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The Relationship Between Brainedness and Handedness

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Introduction

Plato: 'It is only the folly of nurses and mothers to whom we owe it that we are all, so to say, lame on one hand. Nature, in fact, makes the members on both sides broadly correspondent; we have introduced the difference between them for ourselves by our improper habits.' *Laws*, 794, d.

Aristotle '... if we were all to practise always throwing with the left hand, we should become ambidextrous. But still by nature, left is left, and the right hand is none the less superior to the left hand, even if we do everything with the left as we do with the right. Nor because things change does it follow that they are not by nature. But if for the most part and for the greater length of time the left continues thus to be left and the right right, this is by nature.' *Magna moralia*, 1194.

The great majority of people, probably in the order of 90%, prefer to use their right hand for complex unimanual skills, notably for handwriting. At least as high a proportion have left-hemisphere dominance for speech, in the sense that left-hemisphere lesions are more likely than right-hemisphere lesions to produce aphasia. Ever since Bouillaud, on April 4th, 1865, raised the question of a possible relationship between handedness and speech lateralization (Riese, 1947), a central question in neuropsychology has been the following: is this relationship merely one of the many correlations between lateral asymmetrical organs, such as that between *situs* of the heart and digestive tract; or does it have a deeper functional and evolutionary significance?

In this chapter we shall review some of the theories that have attempted to account for the relationship between speech dominance and handedness. It

will help at the outset to classify the various theories; first, according to whether individual learning or past evolution accounts for the association; and second, by the postulated order of priority between speech and handedness. *Learning theories*, not now very popular, maintain that preference for one hand biases the individual towards developing speech mechanisms in the same hemisphere that controls the preferred hand; or alternatively, that the presence of speech mechanisms in one hemisphere biases the individual towards use of the contralateral hand. *Evolutionary theories* suppose the association between speech dominance and handedness to be inherited and laid down in the evolution of the species: a critical feature of such theories is that they postulate a selective advantage to the normal arrangement of having speech and control of the preferred hand in the same hemisphere.

In either kind of theory, it is possible to have versions claiming that handedness preceded speech lateralization, or the reverse; that one pre-adapted the brain for the development of the other (Varney and Vileasky, 1980). In practice, as we shall see, the priority of handedness has been the more popular alternative in evolutionary theories, because there is evidence that hand preferences appeared very early in human evolution.

An alternative to the Learning and Evolutionary theories will be referred to rather clumsily as the *Correlational Theory*, which maintains that the association between handedness and speech dominance is accidental, or at most, dependent upon a third variable. The critical feature of this kind of theory is that the association has no particular selective advantage; nor is it learned. For example, it has been suggested (Morgan, 1977; Corballis and Morgan, 1978; Morgan and Corballis, 1978) that handedness and speech lateralization are both reflections of an underlying developmental gradient slightly favouring more rapid movement of the left hand side of the body.

We consider first the formal nature of the evidence required to distinguish between the different theories. If it is possible to classify individuals as right or left speech dominant and right or left-handed, the simplest situation to analyse is that in which an entire population is both right-handed and left-speech dominant (*Figure 1(a)*) but, while this situation is descriptively simple, it is causally intractable, since in the absence of variance there is nothing to analyse, and hence no possibility of teasing apart cause and effect; technically it is not even possible to say in such a case that handedness and speech dominance are correlated. Consider now the situation in which the population proportions are as in *Figure 1(b)*, where we assume that 10% of the population are left handed and 10% are right-speech dominant; here the correlation between speech dominance and handedness is one. We now have variance, and this can be considered in terms of three possible causal models, shown in *Figure 1(b)* in terms of path-analytic type models, where the

(a)

		Speech	
		L	R
Hand	R	1.	0
	L	0	0

(b)

		Speech	
		L	R
Hand	R	.9	0
	L	0	.1

(c)

		Speech		
		L	R	
Hand	R	.81	.09	.9
	L	.07	.03	.1
		.88		.12

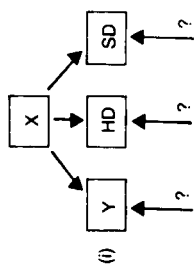
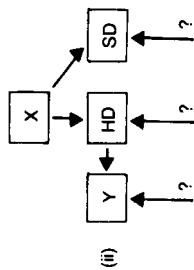
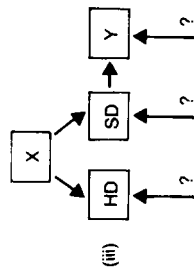
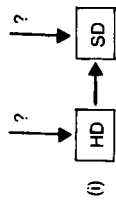
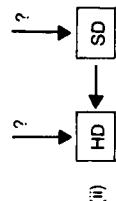
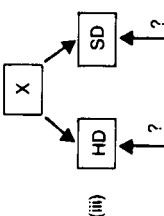
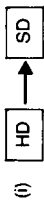
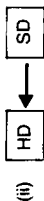
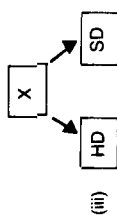


Figure 1

arrows indicate direct causal influences (see Kenny, 1979 for an excellent introduction to path-analytic modelling). In (i) hand dominance is prior to and directly causes the speech dominance; in (ii) speech dominance is prior to and directly causes the hand dominance; and in (iii) both hand dominance and speech dominance are directly caused by some third factor (X).

All of these models predict a correlation of one between hand dominance and speech dominance. In each case some prior influence is pre-supposed which establishes the apparently 'primary' dominance. *Figure 1(c)* shows a more likely situation in which handedness and speech dominance show a more moderate correlation. Here we have three similar models to before, except that each variable has a degree of unattributable effects causing some of its variance (symbolized by '?'). By appropriate choice of parameters such models will predict the correlations shown in *Figure 1(c)*. The unattributable error may represent either errors of measurement, or other unknown causes of laterization.

Thus far we may not seem to have advanced beyond a restatement of the truism (albeit a disputed one) from elementary statistics classes, that one cannot infer causation from correlation. The advance is not in the production of new theoretical insights, but rather in the precision and clarity with which they may be stated. Consider as an example a recent suggestion by Marin, Schwartz and Saffran, (1979):

'The choice of the left over the right hemisphere as the locus for motor speech almost certainly had to do with an earlier established right-hand preference in the hominid line (Dart, 1949). Verbal sequencing and manual sequencing may depend on the same basic type of neural organization, a possibility that receives some support from the association between linguistic and apraxic disturbance with posterior left-hemisphere lesions (Kimura, 1976). Given that motor control for language had become established in the left hemisphere, there might then have been a tendency for other language functions to organize themselves in proximity to the motor speech cortex; thus the left hemisphere would have been the locus for the increasing specialization of auditory mechanisms that would provide the perceptual basis of verbal learning, as well as for the development of syntactic mechanisms involved in the higher-order programming of motor speech input. Aspects of lexical representation might develop, to some extent, in both hemispheres, because of their relationship to perceptual function.' (p. 208)

Without wishing to discuss at this stage whether there is evidence for these claims, we note that the model can be redrawn in the path-analytic model of *Figure 2*. Whether this model is really what the authors meant is not clear, but it is what they apparently said, and the model is now specified far more precisely. The model also raises explicitly the question of *when* the postulated causes are occurring: during the development of the individual or of the species? Unless we wish to subscribe to the strict (and probably erroneous) notion that ontogeny recapitulates phylogeny, then we must be willing to

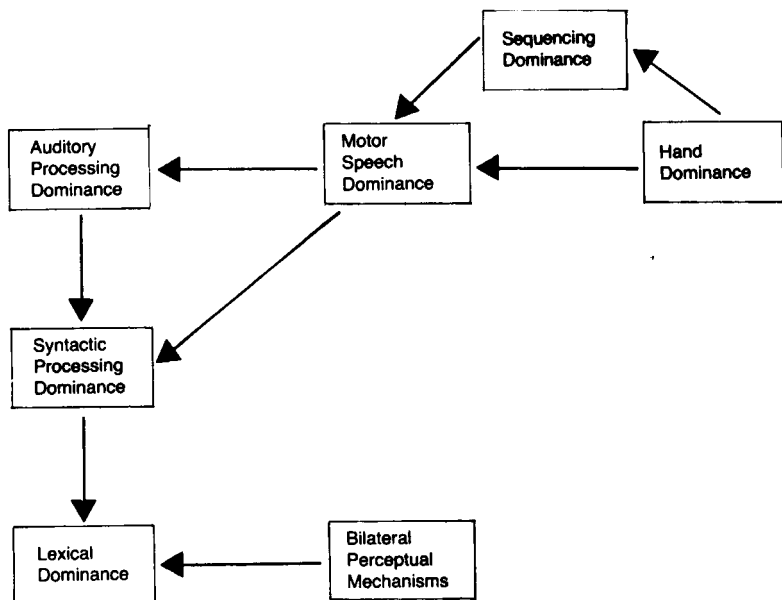


Figure 2

accept the possibility that separate causal models may be necessary for the two forms of development.

Path-analytic diagrams also force certain other conclusions. Consider model (i) of *Figure 1(b)*; it is apparent that if we wish to subscribe to this model then we must accept that in the absence of hand dominance, for whatever reason, there can be no speech dominance. The diagram also makes one realize that the hand dominance in such a case must be arising from somewhere; chance processes in general will only result in a lack of dominance and we must therefore continually look for prior causes, until we eventually arrive at some acceptable first cause (of which perhaps the only acceptable forms will be genes, asymmetry of biological molecules, or sub-atomic asymmetries).

A further question concerns the meaning of dominance. In man there is speech dominance in two very distinct senses:

1. In any individual one hemisphere is the major hemisphere and is primarily responsible for producing speech.
2. In a population, a majority of individuals have a particular hemisphere controlling that function. We may refer to these two forms (along with Denenberg, 1983) as *individual dominance* and *population dominance*. Most of the models of *Figure 1* could be conceived of in terms of either type of dominance, and once more, it is possible that different models may be responsible for each type of dominance.

