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INTRODUCTION

In this chapter I do not intend to violate the Paris Ban of 1866 on speculations about the evolutionary origin of human language, in the sense of discussing whether human linguistic skills were initially prompted by the necessities of co-operative hunting, the division of labour, or extraterrestrial intervention. Instead, my starting point is Hughlings Jackson's discussion of the evolution and dissolution of the nervous system, which makes connections between biological evolution, the brain, and language disorders.

Jackson was a fervent and uncritical admirer of Herbert Spencer, whose metaphysical speculations are rather out of place in the modern neoDarwinian climate, and indeed Head (1926) suggests that Jackson's insistence on putting his observations in Spencerian terms led to obscurity and the neglect of Jackson's writings by his contemporaries. But Head's own championing of Jackson's clinical expertise and theoretical subtlety has meant that many of Jackson's Spencerian ideas, such as the concept of an evolutionary hierarchy of nervous centres, have not been forgotten.

Jackson, following Spencer, used the term "evolution" almost synonymously with "hierarchy": Evolution is a passage from the least to the most organised; from the simple to the complex; from the most automatic to the most voluntary-and in anatomical contexts, from the lowest to the highest centres. (See, especially, the Croonian Lectures; and other papers reprinted in the sections on "Evolution and Dissolution of the Nervous System" in Jackson, 1932). What interested Jackson most about evolution was the peculiar concept of "dissolution;" this was Spencer's term for the reverse of evolution, and the Jacksonian generalisation was that all instances of brain dysfunction could be categorised as local or uniform reversals of evolution, including in particular of course epileptic seizures and aphasia, but also encompassing various forms of intoxication and insanity. This makes very little sense in the context of the Darwinian principle of natural selection. However, as an empirical generalisation it was helpful to stress the reduction from the voluntary to the automatic in many kinds of pathology, and to separate out syndromes according to a hierarchy of nervous centres supposedly affected.

The idea that psychological symptoms resulting from organic brain malfunction represent progressive loss in a hierarchy of centres of organisation, rather than an all-or-nothing loss of discrete psychological functions, may still be a useful one. However, I wish to use Jackson's complex and elaborate theories as an introduction to two other issues: (1) the relation of human language to cognition and communication in other species; and (2) the relation of language disorders following brain damage to principles of brain organisation shared with other species. In each case I shall narrow down the issue.

In the first case it is clear that on Darwinian grounds the capacities of our closest living relatives, the great apes, should be of most relevance, and I shall therefore review the evidence on the abilities of chimpanzees to utilise artificial systems of communication, such as gesture- sign language, which they are exposed to by human intervention. This work has added interest insofar as it involves attempts to establish linguistic skills in subjects who lack them as a matter of species constitution-training methods that prove successful in these instances might be expected to suggest techniques for the rehabilitation of human patients whose organic deficits are less profound. Jackson himself frequently discussed the use of "pantomimic actions" in aphasic patients, and made the connection with the symbolic use of homologues of these in lower animals (e.g. Jackson, 1883, 1932; p.210).

In the second case, that of principles of brain organisation, I shall refer to the vexed issue of localisation of function. Jackson was a moderate on this, claiming to be neither a "localizer," nor a "universalizer" (1883/1932; p. 35), being most concerned initially with the implications of spread and sequence of epileptic spasms for the nature of motor representation in the cerebrum. But his emphasis on the separation of motor and sensory functions within each hemisphere, the separation of productive and voluntary speech in the left hemisphere with automatic and receptive processes in the right, in addition to his anatomical distinctions drawn within the hierarchy of centres, provides a framework for the discussion of the relation of speech disorders to brain function.

PHYLOGENY, COMMUNICATION, AND VOCALISATION

Insofar as language is unique to the human species, biological facts concerning other animals might be thought irrelevant. Jackson was very much aware of research such as that of Ferrier on the motor cortex of monkeys and dogs, but his interests in cross-species comparisons were confined to mammals. However, although human linguistic abilities may be unique, certain subsections of these skills may not be: Vocal production, hearing, vision, and perceptual and motor semantic organisation may be found in a wide range of species other than our own. I turn first, therefore, to the phylogenetic basis for cross-species comparisons. There should be no need to argue the point that the human species is phylogenetically closer to the apes than to any other group of animals-the only matter for debate is the precise assessment of the evolutionary distance between *Homo sapiens* and other primates in biological terms. This may be to some extent imponderable, but all physical measures indicate that, given the great psychological gulf separating people from other vertebrates, the purely biological differences between man and the great apes are remarkably minor. I shall discuss brain organisation in more detail later, but nothing has emerged in the last 100 years to invalidate Huxley's comment that the differences between the brain of a chimpanzee and that of a man are negligible by comparison with the differences between the brain of a chimpanzee and that of a small primate such as a marmoset.

Detailed biochemical investigations into the structure of haemoglobin, the immunological response to proteins from another species, and the structure of DNA, confirm the view that, if anything, apes are more closely related to *Homo* than they are to other primates (Goodman, 1974; King & Wilson, 1975). However, according to most interpretations of the fossil evidence, hominid precursors diverged from the line leading

to the anthropoid apes at least 15 million years before the present. By comparison, murid rodents (rats and mice) are estimated to have first split off from other rodent orders only 10 million years ago (Radinsky, 1976). The fact that rats and mice are a very recent type of rodent does not of course necessarily make them interesting as models for human behaviour, although it is possible that early rodents derived from early primates rather than (as do all other mammalian orders including primates) from early unspecialised insectivores (Radinsky, 1976). Next to the apes, the primates most closely related to ourselves are the Old World Monkeys, such as the rhesus macaque and the baboon, which separated from the Hominoid (apes and man) line about 40 million years ago, while the New World Monkeys (e.g. the squirrel, spider, and rebus) are somewhat more remote phylogenetically, and are guessed to have evolved from a line which diverged from human ancestry up to 50 million years ago (Simons, 1976).

If one defines communication as the transmission of information from one individual animal to another via sensory channels, then the whole range of vertebrate and invertebrate life could be surveyed, and the use of tactile, visual, and chemical signals in inter-individual exchange of information in the social insects would have pride of place. But for reasons of plausibility, as well as of space, I shall here concentrate in the first instance on the primates, within the background of communication in other air breathing vertebrates. Although isolated species of fish produce noises (usually by teeth grinding), the evolution of human speech might be said to begin with the air breathing of amphibians, about 350 million years ago. Early amphibians gave rise to reptiles, which have the phylogenetic distinction of being ancestral to both mammals and birds. One would have to go back over 300 million years to find a common ancestor of birds and primates but it would be worth paying some attention to birds on the ad hoc ground of their elaborate vocalisation. Twenty years ago birds might have been excluded from a survey of the relationship between brain function and vocalisation due to their lack of cerebral cortex, but it has become increasingly apparent that forebrain function in birds is not so radically different from that of mammals as this superficial anatomical distinction might suggest (Nauta & Karten, 1970; Karten, 1979).

Communication and Social Interaction

It is certainly part of the biological context of the evolution of human speech that many species in all vertebrate classes have well-developed forms of inter-individual exchange of information. There is a logical imperative for any vertebrate species to possess social signals sufficient at the very least to accomplish sexual reproduction, and the doctrines of inclusive fitness and sexual selection propose that the physical and psychological mechanisms involved in mate selection should have very high evolutionary priority. Systematic types of social organisation directly or indirectly related to courtship, including distinctions based on rank and territorial space, also occur in all vertebrate classes. These require more or less elaborate sets of instinctive social signals with some modification according to experience, since both territory and rank are often acquired in animals by personal accomplishment rather than by birth. It was because of the very general connection between communication and sexual reproduction that Darwin developed his own theory of the origin of human speech. That it started as singing, used to charm potential sexual partners, or to impress rivals, and only later acquired its spoken and linguistic properties (the hypothesis that propositions began as propositions: Darwin, 1871/1901, pp. 133 & 872). The eventual complexity of grammatical constructions in human languages, even the "most barbarous" ones, Darwin suggested,

should be explained by a process of linguistic evolution analogous to biological evolution.

A more widely applicable Darwinian thesis was that communication in animals could be viewed as the expression of the emotions. In the animal world the emotions expressed are usually various gradations of lust and hostility, but nevertheless there is perhaps more in common between "non-verbal" communication in man and other primates (for instance in facial expression; Van Hoof, 1972) than there is between human speech and primate cries and coos.

Auditory and Visual Channels of Communication

Of the five senses, taste could probably be excluded as a significant channel of inter-individual communication in most vertebrates. Touch is certainly a crucial proximal stimulus in sexual interactions, and hugging, stroking, grooming, biting, scratching, and so on form part of the communicative repertoire of many reptiles and mammals. Olfaction is a crude but effective method of transmitting social signals in some reptile species, and in many mammals, but is usually considered to be of relatively minor importance in primates; in general olfaction is even less important to birds than it is to primates. Clearly the vocal-auditory channel is the basis of human speech, but the visual cues of posture, gesture, and facial expression have interest as supplementary methods of human emotional exchange and social interaction. As a rule of thumb we may say that species in all the airbreathing vertebrate classes commonly make use of all four sensory channels of social communication, but the vocal- auditory channel is used for more elaborate signals in higher vertebrates (birds and mammals) than in amphibians or reptiles. There is something to be said for Spencer's (and Aristotle's) opinion that touch is the highest of all the senses, since mammalian fur and whiskers are more sensitive than the skin scales or feathers of other classes. It might also be claimed that the anatomical differentiation of the inner ear in birds and mammals, by which reptilian jawbones were converted to a mechanism for sound transmission, support the case the hearing is the most phylogenetically advanced modality.

The croaking of modern frogs and toads announces the origins of tetrapod vocalisation, and is involved in some fairly complicated rituals of male competition (one species of toad typically competes in trios, and there is chorusing in several species, but intensity and pitch are probably the main distinctive features detected). Reptiles as a class can be said to use the visual rather than the auditory channel for social communications (see below), but several species of geckos (a family of lizards) are highly vocal. Most of these are nocturnal, and either arboreal or burrow-dwelling (e.g. *Ptenopus garrulus garrulus*), which habits provide obvious reasons for developing the auditory modality, and some species go so far as to utter "polysyllabic" chirps (Stamps, 1977). Others vocalise only when paired during the breeding season, their vocalisation appearing to be primarily male device for territorial assertion or courtship. Turtles and tortoises also produce sounds but little is known of their social function: Various of the chelonians have been reported to cluck like a hen, quack like a duck, me like a cat, or whistle like a tea kettle, but no single species appears to make more than about half-a-dozen separate sounds (Carpenter & Fergus 1977). Although reptilian vocalisation is thus rather limited, neural organisation in both the peripheral and the central auditory pathways is roughly similar to that found in higher vertebrates (Foster & Hall, 1979; Mulroy & Oblak, 1985).

