

## **Lateralization of functions in the vertebrate brain: A review**

**S. F. Walker**

---

That the human left and right cerebral hemispheres perform different functions is widely accepted; but there is little evidence of whether or not similar functional asymmetries exist in non-human vertebrates. In this paper, neuro-anatomical similarities between human and other vertebrate brains are considered, and data concerning physical asymmetries reviewed. The defining features of human lateralization are taken to be right-handedness, as a skewed but continuous distribution of preferences, and a greater involvement of the left hemisphere in species-specific vocalization, with right-hemisphere superiority in spatial perception and emotionality less well-marked characteristics. Rodents, cats, at least one species of marsupial, and macaque monkeys have consistent hand preferences for food reaching. These may result from constitutional factors, but in every species studied the distribution of preferences is unskewed. Canaries appear to have left-hemisphere dominance of vocal production, and there is limited support for the conjecture that macaque monkeys have left-hemisphere dominance for reception of species-specific cries and/or for short-term auditory memory. Left and right unilateral hemispheric damage may have appreciably different effects on emotionality in rats, sound localization in cats, and tactile discrimination in monkeys, although the available evidence is equivocal. It seems possible that asymmetries of cerebral function are widespread in vertebrates. In particular, left hemisphere dominance of species-specific communication might be common in birds and primates: left-hemisphere dominance of human speech may be an example of a general vertebrate tendency towards unilateral control of vocalization.

---

The assignment of different functions to the right and left hemisphere of the human brain is a crucial element of current neuropsychology (Ornstein, 1972; Popper & Eccles, 1977; Gazzaniga, 1979). The left hemisphere contains mechanisms responsible for speech, and is said to operate in a manner suitable for mental arithmetic and logical thought. These are important characteristics, and the left hemisphere was formerly held to be 'dominant' over the 'minor' right hemisphere. But more emphasis is now given to the minor hemisphere's own specializations — perception and expression of emotion ; knowledge of spatial relations, especially in connection with visual input; and generally, operations that take place in a wholistic, global, or Gestalt fashion.

The purpose of this review is not to examine in detail the nature of these asymmetries in human brain functions but to consider the extent to which differences between the left and right hemisphere mark off man from all other vertebrates. There are various ways in which lateralization of function could be related to uniquely human capacities of the brain. For instance, lateralization would be secondary to language, if it could be shown that possession of language induces cerebral asymmetry, rather than vice versa. Any other asymmetrically represented process could conceivably be the driving force behind lateralization, but linguistic competence is clearly a strong candidate. Possible alternatives are right-handedness (Hardyck & Petrinovitch, 1977) and the existence of a conscious self which communicates directly with only the left hemisphere (Popper & Eccles, 1977). In each of these cases we might suppose that human brains become lateralized only as a consequence of the development of language, handedness or a perceiving self, and would therefore be surprised to find evidence of lateralization in non-human species which lack these characteristics.

A more direct hypothesis of the cause of lateralization has been put forward by Levy (1977). She suggests that a division of labour between the hemispheres ‘almost doubles’ the overall cognitive capacity of the human brain. In other words, space in non-human brains is used up by symmetrical duplication of behaviour-controlling processes; abandoning this precaution produces a large quantitative bonus. The ‘dividing and doubling’ idea emphasizes the uses of the minor hemisphere. It bears on why there should be qualitative differences between the hemispheres, and assigns lateralization a special evolutionary role — if it is inferred that the distinctiveness of the human species is achieved only by making use of extra capacities attainable with hemisphere differences.

Semmes (1968) and others have stressed other advantages of having two different kinds of processing strategy available — the analytic and serial in one hemisphere, and the diffuse and global in the other. Hypotheses such as these may be tested within the human species by comparing the abilities of groups of individuals with differing degrees of functional lateralization, and there is some support for the view that lack of lateralization, insofar as it occurs in moderately left-handed people, is associated with reduced cognitive capacities (Levy, 1969; Miller, 1971). However, these differences are not as large as one might expect if lateralization doubles, or qualitatively improves, human intelligence; indeed there is considerable doubt as to whether reliable differences in ability correlated with degree of lateralization exist at all (Hardyck, 1977).

As overwhelming advantages of cerebral asymmetry are not easily established by the study of individual differences in man, it is all the more important to investigate other sources of evidence as to its origin. Implicit in most theories is the view that lateralization is inextricably linked with especially *human* intellectual characteristics — if this is the case, the absence of lateralization of brain function in animals needs to be convincingly demonstrated. On the other hand, if anatomical and functional precursors to human cerebral asymmetry can be found in species other than *Homo sapiens*, we might be provided with new clues concerning its existence in ourselves. I will discuss, first, some relevant aspects of comparative neuro-anatomy; second, what may be taken as firm features of human cerebral dominances; and third, evidence concerning the occurrence of these features in other animals.

## **1 Neuro-anatomical considerations**

In a sense, a necessary condition for cerebral asymmetry is symmetry — in the form of paired, roughly symmetrical hemispheres. This condition is satisfied in all vertebrates, although both hemispheres are small in lower vertebrates (fish, amphibians and reptiles) and make up a much bigger proportion of the brain in higher vertebrates (birds and mammals). The vertebrate brain is a paired organ, from the spinal cord up (Dimond, 1972; Pearson & Pearson, 1976). This duplication of brain halves is associated with what may be termed symmetrical lateralization of sensory and motor functions. For cutaneous sense, and motor control, each half of the brain, or spinal cord, usually has dominant responsibility for one half of the body. This system is complicated by the fact that each half of the nervous system is often connected to the *opposite* sided sensory and motor devices ‘crossed-lateral’ control. The reasons for the cross-over are obscure. Sarnat & Netsky (1974) suppose that primordial defensive reflexes in, for instance, the vertebrate precursor, *Amphioxus*, required that tactile stimulation from one side of the body elicit muscle contraction on the opposite side and that cross-overs were thus built into the vertebrate nervous system from the start. This does not go far in explaining the great variety of decussation in higher vertebrate brains — these may have embryological and functional advantages, but their nature remains a mystery.