A final methodological point concerns the relationships we may expect to find between handedness, speech dominance, and a third dominance variable. Consider a model of the type shown in *Figure 1(c)*, *iii*, in which X, with some error, causes both hand dominance and speech dominance. A third dominance variable, say, Y, may be causally related to either X, HD or SD (*Figure 1(d)*). In case (ii), the correlation between Y and HD will be higher than that between Y and SD or HD and SD. In case (iii) the correlation between SD and Y will be higher than that between Y and HD or HD and SD; finally, in case (i), the correlation between Y and HD, Y and SD, and HD and SD will be identical (assuming path coefficients from X to be identical). Finally, of course, there may be independence of Y from X, HD and SD. In general we cannot easily measure SD but can measure HD, and have little hope of measuring X. The use of variables such as Y is of interest since, if the correlation of Y with HD is too high, we suspect that it is merely an alternative measure of it, while if the correlation is too low, we suspect that the variable is of no interest. If there is a moderate correlation we cannot be sure if the measure is assessing SD, or perhaps is actually a third, truly independent dominance in its own right. It thus appears that moderate correlations are of maximum theoretical interest. But perhaps the major conclusion is that without the set of all possible correlations between X, Y, HD and SD, we cannot strictly interpret the results in causal terms, and yet in general we rarely have such information.

After this preliminary analysis, we turn to consider the main classes of theory.

Learning Theories

Gowers (1878) and Bastian and Horsley (1880) reported post-mortems of individuals with a missing left-hand; in both cases the contralateral parietal lobe was apparently atrophied and vestigial. It was probably cases such as this which provided the neurological justification for theories which stated that the lateralization of language functions was entirely secondary to hand dominance, and that it was, in some sense, 'learned'. Wernicke (1906) felt that 'the left hemisphere may lose the speech functions it previously had developed if use of the left hand replaces that of the right . . . localization of the speech centre is a functional acquisition of each individual'. A similar view may be found in the writings of Jackson (1880), Paget (1887) and Bastian (1898). The theory was attractive in part because it explained the strange problem of why lateralization of function was only discovered in the mid-nineteenth century (see Benton and Joynt, 1960 for a review of early failures). Moxon (1886) suggested that 'the brain of educated individuals is manifestly more unsymmetrical than the brains of uneducated individuals', and

Kinnier Wilson (1926) reiterated the view of Weber (1904) that 'the dissemination of the accomplishment of writing among all classes determined the lead of the left hemisphere over the right, and at the same time finally established the localization of the speech centres in the cerebral cortex'. Thus it was only with universal literacy that Broca *could* have made his discovery. The theory also gave the possibility of therapy, or even, to use the title of a paper by Coley (1909), *The Prophylaxis of Aphasia*; 'my suggestion is that a graphic centre should be made to develop in the right side of the brain by practising writing with the left hand'. The theory also resulted in the development of the 'Ambidextral Culture Society', ambidexterity conferring upon its possessors a myriad of advantages (see Harris, 1980 for a review). The therapeutic potential was considered by Burt (1950). 'At the special schools in the Lingfield colony for epileptics a group of children who were stationary in learning were given a training in left-handedness in the hope that "additional" centres in the brain might be opened up'. The recent enthusiasm for 'two brain education' seems to support Marx's view that history repeats itself, the second time as farce.

The concept continued to have explanatory use to neurologists well into the twentieth century e.g. by Needles (1942), Zangwill (1955) and Weisenburg and McBride (1955), for whom the right brain 'is in a state of receptivity for language acquisition, the degree varying in accord with the use of the left hand for writing, Wechsler (1976) described a case of crossed aphasia in a dextral and concluded that 'the neural mechanisms involved in learning to read and write may be necessary for the complete establishment and maintenance of language dominance.'

Various objections may be found to the hypothesis that speech lateralization is acquired secondarily to hand dominance:

1. Goodglass and Quadfasel (1954) and Gloning *et al.* (1969) reported studies on brain-damaged left-handers some of whom had used their left hand for writing ($n = 50$), and others of whom ($n = 57$) had used their right hand for writing (subsequent to educational pressure). In neither case did the incidence of left-sided speech dominance relate to particular hand usage.
2. Damasio *et al.* (1976a, b) investigated the suggestion (Critchley, 1956) that illiterates rarely became aphasic since they have a more bilateral organisation of their speech centres as a result of the absence of writing. They examined 247 right-handed adults with focal brain lesions, of whom 38 were illiterate; in summary there seemed to be no difference between the illiterates and the literates in side of aphasia-producing lesion, or in quality or degree of aphasia.

A variant of the learning theory concerns the lateralization of language function in bilateral individuals. Albert and Obler (1978) concluded that:

'[first] ... the language organisation of the average bilingual may be more ambilateral than that of a monolingual; second, that the organizational systems of the two or more languages of the bilingual are not necessarily disturbed equally with respect to cerebral language dominance ... [third] ... differential dominance patterns are not random; rather they may be influenced by such acquisition parameters as age, manner and modality of second language acquisition'. (p. 239)

Much of the evidence for such hypotheses comes from clinical cases in which bilingual patients lose just one language as a result of brain damage. The relationship to theories of illiteracy is seen in the case of the 94-year-old patient of Gorlitzer von Mundy (1959), which was retold by Paradis (1977). A 94-year-old man suffered a left hemispheric embolism which left him with a right hemiplegia and a selective aphasia. For the previous 40 years the patient had spoken German in a German environment. Until the age of 30 the patient was illiterate, ambidextrous, and spoke only Slovenian. He was then conscripted into the Austrian army for 12 years where 'he learned simultaneously to manipulate weapons with the right hand and to speak German, and thus, according to the author, German became localized in the left hemisphere. However Slovenian remained in the speech centres of both hemispheres. Consequently, when the left hemisphere was damaged, the patient lost his German and the portion of Slovenian that was stored there, but kept the Slovenian that was stored in his right hemisphere'. (Paradis, 1977, p. 93).

On the basis of such cases, Albert and Obler speculate that 'it would no longer be correct to accept the traditional dogma that the left hemisphere is necessarily dominant for language in right-handers' (p. 253).

The problem with such theories is partly that they are very imprecise (in some cases arguing that the second language should go 'into the right hemisphere, or in others, as Paradis above, that it will go into the left hemisphere), and partly that they are primarily based in clinical studies, from which almost every possible combination of recovery pattern has been observed (*see* Paradis, 1977). More damning, perhaps, is that in the careful study of right-handed Hebrew-English bilinguals by Gordon (1980), no evidence was found for differential lateralization of the two languages (although there was, surprisingly, a 27% incidence of left-ear advantages in these right-handed subjects, and McManus (1983) has suggested, after a statistical re-analysis of the data, that some 7% of the individuals show evidence for differential lateralization of the two languages). As a demonstration of the confusion in the literature we also note that Tzavaras *et al.* (1981) claim that illiterates are *more* left hemisphere dominant for speech (on the basis of dichotic listening tests). Sussman *et al.* (1982) have recently presented evidence that the age of acquisition of the second language affects its lateralization, early second languages (before six years of age) being left

hemisphere dominant, while later acquired second languages show a more bilateral pattern.

In summary, the conclusion of Albert and Obler seems to be premature, and we may, at least for the present, assume that the monolingualism of most subjects of study has not dramatically altered their lateralization patterns.

Further Objections

Most strongly left-handed people turn out to have left hemisphere dominance for speech (Zangwill, 1960); there are also well-documented cases of 'crossed aphasia' in dextrals (Zangwill, 1979). These cases appear to be much more damaging to learning theories than to their evolutionary counterpart, because of the postulated nature of the causation. Evolutionary theories claim that the association between handedness and speech dominance has evolved because it is advantageous: but clearly such an explanation still permits genetic variability, as in the case of other desirable traits, such as having a cerebral cortex. In learning theories, however, the nature of the postulated causation is direct, in the lifetime of the individual, so exceptions are much harder to accommodate unless one postulates that the causal mechanism is only weak. Nevertheless one has to postulate only a relatively weak causal link, or alternatively the presence of several different causal processes, in order to be able to 'explain' such apparent counter-examples.

Children with congenital unilateral aplasia, or absence of one hand, should develop speech dominance contralaterally to the remaining hand if learning theories are correct. We know of no evidence to test this possibility. Loss of a hand post-natally may also be expected to have a similar effect if it occurs early enough in development. Bramwell (1899, cited by Harris, 1980) described a patient who was originally right-handed, but who shifted to use of the left-hand at the age of 17 following an accident. At the age of 57 this patient became aphasic in association with left-sided hemiplegia. Bramwell argued that speech had shifted to the right hemisphere because of the shift in handedness. A similar case is reported by Nielsen (1946). (This explanation is considerably weakened, however, by the finding of 'crossed aphasia' in dextrals who have not changed their hand preference (Zangwill, 1979)). The absence of a control group in such cases and, particularly in the case of Nielsen, the fact that the individual had left-handed relatives and hence was more likely to have right speech dominance, make the interpretation of such cases almost impossible.

There is little support from the developmental literature for the notion that handedness precedes left hemisphere specialization for language. The literature is not clear on the question of when, exactly, 'handedness' and 'speech lateralization' emerge, probably because different aspects appear at different ages. For example, infants under 1 year of age show few signs of

spontaneous preference between the hands when manipulating objects, yet they may show a preference for extended reaching with the right arm (Baldwin, 1894; Wooley, 1910), and even 1–4-month-old infants have been described by Caplan and Kinsbourne (1976) as holding on to a rattle longer with the right hand. What is abundantly clear, however, is that at least some aspects of speech lateralization appear before practice of the right hand with writing and drawing. Witelson (1977) provides a number of useful tables summarizing the developmental evidence and her table 1 reveals 'a marked consistency for greater right than left [ear] scores on dichotic verbal listening tests for children as young as two or three years of age'.

Electrophysiological evidence (reviewed by Molfese, 1977) appears to support the view that there are asymmetries in response to speech sounds in infants, and even neonates. Studies with brain-damaged children, despite the widespread belief in 'equipotentiality', also indicate that speech loss is more frequent after left than right hemisphere damage, and this is true even at about 2 years of age, which is as early as language assessment can be carried out (Witelson, p. 247). These findings add weight to Kinsbourne's (1980) contention that the fundamental mechanisms of lateral asymmetry are probably present at birth. There is thus very little evidence to support the hypothesis that handedness precedes speech lateralization in development.

Evolutionary Theories

The principal ideas we shall try to examine in this section are the following: (1) the tool theory; (2) the gestural theory of language origin; (3) Brain's 'tongue muscle' theory; (4) Levy's theory of 'cognitive style'; (5) the theory of the 'leading hemisphere'; (6) Kinsbourne's attentional theory. All these attempt to provide a rationale for the strong association between right handedness and left hemisphere dominance of speech. They all make implicit assumptions about the actual evolution of handedness and speech dominance, and it is worth briefly considering the limited data on this question. It is also worth stressing that many modern accounts, written from an academic perspective in the late twentieth century, make the implicit assumption that the most crucial thing in the evolution of man is the sudden emergence of a larger brain, and that all other characteristics, in particular an upright posture, evolved secondarily to the larger brain. However, modern anthropological work (see for example Gould, 1980) supports the early nineteenth century view (reiterated in modified form by Freud in *Civilisation and its Discontents*) that the upright posture, with its freeing of the hands for skilled work, evolved *before* the evolution of a larger brain, bipedalism appearing by at least three million years B.C. (Leakey, 1981).