The vocal channel of social communication is of course more conspicuously developed in birds than it is in most mammals. The main lesson simply that a large

primate brain is not a biological necessity for perception and reproduction of human phonology, as this can be achieved by parrots and mynah birds among others. But there is an enormous diversity of innate and experiential determinants of avian vocalisation (Marler, 1970). Social learning of vocal production and auditory discrimination presumably functions for the recognition of particular individual or of individuals sharing local dialects. Young terns respond selectively to the recorded vocalisations of their own parents when only four days old (Stevenson et al., 1970); there are undoubtedly "critical periods" of early vocal learning in some species, but in others vocal learning may be very protracted. Thorpe (1972) reports that individual pairs of an East African shrike develop idiosyncratic antiphonal duets, which he presumes serve to enable the members of a pair to keep in touch even in very dense foliage. The skills of acoustic pattern recognition and complex vocal production thus not in themselves exceptional among higher vertebrates, the human species generally being differentiated more from other primates than from higher vertebrates in these respects. There are no doubt very profound differences in the mechanisms employed in the bird and human brain to produce control of vocalisation: For instance, it has been discovered the annual learning of new songs in canaries is accompanied by annual cycles of neuronal growth and degeneration (Paton & Nottebohm, 1970; Burd & Nottebohm, 1985). This is a special case but may provide a model for other relationships between brain growth and complex vocal learning.

It is conceivable that rather more vocal learning occurs in monkeys and apes than is immediately obvious (Seyfarth & Cheney, 1984). Since sounds produced by any single mammalian species are universal throughout the species and usually directly related to emotional states, it is reasonable to classify them as merely reflexive cries. In monkeys and apes (as also in domestic cats) a fairly wide range of emotional signals may be transmitted vocally—from 15 to approximately 30 sounds being categorised separately by human observers (Marler & Tenaza, 1977)—but it is not necessarily the case that primate cries never have any representational context, or external referents. Seyfarth, Cheney, and Marler (1980) suggest that vervet monkeys extend the meaning of warning cries on the basis of experience and, as adults, discriminate between warnings of "leopard," "snake," or "eagle" by adopting alternative defensive manoeuvres.

Be that as it may, such niceties do little to ameliorate the enormous disparity between primate vocalisations and human speech. In the context of primate communication, one of the most remarkable things about human spoken languages is their phonological diversity. If there was a plentiful supply of obvious linguistic universals, such as aspirated sounds at the end of vocal units always meaning a request, vowel alternations always indicating case—in other words if there were human species-specific sound-meaning universals—it would be possible to ask how these might have evolved from other primate species-specific vocalisations, rather as one can ask similar questions about facial expression (Jolly, 1972). Ignoring, for the moment, whether language expresses unique inner faculties or reason and thought, it is obvious from the diversity of human languages that vocalisation in the human species is serving radically different purposes from those accomplished by the use of the auditory-vocal channel in other primates. But it is worth noting that these unique functions of the vocal organs are accompanied by fairly minor changes in the 'vocal apparatus'. It is possible to trace changes in the human supralaryngeal vocal tract that allow for more varied speech sounds (Lieberman, 1975) but by evolutionary standards this is a trivial anatomical change. Other primate species for which intensity rather than variety of vocalisation has become important, such as the New World howler monkey, or some of the lesser apes, have developed large vocal sacs on the throat. These provide a much clearer anatomical

sign of a selection pressure than the anatomy of the human vocal organs. Similarly there are no obvious changes to the human ear, either internal or external, which are associated with the perception of speech.

The use of the visual channel for social communication may be said to be phylogenetically older than the vocal- auditory channel in the sense that visually detected social displays are common in fish, and in reptiles, as well as in birds and mammals. Perhaps the most primitive displays are colour changes in the skin-like elaborate forms of blushing. These point up the fact that although colour vision is a distinctively primate capacity among mammals, it is well developed in other vertebrate classes. Changes in the appearance of the head by extensions and colourings of dewlaps, crests, and frills are very common as social signals in lizards, and might be considered as specialised forms of facial expression. Lizards also have gestures such as submissive and aggressive circular forelimb waving, tail lashing, head bobbing, back arching, and so on (Carpenter & Fergus 1977). Therefore, lizards do not merely perceive simple colour cues but distinguish also form and movement as visual social signals. Most lizards, like most birds, have a well-developed cone-packed fovea in the retina the eye-again a feature which humans share with primates, birds, a lower vertebrates, but not with other mammals. Many birds have two fovea in each retina: the standard one in the centre, which points to the side the visual field, and an extra temporal fovea which, in both eyes, picks the central region of the visual field in front of the head. I mention this to counter the impression sometimes given in discussions of human reading that the evolution of the fovea post-dated the invention of writing, or least post-dated primate binocular vision.

Phylogeny and Pre-adaptation

The general conclusion I wish to draw concerning the use of the vocal-auditory channel for social communication is simply that human speech has a general biological context, and did not evolve in a complete vacuum. Although conventionally one separates out courtship displays in reptiles or birds as merely "innate releasing mechanisms" of a reflexive stimuli response kind, it is arguable that by these mechanisms a considerable variety of vocal or visual signals are obtained which possess a certain behavioural and emotional meaning for the animals involved. The task the nervous system, even in these nonmammalian species, in detecting and reacting to the array of possible interspecies signals, is much more complicated than a series of lock-and-key releasing circuits. One may thus claim that both the auditory and the visual modalities have a long evolutionary history as channels of social communication.

The human species patently does something quite new and different with these channels, but at the same time makes use of many pre-existing anatomical and neural devices. At any rate, the eyes, ears, and throats hominids did not have to change very radically to achieve radical results. I will discuss possible neurological changes later. However, the theme will remain that of achieving something new with pre-existing devices. One needs fingers and foveas to sight-read a piece of music on the piano violin, but the fingers and foveas we use for this purpose have a phylogenetic history even though sight-reading does not. One needs a larynx and cochlea in order to speak and understand a human language, and these bits of anatomy are inherited from other primates, even though talking is not. Some of the brain circuits between the cochlea and the larynx similarly have an evolutionary history, even if propositional speech does not.

LANGUAGE AND PRINCIPLES OF PRIMATE BRAIN FUNCTION

As many and various cognitive disorders are caused by brain dysfunction, there ought to be at least a partial overlap between theories about cognition and theories about primate brain function. Given the mysteries and complexities of brain function, one may prefer to construct psychological theories and classifications of disorders of cognition and language without reference to the primate brain, or even to the human brain (Patterson, 1981). Moreover, the relationships between primate brain function and human language might be of the kind that human cognitive and linguistic disorders have absolutely nothing to do with primate brain function, as the uniqueness of human language means that the human brain works in a completely different way from all other primate brains (Geschwind, 1965). However, in our present state of ignorance about these matters it is surely a legitimate enterprise to continue to examine relationships between human and primate brain function (Weiskrantz, 1977).

On phylogenetic grounds we would look first and foremost at primate brain function, but in many cases the same theoretical issues apply to other mammals, and in some cases, even to rats. The most general theoretical issue, which has a particular history in connection with language, but bedevils all discussion of mammalian brain function, is the question of the anatomical localisation of psychological function. It is a very old and very strong tradition to distinguish separate psychological faculties, and identify them with different locations in the body. For more than a millennium before the 17th century it was a popular view that "common sense" (i.e. supramodal perception), reason, imagination, and memory could be located in the four brain ventricles. (A 15th-century illustration in Brazier, 1979, has "virtus imaginativa" in the left lateral ventricle and "virtus cognitiva" in the right, with "sensus communis" centrally in the third ventricle and "memoria" further down in the fourth.) Clearly this was a mistaken view, but it does not follow that all other attempts at localisation are equally mistaken (cf. Fodor, 1983). In the 17th century the ventricles lost their popularity and similar mental functions were assigned to more reasonable locations in the brain: The English anatomist Willis put common sense in the corpus striatum, imagination in the corpus callosum, memory in the cerebral cortex, and motor reflexes in the cerebellum-this is not too far from what one may find in current texts (Brazier, 1979). Creutzfeldt (1979) still puts consciousness in the corpus striatum (the basal ganglia) on the "sensus communis" grounds that multi-sensory inputs from the cortex converge there. In Spencer's *Principles of Psychology* (1855/ 1899; p. 105) it is asserted that "the seat of consciousness is that nervous centre to which, mediately or immediately, the most heterogeneous impressions are brought." Jackson often quoted this passage, although he himself located the "substrata" of consciousness in the cerebral hemispheres fairly generally, with different kinds of consciousness in different places (Jackson, 1931; p. 152). Penfield, however, when quoting the same passage from Spencer, deduced that the seat of consciousness was in the thalamus-this is Penfield's "centrencephalic" theory (Penfield & Rasmussen, 1950; p. 235; also Penfield & Jasper, 1954; Penfield & Roberts, 195 p. 247).

The first experimental basis for the anatomical localisation of function was the discovery of the separation of sensory and motor pathways into the dorsal and ventral roots of the spinal cord, made independently by Charles Bell and Francois Magendie. This holds for all living vertebrates with the exception of very primitive fishes such as

the lamprey, whose spinal cord was the subject of Sigmund Freud's first publications, ten years prior to his work on aphasia (Suloway, 1979). (Bell had clinical interests and travelled to Spain in 1809 and Belgium in 1815 to study and treat the effects of gunshot wounds sustained in the battles of Coruna and Waterloo.) Extensive experimentation on laboratory animals took place in the 19th century in parallel with the localising claims of clinicians such as Broca and Wernicke: Ferrier's *The Localisation of Cerebral Disease* (1878), based largely on his experiments with monkeys and dogs, was accepted as conclusive by Jackson among many others, but controversies concerning cerebral localisation continued, as between Goltz and Munk over the visual functions of the occipital lobes (Weiskrantz, 1972). To a degree, these have continued to the present day, since there are some such as Barlow (1972, 1985) and Konorski (1967) who put forward theories in which individual neurons are supposed to have specific cognitive functions, while others (Anderson, Silverstein, Ritz, & Jones, 1977; Wood, 1978, 1982) would not only prefer to avoid giving individual neurons specific functions, but are prepared to support the extreme proposal (Lashley, 1950) that "all of the cells of the brain, are participating, by a sort of algebraic summation, every activity. There are no special cells for special memories (p. 477)."