The important fact is that it is common for one half of the paired structures to act independently of the other in terms of sides of the body. There are consistent differences, across vertebrate classes, between the type of symmetrical lateralization employed for the

various sensory modalities. Olfaction is predominantly ipsilateral, with olfactory nerves and subsequent tracts going through cerebral hemispheres on the same side as the nostril from which they begin. For vision the basic plan is for the left visual field to project to the right side of the brain (in both mid-brain and forebrain routes) and vice versa. In non-mammals, the rule (with some exceptions) is for optic nerves from each side-facing eye to go to the opposite side of the brain, while in mammals, partial decussation at the optic chiasma ensures that the left visual field from both front-facing eyes reaches the right side of the brain (Ebbesson, 1970). With hearing there is a greater degree of duplication of hemisphere function in mammals, since each ear projects to both sides of the brain, due to a variety of decussations and commissures starting in the medulla (Pearson & Pearson, 1976). A similar arrangement of the auditory pathways occurs in birds (Boord, 1968) and reptiles (Foster & Hall, 1978). The contralateral auditory projection is, however, the most direct, and it has been proposed that in the event of conflict between information from the two ears (as in the dichotic listening paradigm with human subjects) the ipsilateral channel may be actively suppressed in mammals (Aitkin & Webster, 1972). Despite this degree of contralateral advantage, it must be stressed that, in terms of hemispheric specialization, audition offers a rather different set of possibilities than vision. A single hemisphere receives information from both ears, and may therefore operate on all auditory input, and make comparisons between right and left auditory fields, without the intervention of the other hemisphere. For instance, a single hemisphere could in theory localize a sound source at any point in the horizontal plane, or decode speech entering either ear, even in the absence of cerebral commissures. By comparison, for visual stimuli, a single hemisphere acting alone is restricted to its own half of the visual field. A mammalian hemisphere and to a limited extent, that of some other vertebrates (Ebbesson, 1970) — has the advantage of being able to compare inputs from the two eyes, arising from one point in the visual field, thus deriving stereoscopic depth. But the nature of the mammalian chiasma tends to retain the left-visual-field-to-the-right-hemisphere system which occurs in lower vertebrates with side-facing eyes.

### *1.1 Integrating symmetrically lateralized information*

This brings up a general requirement which follows from the symmetrical separating out of left and right sensory and motor information. For vision, it would clearly be a disadvantage, even for the simplest vertebrate, if an object detected in the left field had to be detected anew when the object, or the animal, moved round so that the stimulus appeared on the right (see Walls, 1942). To prevent this sort of double vision, it would be necessary that information as to the identity of the object is passed from one side of the brain to the other. It is usually taken for granted that facilities for such a transfer of information exists in man and other mammals, in the shape of the corpus callosum (Pearson & Pearson, 1976). However, it has also been established that some inter-ocular transfer of learned visual discriminations takes place in goldfish (Yeo & Savage, 1975; Ingle & Campbell, 1977), and pigeons (Cuenod, 1974; Zeier, 1975) by means other than transmission via corpus callosum. The method involves training with one eye covered, and subsequent testing for the performance with only the other eye available, with or without surgical lesions of putative transfer routes. In goldfish, sectioning the tectal (midbrain) commissures does not necessarily stop inter-ocular transfer of shape discrimination (Yeo & Savage, 1975) but alternative forebrain commissures appear to be necessary (Ingle & Campbell, 1977). In the pigeon, Cuenod (1974) showed that transfer of colour and shape took place via the supra-optic decussation, from the thalamus to contralateral hemisphere, and not via mid-brain commissures. Electrophysiological recordings establish that each hemisphere of the pigeon contains neurons responsive to ipsi- and bilateral, as well as contralateral inputs: it appears that in

birds a single hemisphere can store and compare information from both eyes, and from both halves of the visual field (Zeier, 1975; Fox et al., 1977).

The point is that, together with symmetrical lateralization of sensory input, vertebrates typically arrange for some kind of bilateral availability of relevant information. Corballis & Beale (1970, 1976) assumed that the transfer is so complete that animals have difficulty in discriminating mirror images about the mid-line. With some kinds of displays such difficulties can occur in man as well as other vertebrates, but information as to whether a stimulus is on the left, or on the right, must be retained in the case of turning responses and the body image. Using the tactile sense, an animal may scratch its right side with either a right or a left limb, and does not normally attempt to scratch bilaterally in response to a unilateral itch.

The presence of a large corpus callosum indicates that the human brain is particularly well equipped for inter-hemispheric communicativeness. However, in higher mammals, the corpus callosum connects some regions of the cortex very well but others very badly, if at all (Ebner, 1969). It should first be emphasized that the small hemispheres of lower vertebrates may be just as well-connected as the larger cerebral structures of mammals, albeit via different pathways. All vertebrate forebrains possess the anterior commissure (which contains several distinct inter-hemispheric tracts) and a 'posterior pallial commissure' (the psalterium between hippocampi in mammals) together with connections at diencephalic levels. Only placental mammals utilize a true corpus callosum, but marsupial mammals have very large anterior and hippocampal commissures, and in some cases 'aberrant bundles' parallel to these (Kappers *et al.*, 1936). The addition of the corpus callosum may be seen as retaining the usual ratio of inter-hemispheric exchange for larger hemispheres rather than increasing the extent of hemispheric cross-talk. The degree of connectedness of marsupial hemispheres can be anatomically assessed by plotting the distribution of degenerating fibres following transection of their forebrain commissures.

By this technique, Ebner (1967) demonstrated that there is an even spread of commissural connections over the entire surface of the hemispheres of the Virginia opossum, a pattern identical to that found in the hedgehog, a primitive placental which has the advantage of a fully fledged corpus callosum. But when the same survey was made of the cerebrum of cats, raccoons and rhesus monkeys — 'higher mammals' with a more substantial corpus callosum than the hedgehog — commissural connections were found to be unevenly distributed, with some areas of the hemispheres, including parts of the somatic and visual cortex, completely free of such fibres (Ebner & Myers, 1962a; Ebner & Myers, 1965).

There is some support, then, for the proposition that the development of the corpus callosum in mammals goes hand in hand with an increase in areas of cerebral neocortex which lack inter-hemispheric coupling. It should be noted that, although marsupials and primitive placentals have relatively homogeneous distribution of commissural fibres, some reptiles possess an irregular pattern more like that of the cat and monkey (Ebner, 1969). It should also be said that Dimond (1972) proposes a rule opposite to that just suggested: he asserts that higher mammals have more widespread commissural interconnections than lower mammals. However, he was led to this assertion by the limited inter-hemispheric projections of the raccoon. As a specialized carnivore (with primate-like performance in laboratory tests) the raccoon is an advanced mammal, and as such was used by Ebner (1969, p. 247) to support the conclusion that 'commissure-free cortical regions of more specialized eutherian (placental) mammals appear at a later stage of the development of neocortex'. The raccoon's hands are well adapted for catching fish and crustaceans by touch (Whitney & Underwood, 1952), and its powers of visual abstraction as measured by success at learning sets (Johnson & Michels, 1958) and patterned string problems (Michels *et al.*, 1961) appear to be considerable. As with cats and monkeys, tactile and visual prowess is accompanied by the

absence of commissural connections to the primary visual and touch areas of the two hemispheres. In the raccoon, the region of somatosensory cortex devoted to the hand, which lacks commissural terminals, is extremely large (Welker & Seidenstein, 1959).