The Evolution of Handedness and Speech Dominance

(i) *Handedness*

Here we may consider two types of evidence — comparative and archaeological. Most studies take as their starting point that handedness is not found in animals, and the results of Collins (1968, 1969, 1970), who found that exactly 50% of mice were right pawed, and 50% were left pawed, are usually quoted here. It is important to note that these mice showed individual dominance, but they did not show population dominance: individual dominance in animals seems to be the rule. There have been repeated attempts at finding population dominance in animals, but these have generally failed to replicate, or to be studied further; examples include the rat (Tsai and Maurer, 1930; Peterson, 1931; Herren and Lindsley, 1935), and the cat (Cole, 1955). Much interest has centred on the monkeys, in view of their phylogenetic closeness to man. Despite some claims that there is a population dominance (e.g. Ettliger, 1961; Ettliger and Moffett, 1964; Brooker *et al.*, 1981) the consensus seems to be that there is only individual hand dominance and not population dominance in the monkeys (Finch, 1941; Cole and Glee, 1951; Warren, 1953; Lehmann, 1978, 1980), a conclusion not convincingly refuted by the most recent review (MacNeillage *et al.*, 1987).

Denenberg (1983) has emphasized that individual dominance may be selected for in lower vertebrates in order to assist in spatial perception, and he cites two studies, by Zimmerberg *et al.* (1978) and Camp *et al.* (1981), in which animals that had strong individual rotational biases performed better on spatial problems than did those without such biases. Of course the fact that individual dominance *might* be selected for does not necessarily mean that all species will show individual dominance — see McManus (1981b) for a negative example in *Drosophila* — although it should also be noted that Collins (1981, 1985) has recently presented evidence for selection and genetic control of degree rather than direction of asymmetry of pawedness in mice, and that Ward and Collins (1985) have shown that such mice show neuroanatomical differences from less lateralized mice.

An interesting case of population dominance may be found in the parrot; Broca himself raised this possibility at the Norwich Meeting of the British Association in 1868 (see Bateman, 1870, p. 165), and it had earlier been suggested by Sir Thomas Browne in his *Pseudodoxia Epidemica* (IV, V). Given the propensity for imitation of speech in these birds, and the clear lateralization of song in some birds (Nottebohm, 1979) it is of some interest that there is good evidence for a population dominance for footedness (Friedman and Davis, 1938; Rogers, 1981). A similar phenomenon in the peacock was claimed by the Chinese Sung Dynasty Emperor, Hi Tsung (Anonymous, 1957).

The general conclusion from comparative work is that man is almost

unique in possessing population dominance for handedness. When did this dominance rise? The study of works of art (e.g. Dennis, 1958; Coren and Porac, 1977) suggests that from the early Egyptian period through to the present day, approximately 7.4% of paintings have shown left-handers, but it must be borne in mind in the interpretation of such material that lateralized artistic representations in works of art are not necessarily veridical — see McManus, 1976 for an example. Prior to the onset of civilization there is less evidence as to handedness. The recent technique of micro-wear analysis of tools provides good evidence that between 6 and 20% of neolithic (about 4000 BC) implements were produced by left-handers (Spennemann, 1984), and that at least some individuals in a palaeolithic Belgian site (8900 BC) were left handed (van Noten *et al.*, 1980). Prior to this we have only the poor and ambiguous data to be obtained from cave paintings (see Uhrbrock, 1973 for a review), followed by a vast gap until the evidence of Dart (1948) that *Australopithecus* (one million years BC) was right-handed, killing prey with a blow to the skull from a stone held in the right hand (although the statistical evidence reported is far from totally convincing). Recently Toth (1985) has argued, on the basis of a detailed analysis of the asymmetric pattern of flaking in stone tools, that right-handedness predominated in sites from the lower Pleistocene (about 1.5 million years BC) and middle Pleistocene (about 200 000 years BC) periods, although his method does not allow any accurate estimation of rates of left-handedness. As a counter-balance to the above theories we also note the eccentric suggestion of Gooch (1977) that Neanderthal man was predominantly left-handed.

In summary, man is probably the only animal with population hand dominance for skilled activity, and this dominance probably arose sometime before the onset of civilization; little else can be said with any certainty. Specific preferences for use of the otherwise *non*-dominant hand are rare in man; Dimond and Harries (1984) have described an interesting example which has evolutionary implications. Face-touching, which is interpreted as a form of emotional expression, is more common with the *left* hand in man, and this is also the case in the great apes, but not in monkeys, suggesting a relatively recent evolutionary origin, perhaps connected with right-hemisphere function.

(ii) Cerebral Dominance

Once more we may consider comparative and archaeological evidence. As far as comparative work is concerned we may look for evidence of functional dominance, be it for language or otherwise. Warren and Nottebohm (1976) concluded that there was no evidence for functional dominance in monkeys, but several lines of evidence suggest that conclusion might be premature. Hamilton *et al.* (1974) reported evidence from seven monkeys which, for several tasks involving movement and orientation detection, suggested right hemisphere dominance; and on other tasks there was evidence of strong

individual dominance in the absence of population dominance. Pohl (1982, 1983) has reported evidence for individual, but not population, dominance in processing of dichotic stimuli in baboons. More excitingly, Petersen *et al.* (1978) have reported work suggesting that the left-hemisphere of the Japanese Macaque contains cells specialized for the detection of species-specific vocalizations, and Heffner and Heffner (1984) have reported that discrimination of such sounds is critically dependent upon the integrity of the left but not the right temporal cortex; if these results are replicable then they must surely be of great importance in our understanding of the evolution of language and dominance. Finally, in a recent review, Denneberg (1983) has presented evidence that might be interpreted as existence of population dominance both in chickens and in rats, especially for emotional behaviours.

A further line of evidence concerns morphological cerebral asymmetries. Since the report of Geschwind and Levitsky (1968) that the *planum temporale* of normal human brains is larger on the left side than the right, a flurry of work has investigated such asymmetries.

Nevertheless, it is worth noting that the asymmetry has not as yet been reported in relation to either handedness, or speech loss after cerebral damage, and in the absence of such data the asymmetry may just as well be interpreted as a correlate of *situs*, or some other anatomical asymmetry. The same criticism does not apply to the work of Le May (1976), where an asymmetry of cerebral blood vessels has been related to handedness. From a re-analysis of the data of Hoadley and Pearson (1929), McManus (1982) has shown that the distribution of human skull asymmetry is bimodal, and infers that this bimodality may reflect two separate types of speech dominance. Morphological asymmetries have been examined in monkeys. Yeni-Komshian and Benson (1976) demonstrated an asymmetry in chimpanzees (but not in rhesus monkeys) and Le May and Geschwind (1975) found asymmetries in the brain of orang-utans. Several studies (Abler, 1976; Le May, 1976) have reported morphological studies of prehistoric skulls and found evidence for asymmetries. Studies of cranial endocasts suggest that both *H. erectus* and *H. habilis* had well-developed Broca's and Wernicke's areas, and that these areas are relatively underdeveloped in Australopithecines and the modern apes (Tobias, 1981; Holloway, 1981).

There is some evidence for functional asymmetries, and better evidence for morphological asymmetries indicating population dominance in the higher apes, and such results are at least consistent with the prehistoric remains of man.

(1) The Tool Theory

There are recent discussions of this theory by Frost (1981), Calvin (1982), and Steklis and Harnad (1976) (although Steklis (1985) has recently withdrawn

his earlier support for the theory). A volume of the Proceedings of the New York Academy of Sciences (1976) was devoted to the 'Origins and Evolution of Language and Speech', and many of the articles contain material relevant to the following discussion. The essence of the theory is this: human beings are distinguished from non-humans by their bipedal gait, by tool-using behaviour, by their preference for using the right hand in complex motor skills and, finally, by language. The Tool theory attempts to link these human characteristics together in a systematic way. To start with, the hominids are the only Primate group for which the primary functions of the forelimbs are other than for locomotion, thus freeing the forelimbs for the making and using of tools, albeit some 1½–2 million years before the first appearance of stone tools in the fossil record (Isaac, 1981). Many tools require different skills from the two hands, as in the chipping of a flint or the throwing of a spear. In many of these cases the left hand merely holds or steadies the object being manipulated, while the right hand performs the skilled action. This meant that the motor mechanisms for the more skilled actions involved in tool making and tool using evolved in the left hemisphere. There then follows the most difficult and crucial step in the argument. Why did the development of motor skills in the left hemisphere facilitate the development of language mechanisms there? We quote Frost (1980) here:

'... the co-lateralization of the neural substrates mediating skilled serial motor praxis and those mediating speech in the left hemisphere is likely to be more than a coincidence. The co-occurrence of these mechanisms in the left hemisphere is very likely related to the fact that speech, like tool behaviour, involves skilled serial motor activity, but . . . it is the actions of tongue, lips and vocal chords rather than arms, hands and fingers which must be precisely timed and sequenced.' (p. 455)

Putting this more fancifully, we may say that the left hemisphere, having acquired the skills to control precise movements of the hands, finds that many of these same skills can be used to control the voice. The upright, asymmetrical, tool using, loquacious ape has evolved, to the satisfaction of theory.

(2) The Gestural Theory

This has a great deal in common with the tool theory and the two accounts have evolved in parallel. A comprehensive historical review by Hewes (1976) will be found in the New York Academy of Sciences Symposium referred to earlier. The psychological implications of the theory have been spelled out by Kimura in several publications (e.g. 1977) and it is Kimura's version of the theory that will provide the principal basis for the account we give here.

The Gestural theory of language origin maintains that '... the initial form of language was gestural, in the sense that the propositional, predicative, or

reporting functions were based on gestural signs, with vocal sounds serving much as they do non-human mammals, for the social communication of affect' (Hewes 1976, p. 482). Manual communication thus preceded vocal communication in evolution, and it is thus in manual communication that we must seek the origins of cerebral asymmetry. The next link in the chains of reasoning is therefore that the *right* hand, and in consequence the *left* hemisphere, took on the major role in manual communication (signing). Why the right hand? Here the gestural and tool theories converge, as Kimura (1976, p. 153) explains:

'One may speculate, therefore, that the necessary condition for the development of the communication system we use was the freeing of the upper limbs from locomotor activity. This permitted the development of tool use and the necessary manual dexterity to handle tools. Given that such manual skills existed, it is reasonable to suggest that hand movements could readily be employed in a communication situation, perhaps initially in a manner imitative of the object described. . . .'

