Human Evolution, 16*, 741-761.

Toth, N. (1985). Archaeological evidence for preferential right handedness in the lower and middle Pleistocene and its possible implications. *Journal of Human Evolution, 14*, 607-614.

Turkewitz, G. (1977). The development of lateral differences in the human infant. In S. Harnad, R.W. Doty, L. Goldstein, J. Jaynes, & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 251-259). New York: Academic Press.

Valladas, H., Reyss, J. L., Joron, J. L., Valladas, G., Bar-Yosef, O., & Vandermeersch, B. (1988). Thermoluminescence dating of Mousterian "Proto-Cro-Magnon" remains from Israel and the origin of modern man. *Nature, 331*, 614-616.

Vallortigara, G., Zanforlin, M., & Caillotto, M. (1988). Right-left asymmetry in position learning in male chicks. *Behavioral Brain Research, 27*, 189-191.

Vauclair, J., & Fagot, J. (1987). Spontaneous hand usage and handedness in a troop of baboons. *Cortex, 23*, 265-274.

Wada, J. A., Clarke, R., & Hamm, A. (1975). Cerebral hemispheric asymmetry in humans. *Archives of Neurology, 32*, 239-246.

Walker, S. (1987). Or in the hand or in the heart? Alternative routes to lateralization. *Behavioral and Brain Sciences, 10*, 288.

Ward, J.P. (1988). Left hand reaching preferences in prosimians. *Behavioral and Brain Sciences, 11*, 732-733.

Ward, R., & Collins, R. L. (1985). Brain size and shape in strongly and weakly lateralized rats. *Brain Research, 328*, 243-249.

Wheeler, P. E. (1984). The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution, 13*, 91-98.

Whitaker, H. A., & Ojemann, G. A. (1977). Lateralization of higher cortical functions: A critique. *Annals of the New York Academy of Sciences, 299*, 459-473.

Wind, J. (1978). Fossil evidence for primate vocalizations? In D. J. Chivers & K. A. Joysey, (Eds.), *Recent advances in primatology Vol. 3, Evolution* (pp. 87-91). New York: Academic Press.

Wind, J. (1983). Primate evolution and the emergence of speech. In E. De Grolier (Ed.), *Glossogenetics: The origins and evolution of language* (pp. 15-35). Paris: Harwood Academic Publishers.

Witelson, S.F. & Kigar, D.L. (1988). Anatomical development of the human corpus callosum: A review with reference to sex and cognition. In D.L. Molfese & S.J. Segalowitz (Eds.), *Developmental implications of brain lateralization*. New York: Guilford Press.

Witelson, S. F., & Pallie, W. (1973). Left hemisphere specialization for language in the newborn: Neuroanatomical evidence of asymmetry. *Brain, 96*, 641-646.
Wolf, M. E., & Goodale, M. A. (1987). Oral asymmetries during verbal and nonverbal movements of the mouth. *Neuropsychologia, 25*, 375-396.
Yellen, J. E. (1986). The longest human record. *Nature, 322*, 744.
Yeni-Komshian, G. H., & Benson, D. A. (1976). Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees, and rhesus monkeys. *Science, 192*, 387-389.
Zappia, J. V., & Rogers, L. J. (1987). Sex differences and reversal of brain asymmetry by testosterone in chickens. *Behavioral Brain Research, 23*, 261-267.
Zimmerberg, B., Strumpf, A. J., & Glick, S. D. (1978). Cerebral asymmetry and left/right discrimination. *Brain Research, 140*, 194-196.