The generality of some degree of point-to-point cross-forebrain associations in lower vertebrates can be demonstrated by the same phenomenon that necessitates surgical callosal sections in human epileptic patients — artificial induction of an epileptic focus in the forebrain of teleost fish, amphibians or reptiles, results in the propagation of a secondary focus at the symmetrically opposite position in the contralateral hemisphere (Servit & Strejckova, 1970).

One may tentatively conclude, then, that vertebrate brains are organised according to a symmetrically lateralized plan which matches one side of sensory input or motor output with one side of the brain. There are differences in whether the same or opposite side of the brain dominates lateral input and output, although crossed lateral control is the norm. For all modalities there are some arrangements for bilateral integration, and symmetrical interchange of information. In general, one side of the brain mirrors the other, functionally and anatomically. This is the background against which any functional or structural asymmetry stands out.

### *1.2 Physical asymmetries of the human brain*

It is safe to say that interest in functional asymmetries has preceded the emphasis of human neuro-anatomical imbalance. But since Geschwind & Levitsky (1968) suggested that disparities between the surface area of the left and right planum temporale on the dorsal horizontal extension of the temporal lobe was related to left-sided localization of speech perception, considerably more data have become available (e.g., Geschwind, 1974; Rubens, 1977; Galaburda *et al.*, 1978). The planum temporale is a triangle of secondary auditory cortex, and is in the vicinity of the neurologically identified Wernicke's area which, when damaged, impairs speech comprehension (but see Bogen & Bogen, 1976, 'Wernicke's region — Where is it?'). Geschwind & Levitsky found that out of 100 brains, 65 had a significantly larger planum temporale in the left hemisphere, compared to the right. Of the remaining 35 brains, 11 had a larger area on the right, and 14 were classified as symmetrical. Others have followed 19th-century investigations in measuring the length of the Sylvian fissure, in which the planum temporale lies (Yeni-Komshian & Benson, 1976; Rubens, 1977). The Sylvian fissure tends to be longer in the left hemispheres than in the right, and in 25 of 36 brains (69 per cent) examined by Rubens *et al.* (1976) it continued further horizontally on the left before bending upward. The human brain thus appears to be typically, if not universally, asymmetrical in the region of the temporal/parietal boundary. Moreover; the primacy of the left planum temporale is already evident in foetal and neonatal brains (Wada *et al.*, 1975; Witelson & Pallie, 1973).

Is this because the entire left hemisphere is larger than the right? If anything, the minor right hemisphere weighs more than the left (Lemay, 1976), and there is evidence that the right hemisphere leads the left in prenatal growth (Chi *et al.*, 1977). Campain & Minckler (1976) found that primary auditory cortex, immediately in front of the planum temporale, tends to be more extensive on the right, although there were enormous individual variations in their sample. A more general demonstration of the nature of hemispheric size differences has been obtained by a radiological brain scan technique (Lemay, 1976). This does not at present allow for measurement of bounded areas such as the planum temporale, but provides a coarse-grained picture of living brains *in situ*. Since fixed brains may suffer up to 40 per cent shrinkage, and mechanical distortion, this is valuable additional evidence.

The results may be summarized as follows: the front of the human brain is wider on the right ; the back of the human brain is wider on the left. This applied to individuals categorized as right-handed. For the left-handers, the frontal lobe still tended to be larger on the right, but was more often equal, and the right occipital lobe was also often the larger of the two.

The contention that left-handers have *less* functional asymmetry than right-handers, rather than the opposite form of asymmetry, thus appears to find support in Lemay's EMI scans.

However, it should not go unremarked that the correlation between left-right inequalities of size and left-right assignment of function is somewhat less than perfect. Of the four major asymmetries of function, three (language reception, language production and fine motor control) are localized in the left hemisphere, whilst the fourth (visual-spatial processing) is thought to be a right-hemisphere specialization. Yet, of these four instances, only in one, language reception, does the physical inequality between the hemispheres go in the obvious direction, insofar as the planum temporale is larger on the 'correct' side in 60—70 per cent of the brains studied. Although language production relies on the left hemisphere Broca's area, this area, along with the rest of the frontal lobe, is larger on the right (Wada *et al.*, 1975). If other frontal motor areas are larger in the right hemisphere, as Lemay's data would suggest, then this is the wrong direction for motor dexterity. Finally, if visual-spatial functions are better represented in the right hemisphere, one might have expected an enlargement of the right occipital lobe, but it is the left occipital lobe which is physically dominant (Lemay, 1976).

Thus, although *any* physical left-right asymmetries may be taken as signs of functional lateralization, the exact implications of the various hemispheric size inequalities in man. are by no means clear-cut (Whitaker & Ojemann, 1977). It may be observed that if the 'division of labour' between the hemispheres were an entirely equitable one, pronounced distinctions between the functions of the two hemispheres might occur in the absence of any difference in gross physical dimensions.

### *1.3 Physical asymmetries in non-human brains*

Systematic searches for physical hemispheric asymmetries in animals which might correspond to those observed in man have, reasonably enough, been confined to primates. Generally speaking, it is assumed that non-human brains are bilaterally symmetrical (Dimond, 1972). However, there are indications that the anthropoid apes (chimpanzee, orang-utan, and gorilla) exhibit anatomical hemispheric asymmetries that are similar to, though smaller than, those observed in man.

Cunningham (1892), having observed that the upward turn of the Sylvian fissure was more acute on the right in human brains, found a similar disparity in the brains of chimpanzee, orang-utan, and baboon (a large Old World monkey), but not in those of a macaque (a typical Old World monkey, smaller than the baboon). Yeni-Komshian & Benson (1976) found a corresponding asymmetry in the length of the Sylvian fissure in chimpanzees. For 25 chimpanzee brains the mean length of the Sylvian fissure was greater on the left than on the right — a minute (457 mm versus 437 mm) but statistically significant difference. For the rhesus monkey (a species of macaque) there was a similar difference in the mean length of the fissure, but it did not reach statistical significance. A difference between monkeys and apes is suggested by other studies. Wada *et al.*, (1975) found no temporal lobe asymmetries in rhesus monkeys or baboons. Lemay & Geschwind (1975) report that the point of termination of the Sylvian fissure tends to be higher on the right than on the left in the chimpanzee, gorilla and orang-utan, but that this difference is relatively rare in the New

World and Old World monkeys. Within the great apes, the orang brains were most, and the gorilla's least, asymmetrical. A considerable proportion of the apes did not show the asymmetry (out of 27 ape brains, only 16 had left/right Sylvian fissure height differences of more than 3 mm).