So the left hemisphere developed motor skills through tool use and these were subsequently transferred to manual communication. The next stage in the argument also resembles the tool theory. When speech finally arrived on the scene, it was able to make use of the pre-adapted motor skills in the left hemisphere, and hence speech became lateralized as well. Thus the more skilled hand and the speech mechanisms are controlled by the same hemisphere for definite evolutionary reasons.

(3) Brain's 'tongue-muscle' theory

Both the tool theory and the gestural theory argue that precise motor control of the hands has eventually led to speech dominance. Brain's theory specifically rejects this proposal and looks at the evolution from the other direction:

'... it seems more probable that the establishment of the left hemisphere in man as the major hemisphere for speech resulted in the development of the right hand as the dominant hand. Emotional noises, both in man and in the lower animals, are simple involuntary performances, and such simple reactions can utilise symmetrical and bilateral pathways. In contrast to this, speech calls for articulation — the precise integration of the small muscles of the lips, tongue, palate and larynx, besides the respiratory muscles, so that these contract synchronously on the two sides with such delicacy that a variety of sounds can be differentiated through a range of fine gradations. This motor integration seems to require that the motor cortex of both hemispheres should be under the control of a single co-ordinating centre, 'the motor speech centre'. Speech, in other words, necessitates localization.' (Brain, 1961; pp. 25-26).

And once speech has been lateralized to one hemisphere then hand dominance would rapidly follow.

It should be noted at this point that the three theories presented are

primarily theories of the correlation of hand dominance and speech dominance *within individuals*. If exactly half the population were right-handed and left-speech dominant, and the remainder were left-handed and right-speech dominant, then the above theories could remain almost unchanged. The theories therefore produce no account of population dominance for speech and handedness, beyond the trivial statement that at least one of them exists, and causes the other. This seems to be a serious defect; in each case the models confuse dexterity with right-handedness.

The following key proposals are shared by the tool and gestural theories, and our first task will be to discuss their validity:

1. Tool use in general involves greater skill and finer control on the part of the right hand.
2. As a result of evolution, the right hand (or more correctly, the left hemisphere) has acquired a greater potentiality for skilled motor control.
3. The skills developed by the left hemisphere do not transfer to the right hemisphere, because duplication of function is avoided wherever possible, in order to make the most economical use of available space; in other words, there is a selective advantage to asymmetry.
4. Manual skills and speech resemble one another sufficiently to share a common neural substrate, at least in part.

We now discuss these issues separately. In so far as these key proposals support both the tool/gesture theories and the tongue-muscle theory, then a lack of specification of the theoretical models is demonstrated.

(a) Tool use involves greater skill in the right hand

It must immediately be apparent that since the world is to a first approximation symmetric, then there is no necessary advantage in using tools with the right rather than the left hand *per se*. Nevertheless it is true that for many skills, for example, chipping a flint, throwing a spear, or scraping a bone, the right hand is usually the one carrying out the more skilled actions. Frost (1980) points out that in such examples the left hand performs merely a holding or steadying role, if it has one at all. The hypothesis may thus very well be true for early examples of tool using behaviour. In passing, however, we should like to express doubts about the over-enthusiastic application of this principle to the great variety of modern manual skilled behaviours. Once it has been decided *a priori* that the left hand is deficient in skill, it is all too easy to explain away any apparent counter-example by special pleading. For example, in the playing of many modern stringed instruments, the left hand has the difficult task of holding down the strings in the correct spatio-temporal pattern, so that the right hand can cause them to vibrate at the correct frequency. On the face of it this seems to demand greater skill by the left hand, but we have seen it suggested that this is just another example of

the left hand holding an object while the right hand acts upon it! This sort of assertion makes it virtually meaningless to claim that the right hand has, in general, greater skill. We shall return to this theme below; in the meantime, we agree that the account given by Frost and others for *early* tool use is a plausible one. However, the study by Wright (1972), in which an orang-utan (probably left-handed) learned, by imitation, to produce and use stone tools, suggests that population right-handedness *per se* is not essential for the development of tool use (although there is interesting evidence that handedness concordance between teacher and pupil can facilitate the learning of manual skills (Michel and Harkins, 1985)).

(b) *The right hand (left hemisphere) has evolved a greater potentiality for motor skill*

It is beyond question that the right hand is much more skilful than the left at tasks that it carried out habitually, such as handwriting. (Of course, this remark applied only to right-handed people; we shall deal with the problem of left handedness later.) But does this mean that the right hand has some *intrinsic* advantage in acquiring skill? We would follow Dimond (1970) in arguing that it does not; as he points out, 'lateral preference is not the same thing as cerebral dominance': thus it may be that the only reason why the right hand is more skilful at writing and other tasks is that it has practised them more, and that this practice has failed to transfer to the left hand, just as skills acquired by the left hand may fail to transfer to the right. It may be objected that no rational account of handedness is possible unless the hands differ in their potential for skill; but such reasoning is erroneous. The origin of the skill difference might be an inherited *preference* for using the right hand, rather than skill coming first and preference second. After all, infants manifest handedness by a reaching preference long before it is possible to demonstrate differences in skill. Might not what is true of ontogeny be also true of phylogeny?

If there is indeed a preference for using the right hand, irrespective of an underlying skill difference, then a skill difference will soon result as a consequence of differential practice. In almost any task involving different functions of the two hands, we would maintain, people are less able to do with one hand what they normally do with the other, even if the original choice is idiosyncratic rather than species-specific. (The same is probably true of which side of the nose is used in pea-rolling competitions, in highly practised competitors.) Thus the superior skills of the right hand cannot be used as evidence for an inherited superiority of the left hemisphere in skilled tasks, unless differential practice can be ruled out as an explanation. In using such an argument we would argue that *preference* may be fundamental, but that this preference should not be regarded as *mere preference*. In the case of another human behavioural asymmetry (hand-clasping), which appears to be purely preferential, one of us has described significant geographical

variations, and evidence of a genetic mechanism (McManus and Mascie-Taylor, 1979). It should also be remembered that in the case of vision, sighting eye dominance bears no relation to acuity dominance, which might have been suspected to be the underlying skill difference upon which the sighting dominance depended (Porac and Coren, 1976).

The clearest evidence for an innate skill difference would be a demonstration that right handers could never acquire, with the left hand, skills that are normally performed with the right hand. One might look here for acquisition of left-handed writing and drawing in right-handed patients with right hemiplegia, if it were not for certain obvious difficulties of interpretation. First, it would be unwise to make too much of a difference in fine motor skill between a brain-damaged and normal subject, or between a brain-damaged patient and their pre-traumatic performance. Second, there may very well be sensitive periods for the development of such skills as writing, and if so it would be unreasonable to expect the left hand to acquire, later in life, skills which the right hand acquired in childhood.

One possible way round these difficulties is to examine children who are born without one or other hand, and to see whether there are left-right differences *between* subjects. Weinstein *et al.* (1964) studied strength and co-ordination of children born with only one upper extremity. The principal motivation of the study was to evaluate the importance of practice in determining skill asymmetry, and it was expected that there would be some superiority of the group in which the right hand had been spared. The data apparently failed to support this hypothesis, from which it is tempting to deduce the important fact that there are no inter-subject differences in skills of the two hands when the opportunities for practice have been equalized. If valid, this argues against the hypothesis that skill differences are primary, and in favour of the alternative that they are acquired by differential practice. However, the results in the paper are published with very little statistical data, and there is a relatively small number of children with terminal arm aplasia. A more difficult problem is that any such study is necessarily a between-subject analysis, and hence the between-subjects design will be far less sensitive to relatively small differences and there is a great danger of a Type I error, particularly if one wishes to 'prove' the null hypothesis.

A further source of data on this question is that of children with limb abnormalities due to maternal thalidomide usage. The only published report of which we are aware (Smithells, 1970) is too brief to be of any help. If anecdote is of any use in such cases, then we could mention an acquaintance of one of us (ICM) who has a symmetric thalidomide deformity involving normal upper arm and elbows, with complete absence of both forearms except for the proximal inch or so, and a rudimentary 'hand', consisting of a single digit. This person states that he has never been in any doubt that he is 'right-handed' — this seeming to be the limb which he naturally prefers to

use for complicated tasks. A further anecdote describes a case of a child with complete upper and lower arm absence, with a rudimentary hand attached to each shoulder. The child in question was finding great difficulty in learning to write with a pencil in the right 'hand'. When the pencil was attached to the left 'hand' then writing developed fluently: the implication is that this child was, in some sense, 'left-handed'. (A related case may be found in Poeck (1964) who reported the case of a child without forearms or hands who said that 'voluntary' movements with the phantom of the left hand were more skilful than similar movements with the phantom of the right hand.) Such cases, as with the cases of unilateral aplasia, are clearly of great potential for disentangling the origins of hand skill and hand preference, although as yet there is little substantial evidence available.

Another way of looking at the problem is to examine left-handers, who are quite frequently forced by social pressures early in life to use their initially non-preferred hand for skills such as hand-writing. If skill differences are dependent upon inherited predispositions of the hemispheres, we should expect skills acquired by the non-preferred hand to be inferior. Is there any evidence for this from left-handers who have been forced to switch hands? In other words, are such people less skilled at writing and drawing than right-handers, or than left-handers who have not been forced to switch? This is a crucial question to which there appears to be no clear answer in the literature; although there have been many claims that enforced changes produce emotional changes, we know of no direct evidence that skills as such are affected. In the case of playing musical instruments, Oldfield (1969) found no evidence to suggest that left-handers were at a disadvantage in having to play right-handed instruments and his conclusion is interesting:

'... handedness is not a matter of superior inherent "dexterity" or the capacity for agility, precision and speed in the [preferred] hand.'

Although here it might be argued that some form of selection has resulted in only the most ambidextrous of left-handers eventually manifesting as professional musicians.

Similarly, Walker (1980) also uses the argument of musicians to support the suggestion that:

'... human handedness is largely a matter of preference rather than a consequence of biologically programmed inadequacies of the minor hemisphere.'