It certainly seems unlikely that a particular neuron should be responsible for a particular psychological property, since a single neuron can do hardly anything on its own. But the notion that all neurons participate in all brain activities, even if logically possible, is in conflict with much empirical evidence that particular neurons do indeed do particular things in mammalian brains (Sperry, 1958; Hubel & Weisel, 1977; Cowey, 1979; Zeki 1978; Kaas, 1982; Perrett et al., 1985). I shall review in the next section evidence of a conventional kind, that stimulating or lesioning specific locations in the primate brain has particular effects on vocalisation. The assumption behind this, of course, is that identifiable processes in the nervous system can be tied to these known anatomical locations. But this assumption is not necessarily incompatible with the notion that *psychologically* defined functions are achieved by serial and parallel and "distributed" sequences of brain circuits, and that it is therefore unwise to imagine that a psychological faculty resides at a particular geographical address in the brain.

Consider for a moment the metaphor of a pair of trousers held up by a pair of braces (suspenders) as well as a belt, each alone being just about sufficient to keep the trousers in place under normal conditions of physical exertion. Where is the function of "holding up the trousers" localised? If we remove both the belt and the braces, but the wearer is sitting or lying down, the trousers stay up anyway, and the supports may thus seem unnecessary (some vertebrates may survive, if hand fed, after the removal of the entire forebrain). On the other hand, if the wearer is standing, and we leave on the belt and braces, but cut all around the trousers below the belt, these garments, to all intents and purposes, fall: even the belt and braces together are not sufficient (optic nerve damage may blind). If we first remove the belt, and then simply snip off the buttons, to which the braces are attached, a dramatic failure of normal trouser stability may ensue—to what extent does the "holding up" function therefore reside in the buttons?

One could go on. The point is that the relationship between the presence and absence of structures, and their possible functions, may be logically complex, and the brain is at least as complicated as the belt and braces system. *But* this does not mean that it is foolish to say that trousers can be held up by belts or by braces, or that these localised items contribute in some way to the behaviourally defined function of holding up. To gather additional evidence for such assertions one might wish to perform more carefully controlled experiments involving the removal of the belt and/or braces under a variety of conditions of physical exertion, but the anatomical position of these physical structures,

in relation to the trousers, by itself strongly suggests an anti-gravity effect. Similarly, in the vertebrate and mammalian brains, anatomical layouts alone virtually ensure some degree of functional specialisation: It might technically be possible to build a robot in which all inputs and outputs are randomly scrambled at a short distance from the sensory and motor peripherals, but brains are not like that. However, as the trousers metaphor indicates, and as discussed in some detail by Jackson (and also by Luria, 1974), it is *components* of functions rather than whole functions which are localised. While the holding up function is clearly distributed both within and between the belt and the braces, it is nevertheless the case that individual functional components of the system are discretely localised—for instance at the buckle and the buttons. Obviously there are limits to the applicability of this metaphor, but it is at least arguable that in the same way, although it would be misleading to claim that a behaviourally defined function in its entirety (e.g. vocalisation), resides at a single location in the primate brain, it is still possible that there are discretely localised brain structures which serve particular components of that function (e.g. premotor and motor cortex, the extrapyramidal motor pathway, and brainstem nuclei which feed the tongue, larynx and lips).

In Jackson's words, it is the "nervous arrangements," rather than psychological entities, that are anatomically discrete. Given this, there are three simplifying dimensions of brain localisation which, as used by Jackson, correspond roughly to the orthogonal axes of the primate brain. First is the up-down hierarchy, from medulla to cortex, but with some parts of the cortex being defined as higher than others. Second is the left/right lateral division of functions between the hemispheres, and third is the "front-to-back" dimension, often stressed by Jackson because it was the relatively novel, with movements and motor organisation in the frontal lobes, and sensory and perceptual functions generally in the rear of the hemispheres.

Hierarchical Control of Vocalisation in Monkeys and Apes

There is a large recent literature on several aspects of primate vocalisation (Steklis & Raleigh, 1979; Sebeok, 1977; Seyfarth & Cheney, 1984) but many ways the most pertinent review for present purposes is that by Ploog (1979), in which a very Jacksonian scheme is put forward involving low middle, and higher levels of neural control of voicing in primates. Ploog's conclusion is that only in the human species is the highest neural level actively involved in the "vocal signalling process," this highest level being localised as the premotor cortex adjacent to the motor representations of the larynx, face, and throat. A corollary of this conclusion is that for human speech is voluntary, sub-human vocalisation being assumed to be emotional and automatic. Thus those aspects of human phonation which are primarily emotional and automatic — crying, shrieking, moaning, screaming, groaning, giggling, grunting, and so on — have more in common with subhuman vocalisation than does articulate speech. Ploog (1979) conjectures that: "the brain mechanisms of vocalisation which operate in the monkey are homologous to those in the human neonate (p. 95)."

In terms of the more peripheral aspects of human voice production, human speech differs from primate vocalisation mainly in the use of supralaryngeal cavities to produce a greater variety of vowel sounds, and the correspondingly decreased importance of sound production during inhalation. An inhaled hiss may indicate a number of signalled emotions between people, from pain to wonder, but vocalisation during inhalation in *Homo sapiens* could be completely ignored without serious loss of information. By contrast, three of the most frequent chimpanzee vocalisations, the pant-hoot, the pant-grunt and "laughing" are typically made both during inhalation and exhalation and, although data

is scarce, it is probably that inhalation is used to produce phonation even more often in the orang-utan than it is in the chimpanzee or gorilla. One orang sound, the "kiss-squeak" is usually produced by sucking through pursed trumpet lips, but some (wild) animals have been observed making a similar noise by sucking on the backs of their hands (MacKinnon, 1974; Marler & Tenaza, 1977). Although observed phonation in the apes (and in other primates) thus has little in common phonetically with human speech, Lieberman (1977) suggests that the external apparatus in apes would be capable of producing a wide variety of phonetic features (voiced/unvoiced, glottal stops, and the consonants, b,p,d for instance). But any nonhuman primate would have to make do with one unspecified vowel. In practice, human observers usually distinguish only a couple of dozen distinct vocalisations at most, in a given primate species, and give them generic labels such as "bark" or "pant hoot" - but this does not deal with the possibility that many gradations within the human categories may be distinguished by the animals concerned.

It should be remarked that practically all of the neuroanatomical work, and most of the behavioural observation, has been done with species other than the gibbons, which are in many ways the most interesting group as far as the evolution of language goes. For the half-dozen species of gibbon, and the Siamang (Tembrock, 1974): "The peculiar structure of the voice apparatus, with an accessory vocal chord, the complete closure of the glottis, the formation of the aryepiglottic folds similar to *Homo*, the m. thyreoideus transversus impar and the extension of the m. cricoarytenoideus give rise to a voice unusually capable of modulation (p. 177)." This is apart from the large air sacs used by the black gibbon and the Siamang. All these lesser apes share with birds a highly arboreal habitat and a social structure based on the two-parent pair bond. Perhaps because of this, they all sing. The songs are made up from repetitions of elements in "stanzas," and repetitions of stanzas in songs, and are thus syntactically more complex than most other nonhuman primate vocalisations. Social co-operation in vocalisation is also complex. In all species of gibbon studied (except Kloss's gibbon) there is duetting, or antiphonal singing, between mated pairs. In the pileated gibbon, the Siamang, and the hoolock, the male and female songs overlap, but in the other species (the white-handed and dark-handed gibbons) the male and female strictly alternate. This "turn-taking" is facilitated by special signals-in the white-handed gibbon (Marler & Tenaza, 1977): "the female signals her readiness to sing by uttering a series of short monotonous notes. When she begins her full song the male normally stops singing until she has completed it, whereupon he adds a short coda, then pauses for several seconds before starting to sing again (p. 1007)."

In Bornean gibbons the male's role seems to be limited to adding the short coda at the end of female songs, and in the Siamang the male sings only stereotyped phrases which overlap with certain portions of the female song. In hoolocks both male and female produce more or less the same sounds, but the male sings in a lower pitch. There are thus large differences in singing style between these closely related species (which often interbreed in captivity), but there is also a considerable degree of variation both within and between the performances of individuals. Apart from male- female duets, the other main occasion for singing is chorusing between neighbouring males, in which individual variations no doubt serve for inter-individual recognition (Marler & Tenaza, 1977). In Kloss's gibbon (the only species without male-female duets), the male pre-dawn chorusing is typically followed by *four hours* of all-female choruses, after the families have left their sleeping trees. Apart from all this, gibbons have a more typically primate selection of food-sighting cries, warning barks, play squeals, and copulatory

grunts. One presumes that the central nervous system requirements for the control of vocalisation in these primates is somewhat greater than average.

Leaving aside the gibbons, on which virtually no neuroanatomical studies seem to have been performed, there is a fairly clear set of conclusions derived from experiments on the larger apes (usually chimpanzees or gorillas) and on laboratory monkeys such as the squirrel monkey (New World) and the rhesus macaque (Old World), which have been reviewed by Jurgens (1979) and Sutton and Jurgens (1985) as well as by Ploog (1979). The main points of these conclusions are that: (1) the basic neuroanatomical pathways for the control of vocalisation are roughly similar in man and other primates; (2) other primates apart from *Homo sapiens* do not make use of the highest levels of their available neuroanatomy in the course of species-specific vocalisations. Three kinds of evidence to support these points may be quoted: neuroanatomical structure; the elicitation of movements or vocalisations by electrical stimulation of the brain; and the effect on vocalisation of various brain lesions. A potentially valuable source of evidence would be electrical recording (or other intra-cranial forms of measurement) during vocalisation, but comparatively little work of this kind has been reported.