Given the vagaries of cortical growth (Richman *et al.*, 1975) it would be a matter for comment if hemispheric asymmetries in individual brains within any species were not observable, with sufficiently precise measurement. What is of interest is whether *systematic* forms of asymmetry appear in species other than man. It appears from the investigations quoted above that the apes may exhibit left/right Sylvian fissure disparities of the same kind as that found in man, but to a lesser degree. In contrast, at present the data for monkeys suggest that their Sylvian fissure left/right asymmetries are not comparable to the human case.

However, the Sylvian fissure is not necessarily the most appropriate test of brain asymmetries. Cain & Wada (1979) have suggested that it would be useful not to concentrate exclusively on the temporal lobe, after finding frontal lobe asymmetries in baboons of the same size as those found in man (with larger measurements on the right). Unfortunately they were not able to compare the occipital lobes, which were damaged, but their data suggest that a more systematic assessment of brain asymmetries than those previously conducted may demonstrate many parallels between the physical asymmetries of the human brain and those of other primates.

Other mammalian species have not been as thoroughly investigated as primates, and in the absence of data it is usually assumed that marked left/right hemispheric asymmetries are absent. *Individual* differences in hemisphere size and fissural pattern are, of course, quite common. Webster (1977), for instance, examined the brains of 33 cats, and found, firstly, that 18 could be categorized as symmetrical in fissural pattern while the other half (15) were asymmetrical, and secondly, that two-thirds (10) of the asymmetrical brains differed in visual, rather than other, areas (although no left/right imbalance was reported). Individual brains of various mammalian species may differ similarly in degree of asymmetry, and thus in degree of individual left/right imbalance, with as yet undetermined implications for species-characteristic hemispheric inequalities (Royal College of Surgeons, 1902).

A possible exception to the general symmetry of the skeletons of mammalian species (apart from higher primates) occurs in the suborder of Odontocete whales. These differ from Mysticete (whalebone) whales, and indeed from most other mammals including man, in having markedly asymmetrical skulls (Slijper, 1962; Ness, 1967; Tomilin, 1967). Not all species in the suborder show the same degree of cranial asymmetry, which is most readily observable in the width of the jaw-bones. Just how readily is illustrated by the case of Bottlenose whales, whose right premaxillary bone may be twice as wide as the left. Clearly there may be special reasons for these peripheral asymmetries, unconnected with functional asymmetries in the brain; for example, asymmetries in the nasal passages may be connected with the use of these passages for sound production in some species. However, marked differences in the left and right nasal, premaxillary and maxillary bones may be accompanied by such cranial asymmetries as, for instance, in the temporal-parietal fossa and the occipital crest. In all cases it is the right side of the skull which is better developed. There is some tendency for the degree of asymmetry to increase with skull size. The Narwhal has a particularly asymmetrical skull, as well as having a single (left) tusk (in the male), but degree of asymmetry does not seem related to the presence of the tusk (Ness, 1967).

The most familiar toothed whale, the Bottlenose Dolphin (*Tursiops Truncatus*), has a relatively evenly developed skull, although Tomilin (1967) gives mean figures for the intermaxillary bone in this species which suggests a sex difference in asymmetry. It is hazardous to infer brain characteristics from peripheral skull measurements, but it seems

more probable than not that systematic physical hemispheric asymmetries of some kind occur in most species of Odontocete whales. Due to the 'hyperfissurization' of whale brains, examination of fissural patterns would be arduous. Published photographs and line drawings of cetacean brains make it quite clear, however, that the fissural patterns of one hemisphere are not always mirror images of those on the other (Slijper, 1962; Morgane & Jacobs, 1972).

In view of the inferences made from fossil human skulls, which are also larger on the right (Abler, 1976; Lemay, 1976), and in the absence of more precise comparisons of the left and right hemispheres of the toothed whales and dolphins, it can only be said that the existence of species-characteristic cerebral asymmetries in this mammalian taxon remains a possibility. It is unlikely that many people have examined the skulls or brains of any non-primate species to see if one side differs from the other by a factor of 1 or 2 per cent. Given the almost universal asymmetry of the other internal organs, slight asymmetries in the skull or brain of any vertebrate would not necessarily be a matter for comment. Some vertebrate brain asymmetries may therefore remain to be discovered. In crocodylians, for instance, very striking individual asymmetries of the skull are not uncommon, but few systematic surveys have been made of this phenomenon (Iordansky, 1973). A rare comparison of right and left hemispheres in the rat (Diamond *et al.*, 1975) suggested that the cortex of the right hemisphere may be between 1 per cent and 10 per cent thicker than the left, depending on which of seven cross-sections is measured, from the sixth day of life onwards. Although the right-hemisphere supremacy was maintained throughout the life span of the animals, the maximum asymmetry, at each of the seven sections, was observed at some point during the first 6 weeks.

All the physical asymmetries discussed so far, human and animal, have concerned overall or surface features of the cerebral hemispheres. It is more difficult to examine internal, subcortical brain characteristics, but these are generally assumed to be bilaterally symmetrical. There is a well-known exception, however, in the diencephalon of lower vertebrates. The habenular nuclei, situated in either side of the third ventricle, are noticeably unequal in size in cyclostomes (lampreys and hagfish), sharks, and some species of teleost fish and amphibians. The left habenular is better developed in sharks, and in those species of frog which have an asymmetry, but the right-hand nuclei are the larger in cyclostomes, and the favoured side varies from species to species in teleost fish (Kappers *et al.*, 1936; Braitenberg & Kemali, 1970; Morgan *et al.*, 1973). When it occurs, this anatomical asymmetry is quite unequivocal, but its functional implications are unknown. The habenulae are traditionally classed as olfactory correlation centres (Kappers *et al.*, 1936) as they have fibre tract connections with the olfactory bulbs, the amygdaloid, septal and hippocampal regions, with the thalamus, with midbrain centres, and with each other (via habenular commissures). Habenular nuclei are retained in mammals and birds, and their connections remain 'surprisingly constant throughout the vertebrate series' (Kappers *et al.*, 1936, p. 1264). They can obviously be regarded as an integral part of the limbic system (Pearson & Pearson, 1976). Since the details of habenular function in any species are not known, it is difficult to draw conclusions from the observed physical asymmetries, but it would hardly be surprising if limbic system function were in some way lateralized in the species in question. To the extent that human emotionality is held to be asymmetrically controlled, functional lateralization in the human limbic system might also be expected.