It could be argued against this that the case of left-handers throws little light on the general question of the origin of skill differences, because left-handers are often claimed to be less weakly lateralized than right-handers and would not thus be expected to show strong differences in motor skill between the hemispheres. On examination, however, this argument is revealed as somewhat circular, in as much as one line of evidence that left-handers are

'less lateralized' comes from skill tests, the results of which are actually in accord with the hypothesis that skill differences result from practice. For example, Benton *et al.* (1962) (cited by Satz *et al.*, 1967) found that many self-classified left-handers showed striking superiority of the *right* hand on a manual co-ordination test. This is just what we should expect if these left-handers had been forced by social pressures to use their right hand, and if skill differences are determined by usage, not by inherited differences between the hemispheres. Similarly, Satz *et al.* (1967) found that in a manual dexterity test (picking up pins with tweezers) left-handers were no worse than right-handers with their right hands: the most striking fact was the inferiority of right-handers to left-handers when using their *left* hand. This is just what we should expect from the practice hypothesis. Left-handers are also claimed to be less lateralized and more variable in their laterality on the basis of handedness questionnaires. McManus (1979) has demonstrated that these differences are entirely due to items for which there is either social pressure (e.g. the hand used to hold a knife and fork) or mechanical pressure (e.g. in the use of items with a right-hand screw thread). Thus these left-handers are 'dextrous' in accord with the demands of society: otherwise they use their preferred hand, and show as strong a degree of asymmetry as right-handers.

At this point it would be desirable to distinguish clearly the two main senses in which the term 'handedness' has been used in the literature (*cf.* Oldfield, 1971; Annett, 1972). The first refers to the subject's preferences in carrying out everyday tasks such as hand-writing and hammering, and is usually assessed by self-report in questionnaire form. The second refers to objectively determined performance differences between the two hands in tasks such as frequency of tapping, reaction time, balancing a dowell rod, or moving pegs around a board (Annett, 1972). We shall refer to these two kinds of handedness as 'handedness/preference' and 'handedness/skill' in order to be quite clear about which we mean in a particular context. Now, it is the essence of the class of evolutionary theory that we are considering to suppose that there is an intimate relation between 'handedness/preference' and 'handedness/skill'. It is claimed that the left hemisphere has evolved special mechanisms for the control of manual skill, which subsequently transfer to the control of speech. But the evidence that humans acquired handedness/skill early in evolution comes necessarily from preference measures, since psychologists were not around at the time with their peg-boards to test differences in skill between the hands. There is thus a rather crucial gap in the theory, and it is important that it should be bridged by convincing evidence demonstrating a clear relation between handedness/skill and handedness/preference.

Unfortunately for the tool theory and related accounts, the evidence is that preference and skill measures are related only rather loosely. As Annett

(1972, 1978) has pointed out, skill difference between the hands show an approximately normal distribution both in left and right handers, with a wide spread in both cases. For example, in Galton's data on grip strength, the distribution of difference scores follows an approximate normal distribution in which the mean is shifted from the zero point by about 0.44 SDs. This means that about 33% of the sample actually showed a *left-hand superiority*: and since this is far too high a proportion to represent left-handers as they would be classified on a preference test, it must be concluded that a number of right-handers (by preference) actually show a left-hand superiority in grip strength. Similarly, Annett's (1974) figures for peg moving show a shift from the mean of 0.5 SDs and 1.10 SDs in males and females respectively, again suggesting that quite a large proportion of right-handers (preference) show a left hand superiority in a skill test.

The National Child Development Study (see McManus, 1981) administered two unimanual tasks to over 12 000 11-year-old children for details of the classification of handedness and background. The first test involved using a pencil to mark as many small squares as possible on a sheet of graph paper in one minute, using first one hand and then the other. The second test required the child to pick up and transfer 20 matchsticks to the other side of the table. In each case a laterality index ($R-L/R+L$) was computed for each child (see McManus, 1985b). The overall distribution of the scores for the square-making task was bimodal with considerable overlap of the distributions of right and left handers. For the matches task the overlap was much more marked, although the means of the two distributions were still in the expected directions. In contrast to these overlapping measures of skill difference, the measures of handedness in the National Child Development Study showed a clear separation (see McManus, 1981a).

It is thus quite mistaken to start from the fact that about 90% of people write with the right hand, and to deduce from this that 90% of people have more skilled right hands. As Oldfield puts it:

'... tasks which in the precise form presented are unfamiliar to the subject, and which he is given little or no opportunity to practice, produce a distribution of indices which, while not symmetrical, is roughly bell-shaped with an outstanding mode not far from the neutral point, and sometimes... another small one near the left hand end. That is to say, the right-left differences displayed by such methods are relatively small and *certainly do not correspond with the gross disparity between the two hands which is manifest in well practised tasks.*' (Oldfield, 1971, p. 97)

We are not denying that some skill tests, such as tracing, and cutting out shapes with scissors (Shankweiler and Studdert-Kennedy, 1975) will discriminate virtually perfectly between hands. But these are highly practised tasks (and in one case involve using an asymmetric tool). In the case of unpractised tasks like Crawford pegs and Crawford screws,

Shankweiler and Studdert Kennedy found virtually zero correlation between asymmetry scores and handedness as measured by tracing and scissors, in a group of self-classified right-handers. This lack of correlation contrasted with the high intercorrelation between scissors and tracing. (Although note here that handedness and skill are being assessed *within* right-handers. It is quite conceivable that there may be a strong correlation of handedness and skill between right and left handers, but no correlation within either handedness group.) Furthermore, only tracing and cutting were significant predictors of ear advantage in a dichotic CV test: the unpractised tasks showed if anything a weighting in the wrong direction. Shankweiler and Studdert-Kennedy conclude from this '... that well-practised tasks, which are nearly always carried out by the same hand, should be used for measurements of manual laterality. This would ensure that differential experience in use of hands, otherwise a potent uncontrolled variable, does not contribute to the variance'. This is one line of reasoning: another might be that cerebral lateralization correlates with preference, and only secondarily with skill, as we are suggesting here.

Shankweiler and Studdert-Kennedy seem to be suggesting that skill differences between the two hands will show themselves best in asymptotic performance. This is a reasonable position, and it may be tested by taking a relatively unfamiliar task like Crawford pegs and training both hands in short, alternating sessions until performance shows no further improvement. Four experiments have been reported which broadly fit this description. Peters (1981) has reported a study on the relatively unskilled task of finger-tapping. In general the dominant index finger has a maximum tapping speed score 10% greater than the non-dominant index finger. Peters examined the effect of long-term practice on the difference between the hands: fourteen subjects completed from 200 to 1150 trials each involving 10 seconds tapping with the right and the left hand. In thirteen of the fourteen subjects there was no evidence of a diminution of the difference in performance of the two hands, despite an improvement in performance with both hands through the experiment. Hicks (1974) asked 160 right-handed subjects to cover sheets of paper in capital letters printed inverted and reversed. Two blocks of ten trials were used, with a quarter of the subjects using the right-hand during both blocks, a quarter using the left-hand during both blocks, and the remaining subjects changing hands between blocks 1 and 2, half from right to left, and the rest vice versa. From the present viewpoint the interesting finding is that the rate of learning was greater with the right than the left-hand, and that the relative advantage of the right-hand increased as the experiment went on. It is also of some interest that in those subjects who changed hands between blocks there was a greater transfer of skill from right hand to left hand than vice versa. Similar results have been found by Taylor and Heilman (1980), and McManus and Stagg (1984).

The third experiment is that of Annett *et al.* (1974) who reported extended practice on the Annett peg moving task. This experiment differed from the previous ones in that in two out of the three subjects there was a significant diminution in the degree of manual asymmetry. Finally, Perelle *et al.* (1981) reported that practice with the Crawford Small Parts Dexterity Test reduced the degree of skill asymmetry to a non-significant amount. Several objections may be found to these experiments. However intense the practice it seems unlikely that it could reverse the habits of a lifetime, particularly in an adult with a non-plastic brain. It might also be questioned whether, in any case, the subjects were sufficiently motivated to learn with their non-dominant hand, given that such learning ran counter to all their previous intuitions of their learning abilities. It is, after all, noteworthy that the high motivation for success found in skilled pianists or typists produces much less performance asymmetry between the hands.

In summary the evidence is confused as to whether the right hand is innately more skilful or merely preferred and hence more practised at the tasks. The case for a more 'skilful' left hemisphere is thus not proved, and we turn to examine the next critical element in the tool and gestural theories.

(c) Competition for neural space has prevented unnecessary duplication of functions in the two hemispheres

This is a central and plausible proposition in both the tool and gestural theories. Once again we quote Frost:

'If we advance the premise that both praxic and non-praxic functioning were essential to the early hominids, it would follow that *both* of the corresponding neural substrates would have to be represented in the hominid cortex: thus neither can be extensively represented at the expense of the other. By consequence of the trade-off principle, any increase in the praxic substrates will enhance the ability to make and use tools while producing a decrement in non-praxic functioning while any increase in the non-praxic substrates will have the reverse effect. The expected evolutionary result of this competition for neural space would be a distribution of the praxic and non-praxic substrates within the cortex which would maximize tool making and using ability while minimizing the loss of non-praxic functioning.' (Frost, 1980, p. 451)

The perfect solution to this competition problem is, of course, to parcel out the different functions in opposite hemispheres. This reasoning accounts very neatly for the specialization of the right hemisphere for visuo-spatial abilities. Exactly the same line of argument has been advanced by Levy (1977) in her 'cognitive style' theory:

'Lateralization appears to provide for a minimization of interference effects in neural activity patterns and a maximization of the computers integrating these patterns. If two very different kinds of cognitive capacities are to be present, then joint optimization of the level of these capacities seems to require lateralization.' (p. 815)

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This is a plausible retrospective account of the origin of lateralization, but is there any way to test it? On the face of it the theory seems to predict that individuals who have not adopted the optimum strategy will be at a cognitive disadvantage; and the obvious group to look at here is those left-handers who have retained left hemisphere language control, while presumably invading the right hemisphere for the control of manual skill (praxis). Such individuals should, according to Levy (1977), manifest inferior visuospatial abilities. Another reason why this should be so is that a right hemisphere contribution to language is more likely in sinistrals than in dextrals, both according to clinical findings on aphasia, and from the results of unilateral ECT and amylobarbitol tests (*see* Bradshaw, 1980 for a review).

From an evolutionary point of view, the hypothesis of a cognitive deficit in sinistrals raises the intriguing question of why left-handedness has remained so common, relative to other genetically deleterious traits such as haemophilia. Possible answers might include the following:

1. Incomplete heritability of the trait.
2. Relaxation of selection pressures against cognitive deficit followed by a random drift upwards in gene frequency.
3. A rather weak selection pressure is in equilibrium with a quite high mutation pressure.
4. An unknown selective advantage of sinistrality, such as higher fertility (McManus, 1979) acts in opposition to the putative cognitive disadvantage and has resulted in a situation of balanced polymorphism (Sheppard, 1975).