Electrical Stimulation

"Artificially induced discharge of what in the monkey is homologous to Broca's region, produces movements of the tongue, palate, lips, etc. (Jackson, 1883/1932; p. 205)." This refers of course to the electrical stimulation of the regions of excitable motor cortex related to the face and throat, which are in the same relative position-at the bottom of the motor strip-in all mammals. Vocal fold movements can be elicited from points in this area (the inferior precentral gyrus) in the chimpanzee (Leyton & Sherrington, 1917), the rhesus monkey (Hast, Fisher, Wetzel, & Thompson, 1974), and the squirrel monkey (Jurgens, 1974). There is thus no doubt that the bottom of the motor strip in primates is associated with outputs which would be useful in vocalisation, but whether they are normally put to this use in nonhuman primates is another matter. Emphasis is usually given to the fact that, although motor strip stimulation may produce isolated lip and laryngeal movements in experimental animals, it seldom, if ever, prompts actual vocalisations. The contrast is then drawn with Penfield's finding that in human patients "occasional growls or grunts" and sometimes a vowel cry, are made involuntarily during stimulation at the bottom of the pre-central gyrus. (And with stimulation at the bottom of the post-central gyrus: In both cases the effect may occur in either hemisphere.) It would hardly be surprising if the human motor cortex was found to be more sensitive in this respect than that of other primates, but no such conclusion can properly be drawn from the stimulation studies just cited, since all the animal work was done under anaesthetic, while in Penfield's work the human patients were awake (Penfield & Rasmussen, 1950/57; e.g. pp. 88-89).

Electrical Stimulation-Supplementary Motor Area

Penfield obtained involuntary cries from awake human patients both by stimulation of the Rolandic facial region (bottom of the pre-central motor strip, as above) and by stimulation within the longitudinal fissure between the hemispheres, anterior to the central fissure, and just above the cingulate gyrus. (Again, even in human patients, this kind of phonation occurs equally often from stimulation of the right and left hemispheres.) Other motor effects were also observed in this region, and on the basis of experimental work with various mammalian species, the longitudinal fissure is expected to contain the "supplementary motor area"-a second map of the body surface, smaller than that on the main motor strip, and having more bilateral effects (Kruger & Stein,

1973). However, the cingulate gyrus, just below this secondary motor area, is classified as "limbic." For present purposes, the interesting thing about this limbic/ supplementary motor region is that stimulating it reliably produces vocalisations in monkeys (rhesus and squirrel: Jurgens & Ploog, 1970; Jurgens, 1979).

Electrical Stimulation-Subcortical Structures

The supplementary motor/cingulate regions of the frontal cortex are certainly not the only parts of the brain from which vocalisations in monkeys may be obtained by the technique of electrical stimulation. Stimulation of many parts of the limbic system, and of brainstem nuclei (in particular, the inferior olive, adjacent to the auditory nuclei of the superior olive) results in phonation, with certain types of vocal call "localised in certain sets of structures (for the squirrel monkey; Jurgens, 1979; 1982)." Shrieking and groaning seems most likely to come from a circuit based in the stria terminalis, and growling from a rather similar set of (limbic) locations, but cackling appears to follow a different path, starting in the cingulate region and continuing down through the thalamus; while chirping is evoked from five separate areas, including the nucleus accumbens, the rostral hippocampus, and the inferior olive. Broadly speaking vocalisation is most likely to be produced by the application of current to electrodes placed in the limbic system. Clearly this raises the question of whether the cries so produced are an indirect result of the induction of motivational states-the shrieks and growls resulting from current applied to the amygdala might well be associated with pain or anger, since lesioning this area produces animals which, on more general behavioural grounds, are judged to be extremely placid, and relatively insensitive to pain. It would of course be expected that species-specific and innately determined emotional signals should be closely linked anatomically with other aspects of the emotions. In fact Jurgens (1976, 1979) found that the majority of his sites which were implicated in the elicitation of cries of any kind also gave rise to intracranial reinforcement effects (i.e. the animals would turn the stimulation on or off themselves, if given the opportunity to do so). The only sites from which vocalisation could be evoked without such obvious emotional connotations were in the cingulate gyrus, or thereabouts, or in the midbrain ("caudalmost periaqueductal grey"), as if emotionally neutral vocalisation circuits were emerging from the top and bottom of the limbic system (Jurgens, 1979; pp. 16-17, 22-25).

Anatomical Pathways for Vocalisation

Anatomical pathways are inferred from various kinds of evidence, all involving a margin of histological error. However, it seems probable that the output pathways utilised in human vocal production are not very different from those present in the chimpanzee, and many features of the human neural circuitry are characteristic also of monkeys. The limbic system and motor pathways through the basal ganglia are undoubtedly involved in both human and primate vocal output. (Fairly severe speech difficulties can occur in connection with disturbances of the extrapyramidal route through the basal ganglia in Parkinsonism: See Lamendella, 1977, for a review of the limbic system and language). In addition to the extrapyramidal pathway, it appears that both in man and in the chimpanzee there is a direct route from the larynx representation in the pre-central motor strip to the nucleus ambiguus in the medulla (from which branches of the vagal nerve supply the larynx, and branches of the hypoglossal nerve the tongue: Kuypers, 1958a, 1958b). But many of the fibres do not run in the main pyramidal tract output of the motor cortex. No direct route between the "cortical larynx area" and the cranial nerve nuclei is thought to exist in the squirrel monkey (or in the

cat), and it is doubtful whether this direct route, observable both in the chimpanzee and the human brain, is shared by the rhesus monkey (Jurgens, 1979). However, many primate species may make use of peripheral feedback circuits with access to sensory input from the larynx (Jurgens & Kirzinger, 1985).

It would be unwise to consider vocal output pathways to be independent of auditory input, but there is no anatomical evidence at present to suggest that the human auditory pathways have become structurally specialised for speech perception. Other primates do not appear to have difficulty in discriminating the phonetic features of human speech: Indeed it has been shown that even chinchillas (rodents) are quite capable of the "categorical perception" of alveolar stops (Kuhl & Miller, 1975; Waters & Wilson, 1976). Ploog (1979) reports that the anatomical substrate for what must be a basic relationship between speech production and speech perception is present in the squirrel monkey: There are some cells in this species' auditory cortex which do not respond to self-produced calls (even those artificially elicited by brain stimulation) but which respond to tape recordings of the same sounds. Recent anatomical work suggests that there is a very high degree of organisation within auditory cortex at the neuronal level, probably comparable to that found by Hubel and Weisel (1977) in visual cortex (Mitani et al., 1985; Winer, 1985).

The Effects of Cortical Lesions on Primate Vocalisations

We should not take it for granted that lesioning any given block of human cerebral cortex would necessarily have a predictable effect on speech. However, it is a safe generalisation that lesions of frontal motor cortex are quite likely to produce speech output difficulties in human patients, especially if they are large, and surround the inferior precentral gyrus in the left hemisphere. Greater specificity of prediction may eventually become possible (Naesser, Hayward, Laughlin, Becker, Jernigan, & Zatz, 1981). A number of experiments have been performed to assess the effect on vocalisation in nonhuman primates of lesions in their frontal motor areas-"Broca area homologues" (Aitken, 1981; see also Sutton, Larson, & Lindeman, 1974; Franzen & Myers, 1973). Often included in the same experiments are "Wernicke homologues"-that is, lesions centred on the superior temporal and/or inferior parietal regions. The results of these experiments are often difficult to interpret, for a number of reasons, including uncertainties involved in selecting the "Broca and Wernicke homologues." However, four tentative generalisations have been made (Jurgens, 1979; Ploog, 1979; Sutton & Jurgens, 1985):

1. Very large bilateral lesions of the frontal lobes may severely impair both vocalisation and other social behaviours in monkeys (Franzen & Myers, 1973; Green & Walker, 1938).
2. Small bilateral lesions of the frontal or temporal lobes do *not* impair vocalisation in monkeys (Aitken, 1981; Sutton et al., 1974).
3. Small bilateral lesions of the cingulate/supplementary motor regions may very severely impair vocalisations in monkeys under some circumstances (Sutton et al., 1974; Sutton, Samson, & Larson, 1978; Sutton, Trachy, & Lindeman, 1981a, 1981b; Aitken, 1981) and this "limbic" area may therefore be needed for volitional control of vocalisation (Jurgens, 1985; Tanji, 1984).
4. Large bilateral lesions of the superior temporal lobes significantly impair the auditory discrimination of species-specific calls (Hupfer, Jurgens, & Ploog, 1977).

Brain Mechanisms and Primate Vocalisations-Conclusions

Ploog's hierarchical theory of the brain mechanisms involved in primate vocalisation, put forward on the basis of the kinds of evidence described earlier, can be paraphrased as follows. Instinctive and species-specific cries can be accomplished with the necessary co-ordination of the vocal organs occurring at the lowest levels (midbrain and medulla). The correlation of vocalisations with emotional states is developed in the limbic system. Of particular interest in primates is the cingulate/supplementary motor area within the longitudinal fissure, categorised as "limbic," which has to do with "readiness to vocalise" (Ploog, 1979) or is the "voluntary call initiation area" (Jurgens, 1979, 1985) in both monkeys and man. The highest level in this model is the neocortex surrounding and in front of the facial and laryngeal parts of the pre-central gyrus, which is used for "voluntary call *formation*" and is thus significantly involved in vocal signalling in only the human species. This is not unlike Jackson's (1883/ 1932) speculation:

I suppose that the motor nervous arrangements of Broca's regions which are correlative with what are psychically words have arisen out of those for the "common place" movements of the tongue, palate and lips and have become greatly or completely detached from the latter and then serve, not for their own ends, but stand for operations. . . . If so Broca's region, in man, differs from the homologous part of a dog in their being in it more specialised, new, nervous arrangements in addition to what we may call the ordinary or old ones (p. 209).

BRAIN MECHANISMS AND HUMAN BRAIN DAMAGE: EVOLUTION AND DISSOLUTION

In one sense, the way in which mammalian brain mechanisms are discussed by Jackson, and by modern comparative anatomists, simply reinforces the naive theories of the localisation of psychological functions put forward by Bastian and the other "diagram makers" (e.g. Bastian, 1898) who were so chastised by Head (1926). On the other hand, Head was able to use Jackson's writing as a stick to beat the diagram makers with, since Jackson's theories are anything but naive (and he refrained from drawing diagrams). Although Jackson (1882/1932) claimed "I am neither a universaliser nor a localiser (p. 35)" he noted that he was attacked as both, and he can be quoted in support of both. The reason for this paradox is that Jackson argued for the localisation of multiple and various physiological components of brain mechanisms which accomplish psychological functions, rather than simplifying the localisation to unitary "speech centres," "writing centres," and so on. He emphasised not only multiple localisation in his evolutionary up-down hierarchy but also, of course, multiple localisation across the hemispheres (the left being for voluntary expression of propositions, the right for automatic expression and propositional reception), and the anterior/posterior separation of motor and sensory centres.