Functional lateralization in the human diencephalon is occasionally referred to in the context of verbal performance: because of its extensive two-way connections with the cortex, the thalamus ought to reflect, if not determine, lateralization of sensory functions, and electrical stimulation of the thalamus in human subjects suggests a degree of left dominance of verbal processes (especially for the pulvinar and ventro-lateral nuclei —Ojemann, 1976; Riklan & Cooper, 1977). It was noticed by Haight & Neylon (1978) that occasional



individuals (about 10 per cent) in a sample of brush-tailed possums, had serious asymmetries in the thalamus, but not elsewhere in the brain. The diencephalon appears susceptible to physical asymmetries which may be embryological in origin.

#### *1.4 Sensory and motor pathways*

It can safely be assumed that the innervation of sensory and motor organs has identical physical characteristics on the left and right side of the body, as a general vertebrate rule, and that the same applies to major sensory and motor pathways within the brain. However, there may be interesting exceptions. Cobb (1964) reported that for a species of owl and for the South American oil-bird, midbrain auditory projections were larger on the left than on the right. Owls make use of hearing for nocturnal location of prey, and several species have pronounced asymmetries of the external auditory meatus, consistent within the species, which may assist this (Erulkar, 1972). The oil-bird also flies under low levels of illumination, and employs a bat-like echo-location system.

A neurochemical, rather than an anatomical, asymmetry has been reported for the nigrostriatal motor system of rats (Zimmerberg *et al.*, 1974; Glick *et al.*, 1977). Normal rats have a 10—15 per cent difference between the dopamine content of the ‘high’ and low side of the nigrostriatal pathway, but the ‘high’ side is as often on the left as on the right. A large dose of amphetamine increases the disparity between ‘high’ and ‘low’ sides to 25—30 per cent, and the difference is accompanied by behavioural side preferences (see later section). This is another example of individual variations in left/right balance within a species, with the bias towards left or right varying randomly. It is conceivable that random irregularities make individual variations in sensory and motor efficiency on the left and right a common occurrence, without contributing to the behavioural characteristics of the species.

For rare examples of an entirely different state of affairs, where a species has a characteristic asymmetry between left and right motor systems, one has to fall back on the flat-fish, where left corresponds to bottom, and right to top, or vice versa according to species (Neville, 1976). Even rarer is a pronounced sensori-motor asymmetry in an upright species: the New Zealand Wryneck is a bird with its entire bill curved sharply to the right, and as a consequence it must adopt a rigidly unilateral approach to the business of turning over pebbles (Thomson, 1964).

## **2. Functional asymmetry in man**

### *2.1 Handedness*

There is little doubt that the study of functional asymmetry in animals is predicated on the existence of a reliable human model. Agreement on the nature and significance of functional asymmetries in man is not universal ; but it is necessary to isolate features of the phenomena that can serve as the basis for cross-species comparisons. The most visible asymmetrical human attribute is, of course, right-handedness.

Human handedness is not quite so fixed and unitary a trend as the quotation of a 90 per cent incidence of right preference implies (Annett, 1970, 1972). Our apprehension of handedness is influenced by its most obvious manifestation — handwriting. This skill is severely lateralized (Annett, 1970) in that writing with the left hand is rare within population samples, and very few individuals can be said to have equal proficiency with the non-preferred hand. However, it is rather unlikely that the human species is genetically specialized for unilateral handwriting as such, since it is not a skill which has had much time to operate as a selection pressure. The most lateralized skill of all those assessed by Annett

(1970) was hammering, which has a long enough history to be a more plausible candidate for special evolutionary selection (e.g., Oakley, 1972)..

Annett (1972) suggests that there is a large group of individuals of 'mixed handedness' who perform some tasks (e.g., writing) with one hand, other (e.g., throwing, or using scissors) with the opposite hand, and some skills (e.g., unscrewing the top of a jar) with either hand. Human handedness, Annett concludes, is a continuous dimension, though heavily skewed towards right-handedness.

#### *Preference, capacity and transferability*

It would be helpful to know whether human handedness consists of a difference in preferred uses to which the two hands are put, or more fundamental differences in the capacities of the left and right hands (or rather, of the contralateral hemispheres that control them). In the context of theories of cerebral dominance, it could be assumed that the right hand is preferred for detailed work, because only the left hemisphere is capable of supporting highly organized sequences of limb and finger movements. Forcing the right hemisphere to undertake control of activities which are properly the province of the left should therefore result in clumsier performance. This is a stronger proposition than simple preference — individual animals, or even particular animal species might exhibit arbitrary preferences without an underlying disparity of hemispheric capacities.

The only thing which can be said with any confidence about human handedness and hemispheric capacities is that the capabilities of the minor hemisphere might not be as limited as the bare facts of hand preference might suggest. The evidence for at least adequate capacities of the minor hemisphere for control of manual skill can be drawn from the existence of individuals with mixed handedness (Annett, 1970) and from forced use of the non-preferred hand in some skills, notably the playing of musical instruments (Oldfield, 1969). Individuals who write with one hand and perform high level skills with the other (for example, in bowling a cricket ball, or using a tennis racket) demonstrate that motor incompetence of one of the hemispheres need not be regarded as a defining feature of human handedness. There is no evidence that 'left-handers' have difficulties in playing 'right-handed' musical instruments (Oldfield, 1969). Most musical instruments require fine motor control of both hands, which in itself indicates minor hemisphere potential. Some, such as the piano, seem to require faster or more delicate performance by the right hand, but left-handers are not known to be disadvantaged by this arrangement. A few instruments, in particular the violin and similar stringed instruments, require very fine control of left-hand finger movements, yet are not the exclusive preserve of the left-handed. It is arguable that movements of the left hand of a virtuoso violinist represent the high point of human dexterity. Oldfield (1969) suggests that this anomaly results from a left-hand preference for holding, exhibited initially when instruments were played by right-hand manipulation of open strings, and retained when changes in technique demanded detailed movements by the holding hand. Similarly, when the French horn acquired keys, the left hand, originally limited to holding the instrument while the right hand altered pitch by occluding the open horn, adopted the 'dextrous' job of key fingering. Oldfield wonders whether the right arm may be more adept at ballistic movements, with left-side capabilities limited to modification of finger holds. But accurate ballistic use of the left hand, by right-handers, is evident in the skilled playing of stringed instruments (and in certain styles of boxing).