The high incidence of left handedness is a general problem for evolutionary theories, because they all attempt to derive the majority state of affairs from some supposed selective advantage. However, it is time to leave this fascinating but unsolved problem on one side for the moment, and ask if there is really anything to explain: is there in fact any evidence for a cognitive disadvantage to sinistrality?

Levy (1977) reported that left-handers had significantly lower scores than dextrals on tests of spatial ability, and not on language tests. Her study was criticized by Newcombe and Ratcliffe (1973) for involving an occupationally restricted group (college students); their own more extensive study of 410 men and 410 women of various occupations found no significant difference in WAIS IQ, either verbal or performance. Heim and Watts (1976) examined this problem with test AH 2/3 and found no evidence that left-handers did less well on performance/visuospatial tasks. (A total of 2165 sinistrals were used ranging from 9-year-old children to adult students.) Curiously, the results did suggest that left-handers —especially if they were male — did better on numerical tasks, a result quite contrary to Levy's hypothesis.

In a more recent large-scale study, of a housing estate in Cambridge

(England), Mascie-Taylor (1980) found that left-handers were significantly worse than right-handers on performance but not verbal IQ. This supports Levy's findings. But in an even larger sample, of 7169 children in the National Child Development Study (NCDS), McManus and Mascie-Taylor (1983) found no significant effects of handedness on non-verbal IQ. They did, however, find that left-handers scored very slightly but significantly less well than right-handers on G, the factor that accounted for 91% of the common variance in the four tests used, Reading, Maths, Verbal Ability and Non-Verbal Ability.

It is difficult to draw firm conclusions from this mass of contradictory findings, unless it be that Levy's suggestion of a visuospatial deficit in sinistrals holds only under special conditions, at present unspecified. There is evidence from the two most extensive studies of a slight difference in favour of right-handers, although it should be emphasized that the effect is very small indeed. We tend to agree with the conclusion of Bradshaw's (1980) review, that '... Levy's hypothesis of a specific visuospatial disability amongst sinistrals is unsupported.'

Finally, we consider the idea that sinistrality, and its alleged cognitive deficit, results from otherwise undetectable left hemisphere damage resulting from 'birth stress' (Bakan, 1977). This hypothesis has been strongly contested by others (*see* McManus, 1981 for a review) and, in a large-scale study of the NCDS dataset, McManus found little evidence to support it. Incidentally, McManus and Mascie-Taylor (1983) found no evidence either to support the idea that the slightly lower G score of sinistrals was due to a severely impaired sub-group: the same effect was found if the lowest-scoring 5% was removed from the sample.

(d) Do speech and manual praxis share a common neural mechanism?

The most difficult problem for the speech and gestural theories is to bridge the gap between the evolution of the left hemisphere as a controller of skilled manual movements, and its role in the control of speech and language. This gap is bridged by the proposal that speech and manual praxis have sufficient in common for speech, when it evolved, to make use of pre-adapted neural mechanisms in the left hemisphere. Thus Kimura (1976) has proposed that 'brain regions considered to be important for symbolic language processing might better be conceived as important for the production of motor sequences which happen to lend themselves readily to communication' (p. 145). Before considering the evidence that Kimura advances for this interesting idea, we shall ask what kind of shared properties have been specified, and try to assess the general plausibility of the argument.

In point of fact, Kimura appears to have offered a variety of ideas relating speech to manual praxis, and it is not easy to know which one to consider as fundamental. Kimura (1976) argued that the special contribution of the left hemisphere both to speech and to manual praxis, is the 'running off or

patterning' of smaller units: phonemes or syllables in the case of speech, single flexions in the case of movements. In support of this idea are the findings of several studies that temporal acuity is apparently greater in the left hemisphere in normals (Efron, 1963a; Hammond, 1981) and in brain-damaged populations (Efron, 1963b; Carman and Nachshon, 1961), and that the perception (Gordon, 1978) and production (Woolf *et al.* 1977; Ibbotson and Morton, 1981) of rhythms is superior in the left hemisphere. In a later article (Kimura, 1977) greater stress was laid on the presence in the left hemisphere of a spatial mechanism for the 'accurate positioning of oral and brachial musculature.' These suggestions are not necessarily incompatible, since the sequencing or patterning function could clearly depend upon accurate positional information; we do wonder, however, whether neural capacities defined in such very general terms are not in danger of explaining too much. Is there any example of a complex behaviour that could not be included *a posteriori* under such an umbrella if it were found to be affected by left hemisphere lesions? Conversely, is it possible to exclude from under the umbrella those functions that are known to have a specific contribution from the right hemisphere, such as visuospatial manipulation?

Kimura (1977, p. 539) acknowledges that the idea of a special left hemisphere involvement in spatial control of body movements may appear implausible given the neuropsychological evidence for a right hemisphere involvement in complex spatial abilities. McFie and Zangwill (1960) described severe spatial disorders following right parietal lesions. As a recent example, Kolb and Whishaw (1980, p. 249) describe Mr P, a 67-year-old man who had suffered a right parietal stroke; he was impaired at combining blocks together to form designs (constructional apraxia) and generally impaired at drawing freehand *with either hand*, copying drawings or cutting out paper figures.

Kimura attempts to circumvent this difficulty by proposing a distinction between spatial control exerted by external visual cues, and control by the internal body schema. Only the latter, she suggests, is the property of the left hemisphere. An immediate objection is that the spatial deficits associated with right parietal lesions go far beyond an inability to deal with external spatial relations: they can include neglect of the left side of the body and difficulties in dressing the left side of the body; and even in more severe cases, problems in dressing extending to the right side of the body as well. Moreover, these impairments are more common following right than left hemisphere lesions (Geschwind, 1965, p. 599).

Another problem is concerned with music production, which clearly shares many of the properties of speech, such as complex sequencing and fine motor control of the lips: and which should therefore involve the left hemisphere according to Kimura's hypothesis. However, left hemisphere lesions and left carotid sodium amytal injections can produce aphasia while

leaving singing ability relatively intact (Kolb and Whishaw, 1980, p. 201). Many severely aphasic patients can hum a tune or sing the words of a previously learned song (e.g. Yamadori *et al.*, 1977). If two such closely related skills as speaking and singing have different neural substrates, perhaps even control from opposite hemispheres, it becomes a bit implausible to argue that speech and manual praxis have common neural substrates, merely because they share certain properties at a highly abstract level of description.

Kimura brings forward four lines of evidence to support the idea of an intimate relation between speech and manual activity:

1. The association between hand preference and speech lateralization.
2. The frequent association between hand movements and speaking.
3. The frequent association between limb apraxia, aphasia and left hemisphere lesions.
4. The association between disorders of manual communication (signing) and left hemisphere lesions in the deaf.

The first point reiterates the fundamental problem: why are people generally right-handed and left hemisphere dominant for speech? Preference is not necessarily the same thing as skill, and there is little evidence for an association between manual skill asymmetry and speech lateralization, once differences in practice have been taken into account. Shankweiler and Studdert-Kennedy found no correlation between dichotic asymmetry and manual asymmetry for unpractised skilled tasks, although there was a clear correlation with practised tasks. The obvious point is also worth mentioning that the association between handedness and speech lateralization is far from being invariable: many left-handers have left hemisphere speech dominance and there are cases of right-handers with right hemisphere speech (Zangwill, 1960, 1979).

Kimura's second argument is the frequent association between speech and gestures, particularly by the right hand. In an observational study (Kimura, 1976) more right- than left-hand movements were found during speaking than during either silent verbal activity or humming, and speaking was accompanied by three times more right hand movements than left. Furthermore, Kinsbourne and his collaborators (cf. Kinsbourne, 1975) have shown in a number of studies that speech interferes with skilled right-hand performance such as balancing a dowel rod, finger tapping and sequential finger movements. The left hand is less affected by vocalization. Kinsbourne uses this and other evidence to argue for 'an archaic . . . relationship between language and right-sided action'. Indeed, McNeill (1985) has argued, primarily on linguistic grounds, that gestures and speech share a common computational stage (or, in more recent terms, a 'module'), and that at a deep level they are functionally equivalent.

Oldfield (1969) made the very interesting observation about left-handed musicians that they have no apparent difficulty in playing right-handed musical instruments, but do find it unnatural and difficult to conduct with the baton in their right hands. Oldfield suggests that the preferred hand has more immediate access to the individual's intentions and conceptions than does the minor hand. Peters (1981) has reported that right-handers find it easier to tap as quickly as possible with the right hand while following a beat with their left, than to attempt the reverse arrangement. Kinsbourne has argued that there is an *attentional* bias towards the left hemisphere, which explains not only why we are right-handed and left hemisphere dominant for speech, but also why we find it difficult to divide attention between speech and right-hand activity. Some recent evidence for an attentional bias is Rabbitt's (1978) observation that reaction times are faster for the right hand when the subject's response involves choice between hands, but not when all responses are carried out with a single hand.

We have mentioned the attentional theory here because it would seem to provide a way of explaining why speech and hand movements are sometimes related, without invoking Kimura's idea that they share a common neural mechanism (except in the trivial sense that they are both in the same hemisphere). It would be interesting to have evidence from left-handers, to see if gestures during speech are made with the normally preferred hand, or with the hand controlled by the hemisphere dominant for speech.

The third line of evidence Kimura uses to support her position is the association between limb apraxia and left hemisphere lesions. The term 'Apraxia' goes back to Liepmann's description of the 'Regierungsrat' case history (see Geschwind, 1967 for an historical and critical review). The important observation for present purposes is that left hemisphere lesions can produce motor disturbances in the right hand, which is to be expected, but also in the *left* hand: so called 'sympathetic' dyspraxia. This suggests that the left hemisphere has some responsibility for both hands in the case of complex movements. The disturbance can be manifested in inability to respond to verbal commands, to carry out imitation movements, and to indicate the normal use of objects by handling them appropriately. Liepmann found this syndrome frequently associated with right hemiplegia and aphasia, but never with the left hemiplegia: he explained his data by the hypothesis that the left hemisphere is dominant for more than speech — in addition it contains the memory for skilled movements.