Arguably, this means that Jackson was different from the diagram makers in being *more* of a localiser, rather than less. The Jacksonian theme is that *everything can be separated out*: The voluntary from the involuntary and automatic; the propositional from the nonpropositional; the receptive from the expressive; representations from re-representations; muscle coordinations from intentional movements. The more it is the case that the physiological components subserving cognitive functions are separated out in the brain, the more likely it is that brain-damaged patients will present with peculiar permutations and combinations of psychological symptoms. Very few, apart from Lashley, have been prepared to maintain that the particular permutation of psychological

symptoms resulting from brain damage has nothing whatever to do with the site (almost always, of course, sites) of the damage. Brain (1965) points out that even Head (although Head was virulently opposed to anatomical centres for functions) becomes "involuntarily a psycho-anatomist" by clearly attributing each of his own four types of aphasia to four kinds of cerebral damage, in a way which is roughly comparable to the theories of the much-abused diagram makers.

According to Head (1926): "Verbal aphasia is more particularly associated with injury to the foot of the precentral and neighbouring gyri"; "syntactical aphasia is associated with lesions in and around the upper temporal gyri and the parts beneath them"; "A lesion situated in the left hemisphere between the post-central fissure and the occipital lobe (i.e. in the parietal lobe) tends to affect more particularly the meaning and categorical use of language"; and "When the lesion lies in the neighbourhood of the angular gyrus and the parts beneath it the defects of speech are liable to assume a nominal form (pp. 500-502)." Lord Brain himself gives a straightforward anatomical account for all the disorders of speech and writing which he discusses. Similarly, Luria (1974) accuses Head of preserving "the same principle of *direct* relation of language and brain (p. 4)" but Luria is willing to attribute "motor aphasia" to "disturbances of the lower part of the premotor zone of the major hemisphere" and to attribute the acquisition and use of "reversible grammatical structures" to "tertiary zones of the parieto-occipital parts of the cortex (p. 7)" (see Arbib, 1982, for a Jacksonian critique of Luria).

Head's (1926) own explanation of why "manifestations differ according to the site of the lesion" is that "Such topographical associations come about because particular parts of the brain were already required for some lower function, which played a part in the evolution of one of the many aspects of the use of language (pp. 431 & 502)." There is thus a considerable measure of agreement, even among those ostensibly opposed in principle to excessive claims for localisation, that the localisation of physiological components of the human brain, which is a result of evolutionary processes and can be predicted from the study of the brains of other primates, determines the way in which "manifestations differ according to the site of the lesion" in human brain damage. The largest measure of agreement is probably for the up-down dimension of the Jacksonian hierarchy: No-one doubts that bulbar paralysis of the face and throat results in a speech deficit that has different psychological connotations from those of a speech deficit resulting from an infarction around the left middle cerebral artery. Left/right localisations are nothing like so robust, but there is no doubt that the lateralisation of cognitive functions is clinically important, even though the biological basis for this remains obscure (Denenberg, 1981; Walker, 1980, 1981, 1985).

The most contentious of the Jacksonian dimensions, but one with many implications for cognitive neuropsychology, is localisation from front-to-back of a given hemisphere. The main evolutionary constraints on this have been known for approximately 100 years, but it is worth saying that the accumulation of evidence concerning mammalian brain function has continuously strengthened the original rough generalisations, even though we are still ignorant of many neuronal details. The first constraint is that the frontal lobes are predominantly motor whereas the temporal, parietal and occipital lobes are distinctly sensory, containing clearly separate auditory, tactile, and visual inputs, respectively. It is hard to imagine ever knowing quite why the occipital lobe receives a visual input, but the temporal lobe an auditory one, *but* we can say beyond a shadow of doubt that the reason why the human occipital lobe receives that optic radiation is that we are primates, and that this is what happens in primates. And the reason why the occipital lobe is visual in primates is that primates are mammals, and there is an optic radiation to the rear of the hemispheres in all mammals (Kaas, 1980).

Similarly, the reception of heard speech is initially in the temporal lobe, despite the uniqueness of human auditory requirements, because that was the immediate possibility offered by the primate brain. Although one might have supposed that the uniqueness of human linguistic demands on the modality of hearing, presumably over a long period, should have entailed the evolution of major departures from the typical primate plan, anatomically the departures are not very radical, either in the temporal lobe or anywhere else (Passingham, 1979, 1982; Walker, 1985). Where uniquely human elaborations of primate organisation can be guessed at, they appear to conform to the general principles of the mammalian system.

The most obvious instance is of course "Broca's area." Broca's original claims may have been excessive, but the clinical consensus surely remains that a large loss of tissue somewhere in the neighbourhood of the bottom rear quadrant of the left frontal lobe is likely to have a deleterious effect on speech output processes. It is clearly no accident that this region is adjacent to (and includes) the face and throat parts of extensible motor cortex (i.e. is close to cortical output to face and throat: Levine & Sweet, 1982). Hence Jackson's hypothesis that the serial co-ordination of the combinations of movements required for vocalisation are in some sense localised here. The argument is that other mammalian species do not possess nervous arrangements for the learned modifications of precise forms of vocal output (or for any grammatical structuring of this output) but that if they did, this is where they would have to start.

By and large, this sort of very coarse localisation of what Head (1926) called "lower functions" is relatively unproblematical, provided that the existence of multiple motor representations in the up-down hierarchy is not forgotten. In some way the striate cortex is involved with visual reception rather than vocal output, even though vision as a psychological function cannot reside in the striate cortex exclusively, and in some way the bottom of the frontal motor strip is involved with vocal output rather than visual reception, even though the frontal cortex is only one level of motor control-these are statements which apply to all primate species. And these constraints alone would be sufficient to account for profound deficits in speech (but not necessarily vision) in anyone deprived of the front half of both hemispheres, no matter how soon in life (and therefore how much time was allowed for brain plasticity to make itself felt) the deprivation began (e.g. Vargha-Khadem & Watters, 1985).

But what of the "higher functions"-the formation of propositions, syntactical organisation, and the understanding of the meaning of a sentence? As these apply only to human capacities, is there any point in even attempting to relate them to primate brain mechanisms? In many cases probably not, but consider the example of higher functions in vision, in particular in reading. First, whatever brain peculiarities may have arisen during human evolution, they most certainly do not include specialisations for reading as such, since the vast majority of all human generations, at least until the last one or two, have been illiterate. When we look at letters, we cannot use anything that has evolved for that purpose. Conceivably a million years or more of naming seen and unseen objects, and more generally applying vocalisation to the perceived and imagined world, has had anatomical consequences, but grapheme-morpheme and grapheme-phoneme correspondences can only make use of these much more general mechanisms for auditory/visual correlations. In evolutionary terms, therefore, there is something odd about Charcot's famous diagram of the 1880s, which includes a visual centre for reading words (and a graphic motor centre for writing them) as useful items built in to the human central nervous system. However, if we were to suppose that a general purpose primate brain had to undertake the task of decoding script, we should expect it to make use of fairly nontopographical combinatorial mappings in the extra-striate cortex for

detecting graphemes and for detected graphemes to be put in correspondence with phonemic motor instructions somewhere in the frontal lobe. Morphemic matters would have to be dealt with much more diffusely, and even for this the brain would need a separate set of motor instructions for writing, near the arm rather than the mouth regions of the pre-central motor cortex. We should in fact end up with something not unlike Charcot's diagram, or Lord Brain's version of it with labels for auditory phoneme schemas and graphic letter schemas (and word-meaning schemas and sentence schemas). On the basis of primate cortical layout, it would not surprise us that many different aspects of visual analysis and synthesis necessary for reading had different locations in the extra-striate cortex (in the parietal and temporal as well as occipital lobes) and that some localised lesions therefore had highly specific and separable effects on reading and writing (Cowey, 1979; Barlow, 1985; Diamond, 1979; Mansfield, 1982; Merzenich & Kaas, 1980; Kaas, 1982).

As specific mechanisms for reading and writing cannot be "given by inheritance," general features of the primate brain can plausibly be put forward as alternative principles of organisation. But both in terms of the plasticity of any individual's output, and in terms of an innate human grammar, speech, as opposed to writing, may be thought to have acquired the evolution of specialised mechanisms in the human brain beyond the predictable primate pattern. As far as plasticity goes, the most remarkable thing about human spoken language (from the point of view of comparisons with other species) is the existence of comparative linguistics. In other species, things that, in Jackson's words, are "given by inheritance" are usually very stereotyped, and this applies to species-specific vocalisations as well as to other behaviours. The observer from Mars, anticipating the emergence of propositional speech from primate calls, would surely have expected that syntax should be species-specific-in other words that linguistic universals in human speech should be very much more obvious than they are in fact. Even if anticipating some hominid enterprise with the same consequences as the Tower of Babel, to cause speech in different human populations not to be mutually comprehensible, the Martian primatologist could be forgiven if he or she predicted frequent cross-language regularities-such as gender always having similar grammatical implications, or word endings or vowel alternations always having at least roughly the same kind of grammatical significance. But, by comparison with the instinctive behaviours of animals or human emotional expression, the symbolic and referential use of language appears to be almost completely free of such inherited constraints (Greenberg, 1966; Swadesh, 1972; Comrie, 1981; Waldron, 1985).

If it is the case that the "commonplace movements" of the tongue and lips have become widely symbolic, then it appears that almost any movement of these organs can stand for almost any symbolic operation. One inference that could be drawn from this is that although the complex set of rules required for motor output of a specific human language are likely to require the successful functioning of extremely powerful combinatorial motor mappings, whatever it is that is innate about meanings and propositions, linguistically expressed, cannot be tied up exclusively with motor speech output. If all human languages signified plurality by putting an "s" sound on the end of words, then one might suppose that the anatomical idea of plurality was localised in Broca's area, and in close association with the movements required to say "s's." As human spoken languages are prodigiously variable, even for such basics as the denotation of sex and plurality, it seems possible that within the vocal-auditory channel general purpose aspects of primate brain function and cognition influence the human use of language, in addition to any uniquely evolved mechanisms for speech.