It is arguable, therefore, that human handedness is largely a matter of preference, rather than a consequence of biologically programmed inadequacies of the minor hemisphere. As a species, humans are right-handed. However, there is a small minority of left-handers, both familial (fairly ambidextrous) and non-familial (strongly left-handed Hardyck & Petrinovich, 1977). Both kinds of left-handers are recognizably human, even if suffering from minor intellectual impairments (Levy, 1969; Hardyck *et al.*, 1976). For the purpose of comparisons

with other species it is all the more appropriate to consider human handedness as a continuous distribution of preferences, skewed towards the right (Annett, 1970, 1972, 1975).

## *2.2 Language*

It is widely held that human language is controlled by the left side of the brain. The strongest evidence for this is neurological — individuals who suffer left-sided damage are more likely to also show language deficits than patients with right-hemisphere damage (e.g., Mimer, 1974; Coughian & Warrington, 1978). Post-mortem confirmation of side of lesions shows that very few patients with language deficits resulting from brain damage have lesions in the right hemisphere (Zangwill, 1960). Other diagnostic techniques support this finding, and even left-handers are found to suffer more impairment of language performance after left-sided hemispheric insult (Milner, 1974).

The neurological literature on various sorts of language dysfunction after brain damage is exceedingly complex: individual differences abound (Ojemann & Whitaker, 1978), and almost every conceivable permutation and combination of impairments and preservations of speech production, speech comprehension, reading and writing may occur (Goldstein, 1948 ; Gardner, 1977). Studies of patients who have undergone section of the cerebral commissures for the relief of epilepsy have confirmed that the left hemisphere is more important for language functions than the right (Sperry, 1968; Gazzaniga, 1975) but also support the contention that the right hemisphere normally possesses some limited abilities, especially for language comprehension (Zaidel, 1978).

We take it, then, that left-hemisphere dominance of language functions is a species-specific human characteristic ; but with qualifications. The right hemisphere is quite capable of accomplishing human language at almost, if not completely, normal level, if the left hemisphere is damaged at an early age (Basser, 1962; Dennis & Whitaker, 1976), and may play some part in language function in all individuals (Searleman, 1977 ; Zangwill, 1978 ; Coltheart, 1979).

## *2.3 Perception*

### *Hearing*

It is difficult to isolate hearing generally from speech reception. When speech is played into the left and right ears simultaneously, in dichotic listening studies, normal right-handed human subjects frequently show a right ear advantage (Darwin, 1974; Springer, 1977). The difference is not a large one; given the success of the mammalian auditory pathways in directing the input from each ear to both hemispheres (Whitfield, 1967) a large difference would not be expected and the technique is not without its critics as a method for diagnosing lateralization of speech functions (Berlin, 1977; Colbourn, 1978). Hearing generally is resistant to impairment from unilateral temporal lobe damage (Whitfield, 1967; Adams & Victor, 1977); but there are some reports that right-hemisphere lesions impair memory for complex non-verbal sounds (Ravizza & Belmore, 1978).

The evidence from professional music performers or composers who suffer unilateral brain damage is not sufficiently consistent to allow an assignment of music perception to one or other of the hemispheres (Gardner, 1977) although the momentum of cerebral dominance theories would place it on the right (Ornstein, 1972). The right hemisphere may have specializations for hearing, but these can show individual, and cultural, variations (Tsunoda, 1975).

### *Vision*

There is a large amount of data on the performance of normal subjects in perceiving stimuli presented to their left or right visual fields (Hardyck, 1977; Springer, 1977) and a somewhat smaller amount concerned with the visual abilities of the left and right hemispheres of commissurotomy patients (Gazzaniga, 1975). The findings fall into two categories: the left hemisphere (right visual field) is better, or quicker at recognizing brief alpha-numeric stimuli ; and the right hemisphere is better at analysing more complex visual-spatial relationships.

In the case of normal subjects viewing visual stimuli in the left or right visual field, differing responses are Of course a matter of degree — significant differences are found with a fair degree of regularity, though not universally, but the differences are small (Hardyck, 1977). Given that the stimuli tare usually words or numbers, it is difficult to isolate an asymmetry in human vision from the left hemisphere language advantage.

Evidence for a right-hemisphere superiority in visual-spatial perception rests on the performance of the individual hemispheres of split-brain patients (Levy, 1969 ; Nebes, 1971, 1974) and of patients with unilateral brain damage (Mimer, 1974). If a three-dimensional shape held in one hand had to be matched with an ‘unfolded’ two-dimensional representation of the shape, presented visually, the left hand (right hemisphere) was more successful than the right hand for right-handed commissurotomy patients (Levy, 1969). Matching an arc of a circle with the circle to which it belonged (from a choice of three) was more successful if both arc and circle were presented to the right hemisphere (either by touch or sight, or in a combination of the two) than to the left, in four out of five similar patients (Nebes, 1971).

#### *2.4 Emotionality*

A final area in which the human hemispheres have been supposed to be differentially S involved is the expression, perception, or experience of emotion. There is some evidence to support the view that emotions are expressed more intensely on the left side of the face (Sackheim *et al.*, 1978). Although it would appear to be counter-productive, if that is the case, observers seem to pay more attention to their left visual field (and thus to the less active side of the observed person) when making judgements of the emotional content of facial expression (Campbell, 1978). More generally, emotional life is assigned to the control of the right hemisphere (Gainotti, 1972 ; Ornstein, 1972; Gazzaniga, 1975).

#### *2.5 Sex differences*

Theories of human sexual differences are not without interest in the context of a comparative survey, insofar as other species, with more pronounced sexual dimorphisms, might be expected to reveal more exaggerated sex differences in behaviour. In terms of the behavioural categories discussed so far, human sex differences have been proposed. Incidence of right-handedness is higher in the human female than in the male (Hardyck & Petrinovich, 1977). Females are found to be better than males at speech-related tasks (Maccoby & Jacklin, 1975) ; females may perform less efficiently than males at visual-spatial tests (Witelson, 1976) and are generally held to be more emotional than males (Maccoby & Jacklin, 1975). These findings do not fall into place in terms of either more or less lateralization but it is usually argued that females are less lateralized than males (e.g., Witelson, 1976; McGlone, 1977). If one were to take all proposed sex differences at face value, it would seem, not that females are necessarily less lateralized, but that they devote the left hemisphere very successfully to speech rather than to logic and mathematics, and use the right hemisphere for emotion instead of spatial perception.

## 2.6 Conclusions

The tendency for individuals to perform tasks with only one hand, and for this hand to be the right hand, is extremely marked in the human species. The evidence that species-specific vocalizations are produced and interpreted by one hemisphere rather than both, and that the dominant hemisphere in this sense is usually the left, is very strong. By comparison, the evidence for other asymmetries in cerebral function, entirely unrelated to language or handedness, is less robust, but it is thought that the right hemisphere may be better than the left at complex visual-spatial perception, and may carry a greater responsibility for various forms of emotionality.