Geschwind (1967) supported Liepmann's findings and his interpretation, and argued against the obvious alternative explanation: that the failure of the left hand is simply due to comprehension difficulty. Thus one of Geschwind's own patients failed badly on verbal commands and imitation and also did poorly on object handling, but could respond appropriately

with single word utterances to difficult questions such as 'What occupation were you engaged in before you became ill?' When asked 'Do you know how to use a hammer?' the patient responded 'Nails', but could not indicate how a hammer should be used. This view is disputed by Ettlinger (1969) who pointed out that, whilst he had been able to simulate human neuropsychological syndromes such as the agnosias by selective cortical removal in monkeys, he had never produced an apraxia, despite the obvious ability of these animals to carry out skilled activities. He then went on to consider the problem of patients with callosal sections who, as Dimond also points out, do not apparently suffer from sympathetic dyspraxia except in response to verbal commands: 'Not a single case was impaired at copying movements or using objects with the left hand, and yet such impairment would have been observed if these actions were always organised in the left hemisphere'. Ettlinger therefore concludes that the fundamental defect in classical apraxia is an inability to perform *verbal* commands, a conclusion supported by the finding of Kools *et al.* (1971) that apraxia in mentally retarded children is primarily related to defects of verbal comprehension.

The association of apraxia with aphasia is problematic. Most authors (e.g. Brown, 1972 (based on a re-analysis of Liepmann's patients), Benson, 1979; Geschwind, 1965; Goodglass and Kaplan, 1979; Heilman, 1979) agree that apraxia is commonly associated with aphasia, although all authors accept that it is relatively common to find aphasia without apraxia and less common to find apraxia without aphasia. This dissociation suggests that two separate functional processes are involved: indeed Geschwind (1955) suggests that 'the relationship is one of anatomical propinquity of lesions; the apraxia frequently accompanies the aphasia but is independent of it' (Geschwind, 1965, p. 609). This relative independence of apraxia and aphasia is also shown by the relative independence of ideational apraxia and ideo-motor apraxia, although the severity of both forms is related to the severity of aphasia, be it Broca's, Wernicke's or global (de Renzi *et al.*, 1968). Although the study of de Renzi *et al.* suggests no difference in the preferential association of apraxia with Broca's rather than Wernicke's aphasia, this has been suggested by Geschwind (1967), and would seem to be a necessary assumption if his disconnection model is to be accepted. However, in a careful study of the localization of cerebral lesions (by computed tomography) and their relationship to apraxia, no tendency was found for apraxics to have anterior rather than posterior lesions (Basso *et al.*, 1980).

A separate problem also arises with the syndrome of facial apraxia, which seems to show a closer relationship with Broca's aphasia than Wernicke's, although it is relatively independent of limb apraxia (de Renzi *et al.* 1966). Geschwind (1967) suggests that *facial* apraxia is only a special form of sympathetic dyspraxia involving a lesion of a slightly different pathway, one which lies closer to Broca's area.

Another approach to apraxia has been to study motor behaviour in individuals with right- or left-sided lesions. Heilman (1975) found that amongst right-handed aphasics with right hemiparesis, tapping rate in the left-hand was reduced in the patients with a clinical apraxia. In contrast Haaland, Porch and Delaney (1980) could find no difference in tapping rate between apractic and non-apractic patients, although they did find deficits on a task of precise steadiness. Haaland and Delaney (1981) could find no differences between right and left hemisphere lesion groups in a study of a number of motor tasks. Similarly Wyke (1971) found no convincing difference between right and left hemisphere lesions in unimanual or bimanual motor tasks, although her earlier study (Wyke, 1968) had found evidence suggesting that left brain lesions impaired contralateral movements far more than did right brain lesions. There thus seems to be a major discrepancy between clinical apraxia and inability to carry out conventional laboratory tests of lateralized motor skill, suggesting that apraxia may well involve a symbolic component which is missing from our more normal description of handedness.

Kimura and Archibald (1974) required patients with vascular accidents limited to either the left or right hemisphere to perform a number of motor tasks. There were no differences between the two groups in single finger flexions or in the copying of a static hand posture, but in the copying of manual sequences the left hemisphere group was worse, whichever hand was used. Kimura (1976) argues that the deficit was not attributable to a language impairment in the left hemisphere group, on the grounds that there was no significant correlation between scores on the aphasia battery and scores on movement copying. This is a double-edged argument, because what happens in these circumstances to the claim that speech and motor control have a common neural basis?

Critchley (1953) suggested that lesions in the left parietal lobe resulted in defects of language of gesture — *asemasia*. Goodglass and Kaplan (1963) found that gesture and pantomime were both impaired in aphasics, although they found that the gestural ability was less impaired than the pantomiming ability; there was also a correlation between severity of aphasia and severity of gestural and pantomiming defect. De Renzi *et al.* (1980) examined gestural ability in 280 patients. In those with left-sided lesions there was a defect in imitating gestures in 80% of aphasic patients and only 50% of non-aphasic patients, but a 'non-negligible minority' of 20% of the non-aphasic patients with right-sided lesions also had gestural disturbances. Kolb and Milner (1981) examined the ability to perform complex arm and face movements in patients who had had unilateral removals of areas of cortex. For arm movements the left parietal removals were more impaired; face movements were impaired by lesions of *either* the right or the left frontal regions. Thus there is a very confused picture as to the role of asymmetric neural functions

in controlling pantomime, gesture and expression. For a review see Peterson and Kirshner (1981).

A problem in all these studies and in Kimura's (1977) study is that they have been carried out almost exclusively with right-handers, so that it is difficult to decide whether the greater involvement of the left hemisphere in motor control is due to the presence of language there, or to the fact that this hemisphere controls the dominant (preferred) hand. This matter could be settled by studying a group of left-handers with left hemisphere language dominance, assessed by the sodium amytal method. If 'sympathetic apraxia' of the right hand were found after right hemisphere lesions, the view would be supported that the hemisphere dominant for handedness contains the memories of motor movements or some such: but it would argue against Kimura's hypothesis that manual praxis is closely related to speech. If the opposite result were found, that is, greater impairment of manual praxis after left hemisphere lesions, as in dextrals, Kimura's hypothesis would be supported, although it would then be something of a puzzle why these subjects should have preferred to use their left hands. Finally, the absence of a difference between left and right hemisphere effects could readily be attributed to a more bilateral representation of language, and thus of manual praxis, in the two hemispheres.

Haaland and Delaney (1981) have re-examined the problem of inter-hemispheric differences in manual praxis and have come to different conclusions from Kimura. They studied performance both of CVA and tumour groups on grip, tapping, static and vertical groove steadiness, maze co-ordination, and grooved pegboard tasks. All brain-damaged groups performed more poorly than controls on the hand contralateral to the lesion, and also on the ipsilateral hands in the case of the more complex tasks. But the pattern of results was the same in the left and right hemisphere groups. Haaland and Delaney point out that, 'The grooved pegboard task requires at least six different movements including reaching, grasping, turning and insertion . . . suggesting that Kimura's hypothesis is incorrect'.

Thus we are not entirely convinced by the evidence of a special language-related involvement of the left hemisphere in the motor control of complex sequences. Even if there were greater agreement about the facts than is the case, there would still be a problem of interpretation. Is the left hemisphere involved in both sets of function because they share some neural mechanisms, or is it just a coincidence? We have suggested that the study of left-handers is vital here, because many of them will have control of the preferred hand by the right hemisphere but speech control from the left. Another problem that has to be faced is the possible role of language loss *per se* in causing apraxic defects through comprehension deficits: Kimura's theory is on the horns of a dilemma here, because correlation of apraxia with aphasia is required to prove the sharing of neural mechanisms, but too high

a correlation is undesirable, because then it is difficult to exclude the possibility that the only underlying deficit is linguistic. A more precise formulation of the degree of overlap between speech and manual praxis would be helpful.

(4) The Attentional Theory

In a highly stimulating attack upon the laterality problem, Kinsbourne has proposed (e.g. 1975) that language and the preferred hand are controlled by the same hemisphere because there is an underlying gradient of attention favouring a turning to the right side of space.

Kinsbourne points out that evidence of behavioural asymmetry in non-human animals frequently involves an asymmetrical orientating tendency. The clearest evidence for brain asymmetry in animals comes from the study of subcortical mechanisms implicated in arousal. Glick *et al.* (1977) described contralateral circling behaviour in rats with unilateral lesions in the nigrostriatal system, and postulated that rotation in normal rats reflects an intrinsic nigrostriatal asymmetry. Subsequently it was indeed found that normal rats have a 10–15% left–right difference of dopamine content in the striatum. Marshall, Berrios and Sawyer (1980) demonstrated that dopaminergic terminals in the neostriatum are critical for orientation: unilateral neostriatal lesions reduced orientation to contralateral touch, whereas similar damage to other dopamine systems did not. Giehrl and Distel (1980) found what looks like a species-specific asymmetry in the Syrian hamster, related to the caudate nucleus. When descending from a centreboard these animals turn more often to their right than to their left (79% of occasions): the tendency was reversed after small caudate lesions.

These studies are exciting because they suggest an actual mechanism for functional brain asymmetries, rather than relying upon unobservable differences in neuronal organization. It is perhaps easier to see how a relatively simple left–right chemical asymmetry could be coded embryologically than to understand how the two halves of the brain could be programmed to develop different circuitry (for a general discussion of the embryological problem see Morgan, 1977 and Corballis and Morgan, 1978): and descriptions of new chemical asymmetries in the brain are appearing at an increasing rate, as neurochemists begin to look for them. To give another example that may have behavioural significance, Gerandai *et al.* (1979) have found a 96% left–right difference in the medio-basal hypothalamus (rat) of the hypothalamic luteinizing-hormone-release hormone. Of course, chemical differences can also underlie structural differences, a rather nice model for this being the unilateral induction of limb defects in rats by the teratogenic compound, acetazolamide.

Kinsbourne suggests that people have an inherited rightwards orientating

tendency, possibly dependent upon asymmetrical hemispheric activation from subcortical structures. A suggestive line of evidence for subcortical involvement in laterality comes from the work of Petrie and Peters (1980) of an asymmetry in the strength of the grasp reflex in infants of 17 days. Pointing out that the grasp reflex can also be elicited in anencephalics, Petrie and Peters note that, 'the possibility that the observed asymmetry is subcortical in origin cannot therefore be discounted.' (As an illustration of the frequent conflicts of evidence in the developmental literature on asymmetry, we should note that Petrie and Peters, in contrast to Caplan and Kinsbourne (1976) found no differences in the duration of rattle holding in their infants, either in unilateral or bimanual tests.)