TRAINING CHIMPANZEES IN SYMBOLIC COMMUNICATION

Much time and effort has been spent over the last two decades in attempts to demonstrate that the general purpose cognitive capacities of the chimpanzee brain are sufficient to achieve a significant degree of linguistic competence, if the chimpanzees' natural inclinations are diverted by human intervention in the form of extended training with artificial systems of signs or gestures. If human evolution was accompanied by very radical changes in brain function associated with the use of language, then one would not expect very much of chimpanzees, however much time was spent on their education. If, on the other hand, human language is a new way of utilising an already existing brain design, then it is conceivable that the chimpanzee brain might be coached well beyond its normal limits.

The results of coaching efforts of this kind have been described and discussed at length (Gardner & Gardner, 1969, 1971, 1985; Premack, 1970, 1976; Savage-Rumbaugh, Rumbaugh, & Boysen, 1978a; Passing-ham, 1982; Walker, 1985). The most familiar technique is the training of chimpanzees in gestures based on the American Sign Language system developed for use by the human deaf. It is appropriate here, therefore, to refer to Jackson's theories about "pantomimic actions." Jackson distinguished pantomime from gesticulation, since the latter is more automatic and emotional, and not necessarily voluntary, and is therefore lower in the hierarchy. He seems to mean "pantomime" partly in the sense of gestural acting out, but also as anything which is referential and symbolic: Pantomimic actions are propositional and are sometimes severely impaired in aphasia. In other cases, loss of speech is due to more limited damage to middle and lower centres, leaving words still available for internal use in mentation. There are also, Jackson supposed, "arbitrary images," unlike symbols derived from words or from pantomimic actions, which allow us to have mental processes corresponding to the proposition "gold is yellow," simply by "thinking that a gold thing is a yellow thing" (Jackson, 1883/ 1932; p. 210). Clearly, if one believes that chimpanzees have mental processes which correspond to the proposition "bananas are yellow," one would hope to be able to train them to make communicative gestures to the same effect. Jackson's discussion of the evolution of reasoning and of the importance of "visual and tactile ideas and words" is involved and Spencerian, but there is a fairly direct assertion about animal mentation (Jackson, 1883/1932): "Since lower animals think, it may be asked 'What are their symbols?' if symbols are necessary in mentation. They have no words but I submit that they have other symbols-inferior symbols, symbols but little symbolic-which serve in their lowly mentation (p. 205)." These symbols, he suggests, are very low homologues of what in people becomes pantomimic, and are like faint visual and tactile ideas, and faint ideas of actions, concomitant with cerebral activity which is disengaged from the lower centres. In any post-Darwinian context, the assumption is likely to be made that in the anthropoid apes "there is reasoning in its lowest form-or at least there is that out of which reasoning has been gradually evolved (p. 209)." But it is no easy matter to tie down what such a lower form of reasoning might consist of. Perhaps the simplest hypothesis is that the chimpanzee brain is equivalent to two small human right hemispheres, with the corollary that if a human being has lost entirely the special purpose language apparatus of the left hemisphere, there will be suffered a dissolution of cognitive capacities of very drastic proportions. Alternatively one could suppose that the larger overall size of the human brain, or a general superiority in its mode of operation, means that no amount of brain

damage short of complete decerebration is likely to reduce human abilities to an ape-like level.

This is partly a matter of rhetoric, but there is now a considerable body of behavioural evidence to suggest that chimpanzees exhibit a substantial amount of cognition of a rudimentary kind, but remain firmly "aphasic" in the sense of resisting efforts to induce either vocalisation, or syntactic skills within alternative forms of communication. The evidence has been discussed extensively elsewhere, and I shall give only a brief survey of it here (Dingwall, 1979; Passingham, 1982; Terrace, 1985; Savage-Rumbaugh et al., 1985).

There are several accounts of young chimps, oranges and gorillas reared in human domestic environments, most of whom adopted civilised habits of dress and decorum, but none of whom showed any tendency to imitate human speech (Furness, 1916; Cunningham, 1921; Kellogg, 1968). The most systematic study of a "home reared" chimpanzee was that undertaken by Hayes and Hayes (1952, 1953; Hayes & Nissen, 1971). Their animal, Viki, demonstrated an extreme lack of ability at voluntary and learned vocalisation (though not a total lack) but a remarkable aptitude at many other kinds of imitation. The Hayes' were encouraged to attempt the training of vocalisation because Viki, when a few months old, appeared to go through a "babbling" stage, but their efforts to improve on babbling met with little success. Perhaps it is not surprising, in view of Lieberman's description of the acoustic limitations of the chimpanzee throat, that Viki could not master vowel sounds. But she seemed to have difficulty even in establishing voluntary control of lip position. The only approximations to spoken English words were forms of "mama" "papa," "up," and "cup." In learning the most recognisable of these, "mama" and "papa," Viki at first kept her lips in the appropriate position for the consonants *by holding her lips with her own hand*. This was after the experimenters had held her lips, but whether or not it was this she was imitating, her behaviour suggests that she had better voluntary control of arm and hand movements than of lip position. In Jacksonian terms, higher motor centres appeared to be readily available for arm movements and skeletal movements generally, but either lip movements simply lack adequate representation in pre-motor cortex, or they are so strongly wired in to innate vocalisation and facial expression that they are not easily learnable in the context of voluntary phonation.

On the other hand, in perceptual understanding and manual dexterity, the Hayes claimed that Viki, when three years old, closely approximated a three-year-old child. This was based on controlled comparisons with human children, when Viki was aged between three and six, on tasks such as number matching and picture sorting (e.g. pictures of children versus pictures of adults), and these support the contention that the absence of vocal learning by Viki was not due to lack of "higher mental abilities" generally (Hayes & Nissen, 1971). Domestic chimpanzees' intellectual strengths appear to be in: (1) visual perception; (2) manual skill; and (3) visual-motor imitation. Because apes (and children) are good at it, imitation is not usually given much weight as a cognitive skill. But if one imagines building a robot that could *watch* someone cleaning spectacles, or holding the telephone, and then, later, copy these seen actions, then visual-motor imitation seems just as difficult in principle, if not more so, than auditory-vocal imitation. For the latter, self-produced output can be matched against the memory of the original model with little transformation; but to know that one's own actions in cleaning spectacles are equivalent to someone else's actions as visually perceived is quite complicated. Head (1926) promoted the use of a particular kind of imitation test in the examination of aphasic patients (the tester touches one of his eyes or ears with a particular hand, and the patient has to copy this exactly).

Because chimpanzees are usually very good at visual comprehension and the imitation of actions, most "language training" methods since that of Hayes and Hayes (1952) have attempted to capitalise on these natural strengths. Three kinds of system involving the visual modality have been tried: the American Sign Language gesture vocabulary (Gardner & Gardner, 1969; Terrace et al., 1979), a manipulable set of plastic tokens (Premack, 1970, 1976), and a computer- controlled keyboard with back-projected visual symbols (Rumbaugh, Gill, Brown, & Glaser, 1973). I will first describe the methods, and then consider the implications of the results obtained by using them.

The American Sign Language (ASL) Gesture System

Gardner and Gardner (1969) first reported the use of this method with the female chimpanzee Washoe. Since then a virtually identical system has been used with several other chimpanzees by Fouts, Chown, and Goodin (1976), Terrace et al. (1979), and Muncer and Ettlinger (1981), while Patterson (1978) has used the same method with gorillas. As far as its use with nonhumans goes, ASL can be considered as a set of between 100 and 200 separate actions, each independent of the others. Many of the individual gestures are iconic or pantomimic: *drink* is the thumb pointed to the mouth; *eat* the fingers placed on the lips; *toothbrush* is the side of the finger rubbed across the teeth; *up* is an arm extended skywards. Other signs appear to be more arbitrary: *dog* is slapping the thigh; *brown* is a flat palm pulled down the side of the face; *banana* is one index finger stroking the other; and there are arbitrary proper names for human and ape individuals. Training with these gestures is usually partly informal, by "total immersion" of the infant animal among signing human companions, but imitation may deliberately be encouraged, and moulding of correct responses, plus shaping by actively rewarding approximations to the correct response, can also be used (Fouts, 1973).

The Plastic Token System

The tokens used by Premack (1970, 1976) are entirely arbitrary. Colour names are various achromatic shapes and *apple* is a blue triangle. Initially the plastic tokens were metal-backed and "written" in a top-to-bottom sequence by placing them against a magnetised board in a vertical line. There were no problems, however, in switching to the procedure of laying out the same tokens on a shelf in a horizontal line in front of the animal. Step-by-step training with individual tokens is the training method, in the first instance with food rewards for correct responses, but later without this expedient.

The Keyboard System

Combinations of individual visual elements were described by Rumbaugh et al. (1973) but as used in practice the symbols on the keyboard can be considered to be arbitrary and unrelated, though formed from a standard set of crosses, circles and straight lines with in-line display units. Particular visual "lexigrams" of this kind were projected on the individual keys of a keyboard array of up to 56 (8 across by 7 down), but the location of each symbol was changed from day to day to ensure the animals inspected the keys they were pressing visually. When the chimpanzee pressed one of the keys, the lexigram on that key was written up in a horizontal display line above the keyboard. The initial training took the form of key pressing followed by reward-if the animal pressed the key designated *tickle*, the trainer came in and tickled it (the chimp), and various foods and drinks were automatically dispensed when appropriate keys were pressed.

More elaborate training for naming has since been reported to be necessary to establish "representational symbolic ability" (Savage-Rumbaugh et al., 1980, 1983).

Satisfaction of Wants

In all the above cases young apes give every appearance of eagerly making use of the artificial methods presented to them in order to achieve certain tangible ends. After making a gesture for *tickle*, or pressing a key so designated, they appear to expect to be tickled, and to enjoy any tickling delivered as a consequence of their communicative activity. It has frequently been pointed out that this does not constitute a very complex linguistic milestone (Terrace et al., 1979; Seidenberg & Pettito, 1979). Sceptics may deny that there is even any intention to communicate- suggesting that the gesture for tickle is like a reflex response to an itch. This does not seem very plausible, but the use of signs simply to satisfy wants is rather similar to pantomimic gestures used by domestic cats and dogs (running to the food bowl, or scratching at doors) and therefore cannot be used as a measure of exceptional primate abilities.