### 3. Functional asymmetry in non-human vertebrates

In asking whether anything similar to human functional lateralization may be observed in other species, two areas — one-sided motor preferences, and unequal use of the cerebral hemispheres in vocalization and communication — appear to have prime importance, and sections under these two headings follow. Most of the remaining findings to do with human functional asymmetry can be discussed in terms of perception, or emotionality, and a final section covers animal work under these headings.

#### 3.1 Lateralization of motor performance

Of work which may be related to functional lateralization in animals the largest category by far concerns putative analogues to human handedness, in terms of forelimb preferences. Many species of mammals, particularly rodents and primates, make regular use of the forelimbs for moving external objects, in the course of finding food, and carrying it to the mouth, or in nest-building and digging. Some carnivores, notably bears and raccoons, are well adapted for manipulative use of the forelimbs, and although little work has been done in these species, use of the forepaw in the domestic cat has received some experimental attention. The data available are therefore not comprehensive, being heavily biased towards rats, cats and monkeys. Use of hind limbs for object manipulation does occur in some species of primate, and in bats and birds, but is less studied, although Friedman & Davis (1938) reported that individuals from several species of parrot showed a preference for the use of the left claw to hold food. ‘

##### *Forepaw preferences in rats and mice*

The standard sort of test for animal forepaw preferences and typical results are described in the monograph by Peterson (1934); these tests were used in the work of his contemporaries and collaborators (e.g. Yoshioka, 1930; Peterson, 1951 ; Peterson & McGiboney, 1951; Peterson & Devine, 1963). The test requires the animal to reach for food contained in a tube or dish arranged in such a way that single-paw reaches are elicited. The relative number of right-limb and left-limb reaches in individual animals is easily measured, and the effect of experimental variables on such numbers may be assessed. The conclusions reported by Peterson (1934) apply to subsequent work on the rat to the work of Collins (1977) with mice.

(a) Most rats show a strong paw preference in food reaching. Although 75 per cent of reaches with one hand is sometimes used as a criterion for handedness, individual animals commonly show almost exclusive use of one paw during daily sessions and across sessions separated by months. On these grounds rats may be said to satisfy one of the criteria of human handedness: most individual rats consistently prefer one limb over the other, in some tasks. It is noteworthy that fatigue, or response inhibition, does not prevent these strong preferences from emerging.

(b) Rat populations contain equal numbers of right-pawed and left-pawed animals on the food-reaching task: the distribution of handedness shows no sign of being skewed, and in this sense rat populations are distinctly different from human populations.

(c) Rat samples contain a small proportion of individuals that alternate from one paw to the other in the food-reaching task. Less than 10 per cent of a sample is usually ambidextrous in this way, with the remaining 90 per cent equally divided between the left and right handers.

(d) Rats that prefer one paw in the food-reaching task do not necessarily prefer the same paw in other tasks (Peterson assessed lever pressing and latch-opening).

(e) The proportion of animals left- or right-pawed for food reaching cannot be altered by selective breeding.

The results obtained by Collins (1968, 1969, 1975, 1977) with inbred strains of mice reaching down a tube for food do not conflict in any way with the above conclusions for rats. The fact that inbred strains (which may be considered to consist of individuals which are genetically very similar to each other) contain equal proportions of left- and right-handers, implies that a random process determines whether an individual will show a left or right preference. Collins (1969) found no change in distribution of preferences after three generations of selective mating for left or right preferences, but did not breed for lack of preference (ambidexterity). His view, however (Collins, 1977), is that the degree of laterality (for food-reaching behaviour) though not the direction of laterality, is subject to genetic variability. There is little evidence for this, since different strains vary only very slightly in degree of laterality (Collins, 1968); but females of the strain most studied by Collins (1977) consistently show a higher degree of lateralization (i.e. have stronger paw preferences with more females making at least 98 per cent of reaches with the same limb) than males.

A similar sort of food-reaching handedness to that observed in rats and mice may be characteristic of marsupials. Megirian *et al.* (1977) studied reaching responses in an Australian species (the brush-tailed opossum, *Trichosurus vulpecula*) using a centrally positioned narrow tube facing the animal, (very like Collins' apparatus for mice). Of the 78 animals tested, 51 per cent had a 'consistent and predominant' preference for using the left forepaw, 45 per cent had the same kind of preference for the right paw, with only 4 per cent (three subjects) being classed as ambidextrous.

#### *Constitutional and environmental determinants of food-reaching laterality*

Since the distribution of handedness for food-reaching in these lower mammals appears to be random, with roughly equal numbers of left- and right-pawed animals, it is possible to entertain an environmentalist null hypothesis; the choice of limb on the first trial is random for each individual, but success on the first trial predisposes the choice of the same limb on the next occasion, with cumulative learning accounting for the observed individual preferences. An alternative hypothesis is that a random embryological or developmental process makes equal numbers of individuals constitutionally left- or right-handed (Collins, 1977; Morgan, 1977).

Asymmetrical layout of the testing space has a strong immediate influence on observed choice of limbs. A physical barrier, which makes it awkward or impossible to use the previously preferred limb, induces immediate use of the non-preferred limb in rats and brush-tailed opossums whose initial preference has been already assessed (Peterson, 1934; Megirian *et al.*, 1977). If the opening of a tube leading away from the animal is situated flush with the side wall, most mice use the limb on that side in the initial exposure to the problem, as opposed to the 50-50 distribution obtained with a tube opening in the middle of the facing wall (Collins, 1975).

The malleability of preference in response to the local geography suggests a strong role for environmental rather than constitutional factors in determining whether an individual

animal will show left or right preference. However, several other lines of evidence imply that the simple environmental hypothesis that preference is due to random behavioural factors plus cumulative learning is not a complete explanation. Collins (1975) tested mice initially with a tube on one side (the left, say) which produced a J-shaped frequency distribution — most mice favoured the limb on the same side as the tube opening but approximately 10 per cent of the populations resisted the environmental pressure, and had preferences of various strengths for the more awkward limb. The same mice were then, after two sessions in the initial apparatus (biased, for instance, to the left), tested with the tube opening on the opposite side (in this example, to the right). Now the distribution of preferences became almost U shaped, with the modal category being mice who showed an immediate and very strong (over 96 per cent) preference for the paw consistent with the current apparatus. But roughly half the mice showed a preference of some degree for the limb which was used in the initial testing; which was now environmentally inappropriate. Collins (1968, 1977) showed that the mice who retained the initial preference when it was inappropriate had also demonstrated that preference more strongly when it matched the environment; whereas the mice which quickly switched to the easy response in the second apparatus, had shown lesser degrees of environmental influence towards the first direction.