Another piece of evidence begins with the observation of Gesell and Ames (1947), confirmed later by Turkewitz and Birch (*cf.* Turkewitz, 1977), that infants spend approximately 91% of their time lying with their head turned to the right of the body midline. There is also a tendency for predominant rightwards head turning in response to sensory stimulation, both aversive and non-aversive (Liederman and Kinsbourne, 1980). Coryell and Mitchell (1978) make the intriguing suggestion that the right turning posture tends to evoke the asymmetrical tonic neck reflex, i.e. the infant extends the limb on the side to which the head is turned. This could mean that the infant gets greater sensorimotor experience with the right than with the left hand, and Coryell and Mitchell claim that 'Knowledge of which hand an infant has had more visual experience of, as a result of its postural preference, reliably predicts the hand which will be used most in a visually elicited reaching test at 12 weeks.' It must be stressed that in considering work on early postural asymmetries there is little evidence that the asymmetry reliably predicts subsequent adult handedness. Thus the prospective study of Michel (1981) only considered handedness at 22 weeks of age. The study of Viviani *et al.* (1978) considered handedness at 7 years of age (when handedness probably correlates well with subsequent handedness; McManus, 1981a) but since only twenty-two children were followed up, of whom twenty-one were right-handed, it is clear that the significant correlation reported can only refer to degree of lateralization, and not direction. As an aside, it is of interest that neonatal head turning in response to tactile stimulation is apparently sensitive to birth stress, as assessed by the Apgar score (Turkewitz *et al.* 1968) while it is highly unlikely that handedness is related to birth stress (McManus, 1981a).

All of this supports the view that manual asymmetries may be a special case of an asymmetrical rightwards turning tendency. But where does language come into the picture? Kinsbourne offers evidence for what he terms a 'synergism' between language and right-sided motor activity:

1. While people are pondering verbal material they tend to move heads and eyes to the right.

2. When subjects think verbally while making a simple visual discrimination (gap in a line) the concurrent verbal activity biases attention in space so that accuracy is greatest in the right half visual field (Kinsbourne, 1975, Expt 1).
3. Notwithstanding the fact just described, there is interference if the subject tries to speak while engaging in skilled movements with the right hand. For instance, dowel balancing with the right hand is more affected by speaking than is the same task carried out with the left hand.

The second two points are difficult to reconcile, since one involves facilitation of right-sided activity by vocalization, and the other a decrement: but presumably the point is that speaking and visual attention do not require a common processor, while speaking and manual activity do. Once again, then, we are back to the idea that speech and skilled manual activity share the same neural substrate. The version of this hypothesis that Kinsbourne seems to favour is that speech originally represented internalized actions and still bears the mark of this archaic association (*cf.* also Reynolds, 1976). As Kinsbourne (1978) puts it:

We emerge with a model of language origins in relation to the right hand and right-sided action. We would suppose that protoman first made utterances that were coincident with and driven by the same rhythm as the movement in question. As this skill further evolved, the utterances became internalized and detached from overt action, so that they became capable of assuming a signalling role in the absence of their referents. A vast degree of further elaboration and transformation would then ultimately result in the highly intricate language systems prevalent in most human societies. However, even in the most sophisticated speaker, verbal activity is not completely free of corollary somatic movement produced on an involuntary basis.' (p. 558)

The asymmetry of speech is explained by saying that there is no need for it to have evolved bilaterally; Kinsbourne differs from most other theorists in seeing no particular advantage or disadvantage to the present arrangement, and he expressly denies that left-handedness confers any cognitive disadvantage. Speech presumably got started in the left hemisphere because of the presence there of the praxic mechanisms (*see* above quotation). The reasoning here is slightly difficult to follow, in the light of the attentional gradient, probably of subcortical origin, presumably the neural *mechanisms* as such for the control of skilled movement are present in both hemispheres: and in these circumstances it is not clear why speech should have become lateralized, unless it is just a coincidence after all.

Many of the comments in previous sections of this chapter are relevant to Kinsbourne's theory. We tend to agree with his suggestion that handedness is in origin a matter of preference (attentional bias) rather than of pre-programmed differences in skill. The argument that speech and praxis share neural mechanisms is similar to Kimura's account, which we discussed in

Section (d). Perhaps the most unusual feature of Kinsbourne's theory is also its weakest point: we refer to the denial that lateralization of *speech* depends upon pre-programmed differences in cerebral organization. The problem here is that the theory would seem to predict that it is much easier than is fact the case for individuals to learn to speak with their right hemisphere after left hemisphere damage: why should this in fact be so difficult if all that is involved is a switch in attention? The shift should be even easier for young children to effect, yet even here it seems that claims for 'equipotentiality' have been considerably exaggerated (Witelson, 1977), a problem further discussed by Kinsbourne (1978, p. 562).

A variant of the attentional bias theory is that of Gazzaniga (1974) who suggests, along with Kinsbourne, that 'structural-genetic factors' (such as the *planum temporale* asymmetry) cause the right hand to move more, and hence to explore the world more. This then results in, and potentiates, engrams being stored in the left hemisphere; as a result the right hand is used preferentially to explore the world, and hence a positive feedback results in left cerebral dominance. Nottebohm (1979) implies that motor asymmetries are present from birth, and manifest in early speech; thus in his own son he observed that early babbling tended to be associated with shifts of the tongue towards the right side of the mouth. The problem with such models is, as Gazzaniga recognised, that left-handers do not, in general, show right hemispheric speech dominance. To explain this away by saying that 'The phenomenon of left handedness is, at best, a complicated affair . . .', is, at best, special pleading.

Correlation Theories

In relation to the theories we have discussed up to now, the correlational theories stand as a null hypothesis, for they deny that there is any functional reason for the association between speech lateralization and handedness. A convenient starting point is the observation that a partial list of lateral asymmetries in man would include: left aorta distributes oxygenated blood to body, liver displaced to right, kidneys at different heights, left testicle hangs lower than right, gut coiling, and higher incidence of breast cancer on the left (for other examples of unilateral disease presentation *see* McManus, 1979). A list in animals would include: coiling in gastropods, the single Narwhal tusk on the left, the epithalamus of amphibia, ovaries of birds, migration of the eye in flat fish (for these and many other examples *see* Neville (1976) and Morgan (1977)).

Since so many asymmetries exist, why pick on just two of them — handedness and speech lateralization — for explanation? Even if we arbitrarily confine our attention to the brain of man, it is becoming clear that

speech and handedness are not the only asymmetries. In particular, there is the well-documented specialization of the right hemisphere for visuospatial processing, and possibly for music. Particularly in the tool and gestural theories, these asymmetries are considered to be secondary to speech lateralization (cf. also Corballis and Morgan, 1978) but there is no strong evidence for this, and it is motivated mainly by a philosophical prejudice that makes the possession of propositional speech the main defining attribute of mankind. If we took a more Celtic view of man as the only animal to invent new songs, or possibly a Polynesian view of man as navigator, we might come to a different opinion about which is the 'leading hemisphere'.

Thus an extreme view might be that speech lateralization and handedness are no more functionally related than, say, speech and the kidneys. On this view, the exceptional cases where they are dissociated would be like cases of isolated dextrocardia, where the heart but not the liver and gut shows reversed *situs*. A less extreme view is that the various forms of laterality may be embryologically related, without there being any particular functional reason for their association (Corballis and Morgan, 1978; Morgan and Corballis, 1978). There is indeed quite strong evidence in the case of other lateral asymmetries that they are not coded for entirely separately in development. This is illustrated by the condition of *situs inversus viscerum et cordis* in which not only the heart, but also the liver and gut, have reversed asymmetry. In amphibia there is experimental evidence that brain asymmetry correlates with that of liver and gut. Von Woellwarth (1950) studied habenular asymmetry (the habenular nucleus is larger on the left than on the right) after various treatments of the early embryo, and found that reversed *situs* of the habenular invariably correlated with reversed arrangement of the internal organs.

On the basis of this and other examples, Morgan (1977) and Corballis and Morgan (1978) argued that there may be a common source of asymmetries, possibly related to molecular chirality, and that this in general tends to favour more rapid development of the left side of the body. A considerable body of comment, much of it pointing critically to possible counter-examples, followed publication of the articles by Corballis and Morgan (1978) and Morgan and Corballis (1978) in *The Behavioural and Brain Sciences*, to which the interested reader is referred for further details.

A different correlation model has been proposed by one of us (ICM) which is related to that of Annett (1978), and in which there is more than a mere chance association of lateralities, but rather each laterality (say speech and handedness) is dependent upon a single gene. The model originates in a genetic model of handedness, in which there are two alleles, D (for Dextral) and C (for Chance). The three genotypes, DD, DC and CD produce progeny containing respectively 0, 25 and 50% of left-handers. Consider DC genotypes. One in four of these individuals are left-handed, with chance

factors alone determining which one in four is left-handed. If we allow the same gene to control speech dominance, then one in four of DC genotypes will be phenotypically right-speech dominant. If these two chance processes are independent, then one in sixteen of DC genotypes will be left-handed and right-speech dominant, six in sixteen will be cross-lateralized, and nine in sixteen will be right-handed and left-speech dominant. When one takes account of the DD and CC genotypes then it can be shown that the model can predict the observed incidences of right speech dominance in right and left-handers (*see* McManus, 1984, 1985a for a more detailed account). Here no functional advantages are required for particular forms of cerebral organization, and there is no functional similarity between speech and manual praxis; the only similarity between the two processes is that their lateralization is determined by the same genetic mechanism.

Conclusion (General)

We have considered a number of theories that try to account for the statistical relationship between speech lateralization and handedness. The theory that the association is learned has, in our view, little evidence to support it. Evolutionary theories share several common themes: that the left hemisphere has developed special mechanisms for skilled manual control; that speech and manual control share a common neural substrate; and that there is a selective advantage to the present system of inter-hemispheric differences. These claims have been considered critically. We have questioned whether the right hand, and the left hemisphere, are really pre-programmed to acquire special skills, rather than being merely preferred. We have also found little evidence, in our view, to support the speculative idea that speech and hand control share an underlying neural substrate; likewise the claim that there is a selective advantage to the present system of asymmetry. Finally, we outline the 'null hypothesis' that the relation between speech and handedness is accidental, in that it is at most a non-functional expression of a common molecular chirality acting during early development or a necessary consequence of a single gene controlling two lateralized processes.

Our conclusion is that evolutionary theories are highly stimulating; indeed, perhaps a little too stimulating, since they necessarily force us to ask (and usually, not to succeed in answering adequately) questions about the entire gamut of human language and cerebral specialization. It is perhaps not journalistic hyperbole to claim that 'All human life is there'.

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