Naming

Chimpanzees trained with the gesture-sign method appear to use the gestures to make comments as well as requests. When leafing through a picture book they may make spontaneous signs, such as rubbing their teeth when they see a picture of a toothbrush. Experimenters also elicit naming by a *what's this?* gesture. All those involved in performing such experiments believe that a large number of gestures are associated with object categories, and various "double-blind" methods have been employed to check the accuracy of these associations (Fouts et al., 1976; Gardner & Gardner, 1985). The most obvious control technique is for the chimpanzee to be shown objects on a screen or placed in a box, out of the view of the human observer, who translates any gestures made by the animal in response to seeing the objects. But even if objects are labelled reasonably reliably, as appears to be the case, many critics remain to be convinced that this is a preliminary to linguistic skill rather than a set of high- level conditioned reflexes. One would like to have some quantitative measure of how far the animals "understand the names" by comparison with human children (or adults). No such measure is directly available, but one can assess evidence for the labelling of absent objects, and for categorisation.

Labelling Absent Objects

Asking for a banana when none are visible could be taken as displaced reference, but would not be a very convincing example of disengagement from context (Bronowski & Bellugi, 1970). A marginally more interesting achievement is referring to a particular banana which was seen a few minutes ago. Two experiments reported by Savage-Rumbaugh et al. (1978a, 1978b), which are of this general type, are valuable both for their experimental controls and for the fact that two chimpanzees used the keyboard system to exchange information, and material objects, between themselves. In the first case (1978b), one animal communicated to the other the identity of a hidden food object. After several preliminary phases of training, the final performance included the following tests. The animals were in adjacent cubicles, separated by a window, each with his own keyboard. One of the apes was led out to another room, and shown one of 11 different foodstuffs being placed in a container, which was then sealed. (The comestibles included banana, beancake, bread, milk, and orange drink, whose names were already well trained. The animal led out alternated from trial to trial.) This

informed animal was then led back to his keyboard and, observed by his partner, pressed one of the keys to produce a symbol recorded on the overhead display. The second chimpanzee then had to key in a request for the particular food in the container. The container was then opened, and both animals shown its contents; only if these corresponded to the final request were they allowed to consume them. The combined accuracy was between 90% and 100% in various phases of this sort of test.

One of the checks was to require the second animal to select a photo graph of the appropriate food item just after he had keyed in the request for it-since the selections were accurate, it would appear that the identity of a distant object had been transmitted from one animal to the other. If the animal who had seen the hidden food item was denied the use of the keyboard, but allowed to interact socially with the other chimp, the second chimp did not succeed in correctly identifying the hidden food; this suggests that the transmission of object identity took place in the form of meanings attached to arbitrary visual signals.

A second experiment (Savage-Rumbaugh et al., 1978a), using the same two chimpanzees (Austin and Sherman), involved requests made by one animal to the other. They were in adjacent rooms, connected by a hatch which could be opened and closed only by the experimenter. In one room there were several problem devices, each requiring the use of a different tool: a padlocked box requiring a key; a bolted box requiring a wrench; a vending device requiring metal discs; and various tubes and containers needing a stick, a sponge on a string, or a straw, to obtain any food or drink placed in them. On a given trial, the chimpanzee in the problem room was shown just one of these apparatuses being baited with food, but not given any of the six possible tools. The hatch was then opened to provide access to the second chimpanzee in the next room, who had possession of all the tools, but did not know (and could not tell) which one was necessary. The task was for the animal in the problem room to key in the symbol corresponding to the correct tool on a keyboard available to him. The ape in the tool room needed to observe the symbol thus projected (sometimes the requesting animal pointed at this symbol), and hand the appropriate tool through the window. When this tool had been used to obtain the hidden food item, the two animals shared out their incentive (initially at the insistence of the experimenters). As the correct tool was both requested and provided on more than 90% of the trials, even when the experimenter was "blind", or absent altogether, it seems necessary to conclude that the identity of a tool could be communicated from one animal to the other. Pantomimic actions did not appear to be involved: When the keyboard was turned off no iconic gestures were observed, and the only success achieved under these conditions was when the tool room animal simply offered each tool in turn. In a later experiment (Savage-Rumbaugh et al., 1983) both Austin and Sherman were able to use the keyboard to indicate (to the computer) which of several objects on a distant table they intended to choose in the near future. On the basis of this evidence it is difficult to resist the conclusion that these chimpanzees formed mental associations between arbitrary visual symbols and object categories.

Category Names

In a further success for Austin and Sherman it has been demonstrated that the "lexigrams" which they used for tools and for the foodstuffs could come to take part in a certain minimal form of semantic organisation (Savage-Rumbaugh et al., 1980). Special lexigrams designated as category names for "foodstuff" and "tool" were taught by training the animals to press the appropriate lexigram on a keyboard when presented with real food objects or tools, or with photographs of objects and tools. After this, they were able to categorise lexigrams of individual foods and tools correctly by pressing the lexigram for *food* or *tool*. For instance, if shown the lexigram *wrench* they pressed the

lexigram *tool*, but if shown the lexigram *sweet potato* they pressed the lexigram *food*. During this experiment the animals neither ate the foods, nor used the tools, which they were labelling. This should count as a degree of disengagement from context, but the view of the experimenters was that the categorising performance was only made possible by the previous experience of using the lexigrams actively, as a means to achieve desired ends in earlier experiments.

Reasoning

The evidence is quite strong that chimpanzees, lacking any assistance from innate linguistic universals or learned phonological codes, can nevertheless be trained to associate arbitrary visual labels with individual object types and class categories. There is very little indication that they are able to go on from this, and learn syntactical rules for the combination of labels that would amount to a functional grammar (see below). But, even when grammar is absent, apes may be not altogether without nous-there are several experimental procedures which allow one to infer the presence in them of intellectual processes that go beyond the mental associations required for symbolic labelling.

Transitive Inference

If one was told that the orange team always beats the white team; the white team always beats the reds; the reds always beat the blacks; and the blacks always beat the blues; then if one had to bet, one would probably bet on the white team beating the black team. It is to be hoped that chimpanzees are indifferent to the overtones of black and white-these stimuli were used in a test of their inferences in order to avoid preferences based on colour (Gillan, 1981) or generalisation from other hues. The testing was a simple choice between members of pairs of containers with coloured lids. After the following training: orange has food in orange/ white; white has food in white/red; red has food in red/black; and black has food in black/blue; it was possible to give chimpanzees the test of a novel nonadjacent pair, black/white, in which preference could be attributed to a "mental representation of order information." The most telling control procedure was that, if the linearity of the sequence was disturbed by the result that the bottom team always beat the top team, all bets were off: If trials were given in which blue has the food in blue/orange, the preference in the black/white pairing disappeared. This result was obtained with only one chimpanzee, Sadie, but there was more variation in the colour sequences tested than I have described here. This particular animal had not had any language training and the result thus supports the hypothesis that linguistic processes are not an absolute necessity for the accomplishment of transitive inference.

Analogical Reasoning

The chimpanzee, Sadie, which appeared to have constructed a mental linear scale of colours in the transitive inference test, failed to demonstrate any comprehension of a matching-to-sample procedure designed as a simple version of analogical reasoning. The bases of the analogy were the concepts of sameness and difference: The sample was always of two objects, and if these were the same-two toothbrushes, say-an alternative of two matchboxes, rather than an array of an ashtray with a cotton reel, should have been chosen. One would have thought that chimpanzees should be capable of perceiving this sort of relationship, but Premack (1983) reports that four out of five of the apes which he attempted to train on this test failed it. Children below about four years of age also failed it.

Only one chimpanzee (and older children) succeeded, this being Sarah, who had more than a decade of training with the plastic token symbols for "same" and "different" behind her. This animal can apparently not only make choices based on sameness and difference, but also place the tokens designated *same* and *different* between pairs of related or unrelated objects. That ability has been utilised to demonstrate what would seem to be a more complicated kind of analogical reasoning (Gillan, Premack, & Woodruff, 1981). According to this report, when shown a peeled apple plus apple peel on the left, and a peeled orange plus orange peel on the right, Sarah places *same* in the centre, but if the orange peel is accompanied by a peeled banana, or orange seeds, she puts *different*. A can with a can opener elicits *same* when paired with a lock with its key, but *different* when paired with a padlock plus a paint brush. Although a very large number of tests of this kind were given, some using controlled variations of geometric figures, it is difficult to say just what cognitive processes might have been responsible for the animal's (usually correct) choices. Premack (1983) concludes that the long years of token training are responsible for the successful performance by Sarah, because they enhanced an "abstract code" only dimly present in other animals of the same species.

Reasoning About Number, Time, and Place

Although it would be valuable to establish whether or not, as Premack (1983) suggests, training with his token system produces greatly enhanced cognitive abilities in primates lacking spoken language, it is also useful to know what mental capacities can be relied on in relatively untutored animals. Sarah, the "language trained" chimpanzee (although not others) could match arbitrary numbers of objects from one to four. But even the younger animals seemed to comprehend the difference immediately between one and two pieces of fruit. Arguably the test used implies an intuition that two minus one leaves one. First a trainer shows a chimp that he has two pieces of fruit in his hand, then the trainer goes out into a field, unseen by the animal, and places the fruit in a large container. The animal is allowed to see just one piece of food being removed from the container. If then released on its own the chimpanzee rushes to the container to retrieve the remaining titbit. The necessary (and more surprising) control is that if the trainer starts off by showing that he has only one piece of fruit, and then this one piece is seen to be removed from the container (Premack, 1983): "after this demonstration the animal does not go out into the field at all, but sits behind the blind, grooming itself or gazing out into space (p. 131)." This result alone might not be convincing, but there is a sufficient amount of evidence to confirm that, in general, chimpanzees without special training have a rich mental mapping of the observed locations of pieces of fruit in external space (Kohler, 1925; Menzel, 1978).

At least after special training, and possibly without it, nonhuman primates may approach the Piagetian "concrete operations" stage, demonstrating, in Sarah's case, something very like conservation of volume (Pasnak, 1979; Woodruff, Premack, & Kennel, 1978; Muncer, 1982).

Syntax and Function Words

Memory for the location of pieces of fruit, and even the association of visual symbols with object categories, could be taken as semantic, visual-spatial, right-hemisphere abilities. There is relatively little indication that nonhuman primates, even those trained with signs or gestures, can develop the skills required for the use of grammar. All the anecdotal reports of the use of combinations of gestures in apes trained in American Sign Language should probably be discounted (Terrace et al., 1979). It is possible, however, that the use of correct gesture order in the context of prepositions such as "in," "on," "under," and "behind" is within the capabilities of chimpanzees.

After about one year of training with ASL gestures for a limited vocabulary, but including the prepositions "in" and "behind," Muncer and Ettliger (1981) gave their single animal a series of "critical trials" (including regular double-blind trials) to assess both comprehension and production of novel phrases concerning a transparent plastic bag and a number of small opaque objects such as: bag in box; box in bag; box behind apple; apple behind box. Cases such as "carrot in bag" where the order cannot be reversed, were used in training, but not in the critical trials.) Test performance was significantly better than chance, though considerably less than perfect. Curiously, more errors were due to choosing the wrong preposition than to choosing the wrong order of gestures (or objects). There seemed to be absolutely no difficulty for the ape in always putting the prepositions second, in groups of three gestures. Semantically, "in" and "behind" could be confused on the grounds that "bag in box" and "bag behind box" both entail the occlusion of the bag by the box.

In a second experiment this chimpanzee was trained to produce and comprehend the signs for *and*, *or*, and *not*, in the context of the animal being instructed to "*take peanut and carrot*" from a display including a banana and an apple; or the chimpanzee signing "*Graham not take banana*," when she herself would get what was not taken by Graham. Performance on critical trials was then measured, in which, for the first time, *not* was combined with *or* and *and*. Three objects not before used with conjunctions were involved in these trials: paper, bag, and box, with raisins placed on these for reward. The animal refused to produce the signs for *not* or *or* under these circumstances. However, comprehension was tested by giving gestural instructions in the form "*not paper and bag*" or "*not paper or bag*." In the first case, taking both or taking just the third choice was scored as incorrect. Under these rules the chimpanzee was significantly above chance (95%) for the NAND operation, but significantly below chance (10%) on the NOR. In both cases what the animal did on most trials was simply to refrain from taking the raisin from the object signed just after *not*, while collecting its reward from the two others. Muncer and Ettliger rightly report this as a "failure to negate conjunctions," but the chimpanzee should surely be given credit for adopting its own syntactic rule, even if this violated Boolean algebra. When instructions were given in the form "*not paper and not bag*" it was capable of refraining from touching both forbidden objects. Taken together, these findings with prepositions and negations using the gesture-sign method lend credence to Premack's earlier claims, that his animals could follow simple instructions of the type *apple dish insert*, or *red card on green card*, transmitted by lines of plastic tokens. Although the skills of combining symbolic elements, either receptively or productively, may be said to be minimal in tests on chimpanzees so far conducted, the ability to modify the interpretation given to one symbol because of the presence of another is not necessarily completely absent in these animals.

NONVERBAL SYSTEMS OF COMMUNICATION USED WITH APHASIC PATIENTS

As the American Sign Language (ASL) system was developed for the use of disadvantaged people-the deaf-it is hardly a new idea to suggest that it could be used with categories of persons in whom the normal vocal-auditory channel is for some reason unavailable. Bouilland recommended the use of nonspeech signals with adult

aphasic patients in 1825. Peterson and Kirschner (1981) have more recently reviewed reports of the training of aphasic persons with visual methods, including pantomime and American Indian signs as well as ASL. There is of course a general difficulty, in that patients with the severest loss of speech production skills may also be impaired in their ability to produce or understand messages in other symbolic systems (Feyereisen & Seron, 1982). However, Peterson & Kirschner's review suggests that there are many patients whose impairments are sufficiently specific to vocal production or heard speech to make training them in the visual modality worthwhile. The case history reported by Kirschner and Webb (1981) is of this type. The patient, having become mute and uncomprehending of speech after a bitemporal infarction, was able to learn over 100 signs including both ASL and Amerind gestures, which she found useful in communicating with her family. Two other findings with this patient may have considerable generality: Some sparing of reading and writing skills is an indication that other ways of making use of the visual channel may be successful; but even so, gesturing in aphasic patients may lack fluency. More optimistically, there are suggestions that gestural and pantomimic training may improve thinking, and may even result in spontaneous verbalisation, in aphasic patients (e.g. Schlanger & Freiman, 1979).

The tangible plastic token developed by Premack (1970) for use with chimpanzees provides a very particular kind of visual channel for communication; it has the disadvantage, compared to gesture, that it requires special (though not expensive) equipment, but the advantages are first that this equipment serves as an external aid to short-term memory, and second that vision may if necessary be augmented by tactile information. A patient must be relatively quick to observe gestures, but a line of plastic chips may be inspected for as long as is necessary. The token system may therefore be useful for minimising the load placed on memory and visual attention. Hughes (1975) conducted what was virtually a replication of the Premack (1971) investigation of the chimpanzee Sarah with developmentally aphasic children. The 14 subjects, whose aphasia was either congenital or of very early origin, were between 8 and 13 years of age, but had vocal language abilities assessed at the 2-year-old level or less. None could use spoken prepositions. But during a twice-weekly half-hour session, over a period of months, they learned to produce and understand "sentences" and to communicate a knowledge of class concepts. They first learned "nouns" by 'associating arbitrary plastic symbols with particular toys, such as a car or doll. Then sentences of the kind *insert doll, dish*" were correctly complied with, and accurate descriptions such as *"experimenter take-out car bucket"* were given of seen events. The preposition "on" was tested systematically by itself: The children either followed instructions like *"green on red,"* by placing a green card over a red card, or gave description of cards arranged by the experimenter, by placing tokens in correct order, from left to right on a magnified board.

Although it might be expected that, even with profoundly impaired linguistic competence, a natural intelligence should easily encompass a set of simple associations between symbols and perceptible objects, and also between symbols and clearly visible relations between objects such as "in," "on," and "under," it is something of a surprise that bits of plastic can just as easily come to represent concepts such as colour in general, or shape in general, which are not so tied to visual images. When certain tokens stood for "colour of" and "name of," the children were able to select *colour of* correctly when the colour word for red was presented along with an actual red circle; or to insert the token for "square," rather than that for "yellow" in the proposition *"blank shape of actual yellow square."* Perhaps this should only be surprising if one assumes the

existence of an all-powerful and transmodal language acquisition device, which ought to be notable by its absence in developmentally aphasic children. But it is also possible that some higher-order concepts are not as difficult as we think they ought to be for primates who exhibit difficulties with spoken or heard syntax. In Premack's original studies the chimpanzee performed even more accurately than usual when she was required to fill in blanks with class concepts, given concrete instances. This was true not only for implying that the token *round* was the *shape of* a real apple rather than its colour, but also for indicating that the arbitrary token for a banana fell into the category *name of*, rather than the categories of colour or shape (Premack, 1976; pp. 162-164, p. 198).

The manipulable tokens have been taught to autistic children (DeVilliers & Naughton, 1974) and to adult global aphasics (Velettri-Glass, Gazzaniga, & Premack, 1973), and a small number of other forms of visual ideographic symbol have been shown to allow for increased communication with some very severely aphasic adults (e.g. Baker, Berry, Garner, Zurif, Davis, & Veroff, 1975; Gardner, Zurif, Berry, & Baker, 1976). Given the ready availability nowadays of computer controlled coloured graphic displays, an obvious direction for future research in both the testing and retraining of human brain-damaged patients with vocal/auditory difficulties will be ideographic and vivid visual communication systems which make use of a keyboard or joystick and a television screen.

CONCLUSIONS AND SUMMARY

My concern has been the biological backdrop of cross-species comparisons, against which the unimpaired human use of language stands out in brilliant contrast. When human abilities are dimmed, it is perhaps easier to catch a glimpse of shadowy scene-shifters, but it is certainly going too far to think of all human disabilities in the extreme Jacksonian fashion, as a set of localised reversal of evolution. Nevertheless, it is arguable that the specialities of human cognition, including those requiring the use of language, do not place human cognition for ever outside the reach of biological comparisons.

No new modalities of sense or new motor organs were thrown up by the evolution of language, and to this extent the apparatus used in speech has phylogenetic precedents. It is the mental content of speech, rather than its physical form, that is most important, and therefore it is the relation between the functioning of the brain in human language, and the principles of brain organisation which apply also to monkeys and apes, where we might expect biological comparisons to stand or fall. The broad outlines of Hughlings Jackson's views of human brain function usually command respect, and two aspects of the details of Jackson's speculations continue to be supported by both neuroanatomical and clinical evidence. Although the multiple representation of body parts and their movements in the Jacksonian hierarchy precludes the identification of unitary centres in the brain responsible for isolated psychological functions, all specifiable components of psychological activity are, in Jackson's scheme, assigned to physically separate "nervous arrangements." A simple corollary of this is that many of the localisations of the nervous arrangements in the human brain can be related directly to the similar organisation of the brains of closely related primates. Thus the special movements of the tongue and lips required for human speech are anatomically adjacent to where more commonplace motor representations of the lips and tongue would be found in a general-purpose primate brain. Physically separate neural specialisations appear to be the rule in primate

brains, and a second corollary is that small-scale components of psychological skills may be anatomically localised in individual brains to a very high degree.

Primate species which lack those specialisations peculiar to human speech may have other abilities which enable them to master a range of manual gestures, or artificial visual symbols, which can certainly be employed for simple descriptions and requests. Although there is no evidence that grammatical rules of ordinary human complexity will emerge from these training experiments, one-to-one correspondence between distinct visual signals and distinct object categories appears to allow for production and comprehension of symbols that refer to such higher-order categories as prepositions and class descriptions (a food, a tool, a shape, a colour, a visual signal). Persons who lack or who have lost some of the cognitive specialisations peculiar to speech may similarly retain many other cognitive abilities, and in some cases recourse to gestural or ideographic alternatives to the vocal/auditory channel may be clinically helpful. As a final word on the degree of specificity possible in cognitive and linguistic impairments which result from brain disorder, and in belated commemoration of the centenary of Darwin's death (Darwin, 1871/1901):

The intimate connection between the brain, as it is now developed in us, and the faculty of speech, is well shown by those cases of brain disease in which speech is specially affected, as when the power to remember substantives is lost, whilst other words can be correctly used, or where substantives of a certain class, or all except the initial letters of substantives and proper names are forgotten (p. 134).

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