Although an explanation for this in terms of individual differences in rate of learning could probably be concocted, the most direct interpretation, as given by Collins, is that a distribution of handedness in mice is present before the first test. Right-handed mice tested in a 'left-handed world' resist the practical advantages of conforming to the environment by comparison with the higher preference scores of the left-handers, and eagerly switch to their natural limb when tested in the right-handed apparatus, whereas the left-handers with the experience of putting their favoured limb to good use in the first two sessions have a tendency to stick to their guns when subsequently tested in the right-handed apparatus.

The resistance of animals to experimental variables designed to alter their demonstrated paw preference is most amply illustrated by the brush-tailed opossums studied by Megirian *et al.* (1977). Large cortical lesions, intended to destroy all sensory and motor areas contralateral to the preferred limb, failed to produce preference shifts in 13 out of 15 animals, who persisted with their previously preferred limb, despite some qualitatively and quantitatively observed loss of efficiency. The cortical lesions did not seriously impair the ability to use the preferred limb. This may be due to greater subcortical control of movement in marsupials as opposed to rats which do tend to switch preference as a result of contralateral lesions of motor cortex (Peterson & McGiboney, 1951). However, almost total impairment of ability to move the preferred limb — by injections of local anaesthetic — did not result in any change of preference. All seven opossums tested for one session (of 1-2 hours) after this intervention continued to make unsuccessful attempts to use the disabled limb instead of switching to the unaffected, but non-preferred, limb. Are marsupials, lacking the corpus callosum, quite unable to transfer skills from one side of the body to another? This is not the case: they are unwilling, rather than unable, to use the non-preferred limb after interference with the preferred limb by cortical damage or peripheral anaesthesia. One is led to this conclusion by the performance of another group of brush-tailed opossums (Megirian *et al.*, 1977), who were persuaded to switch preference by the presence of a physical barrier. The normal reaching practice was to squat on one side of the tube opening and insert down the tube the limb thus positioned in front of it. When a large block of wood was bolted to the inside of the cage, where the opossums normally squatted, 10 out of 12 subjects had, within 5 minutes, simply adopted the habit of squatting on the opposite side and using their non-preferred limb in a mirror image version of their initial performance. This indicates that the animals normally have the capacity to make use of their non-preferred limb if they perceive the necessity for it. But the forced practice induced in these 10 subjects did not change the

original preference when the barrier was removed they reverted to their initially preferred paw. The strength of the initial preference, even if capacity in the non-preferred limb is available, is also indicated by the performance of the other two subjects in the group confronted with the physical barrier where they normally squatted. Instead of laterally reversing their stance, these animals employed other postural strategies which enabled continued use of the preferred paw; for example, an 'up-down' reversal of hanging upside down above the tube opening (Megirian *et al.*, 1977).

These results make it extremely unlikely that the limb preferences observed in these marsupials were learned during the testing period. Rather, the animals had a behavioural or constitutionally derived preference revealed by the test. It was noted above that some individuals in this species have a strong anatomical asymmetry in the thalamus (Haight & Neylon, 1978).

It is possible that food-reaching preferences in rats are more subject to environmental influences than preferences in marsupials, since Peterson (1951) was apparently able to reverse initial preferences by forced practice with the non-preferred limb. However, only some individual rats showed the change in preferred limb, and the forced practice was very extensive (up to 1000 trials), so there may not necessarily be species differences between brush-tailed opossums and rats.

Peterson (1951) assessed the influence of three experimental procedures on subsequent expressed limb preference. In one group, animals were allowed to eat from a dish having a flange which prevented use of the preferred limb. A second group fed from a symmetrical dish but had the preferred limb strapped to the body with adhesive tape. A third group lived through the testing period with their preferred forelimb strapped to the body, but were not exposed to the reaching apparatus (though they fed themselves as usual in the home cages). Animals in the first two groups, given specific training with the non-preferred limb, shifted their preference. Animals in the third group might be compared to the local anaesthesia condition of Megirian *et al.* (1977), since they experienced stiffness in the initially preferred limb when it was unbound, but showed no signs of switching to the more physically able, but less preferred, paw (Peterson, 1951). Like the brush-tailed opossums, rats may sometimes persevere with the use of the preferred paw in the presence of a barrier designed by the experimenters to discourage them from doing so (Megirian *et al.*, 1974).

It may be concluded that rats, mice and the brush-tailed opossum tend to show strong, consistent forelimb preferences for food reaching, which are not acquired during testing, and which are resistant to various anti-preference measures. In all these species the proportion of left-pawed animals is the same as the proportion of right-pawed, with very few ambidextrous individuals.

#### *Rotation and other side preferences*

Rats can be made to turn around in circles by lesioning the subcortical basal ganglia of one hemisphere, or by unilateral lesions at other stages of the extra-pyramidal motor pathway (Crow, 1971). They always turn towards the side of the lesion, or towards the less active side of the nigrostriatal system, and this phenomenon has been very useful for psychopharmacological investigations since recovered lesioned animals will rotate in response to dopaminergic drugs (Christie & Crow, 1971). As mentioned in the previous section on anatomy, there seems to be a slight pharmacological asymmetry of the nigrostriatal motor pathway in normal animals, which is enhanced by the administration of amphetamine. This sort of asymmetry in motor pathways would provide an example of a 'constitutional' substrate underlying lateralization of motor behaviours, including forepaw reaching. There are no data on whether handedness in food reaching is correlated with physical asymmetries of motor pathways, but there is some indication that nigrostriatal asymmetries affect rotation, T-maze choices and bar-pressing (Glick *et al.*, 1977).



Intact rats will make frequent rotations (in the horizontal plane) in response to certain doses of amphetamine (especially if placed in a spherical enclosure), and individual animals exhibit a preference for one or other direction. Glick *et al.* (1977) believe that this preference reflects the underlying nigrostriatal asymmetry. Their view is supported by their finding that the direction of turning when rats are first placed in a spherical enclosure, or when activity therein is elicited by air puffs or shocks, is the same direction as that shown when rotation is due to a small dose of amphetamine.

Glick *et al.* (1977) also report that side preference in a T-maze is related to higher concentrations of dopamine in the contralateral striatum. Rats were shocked in the central arm of the maze, and allowed to escape into either the left or the right arm. On 10 consecutive trials, they showed side preferences that were stable from day to day and from week to week. Subsequent bilateral assays of dopamine showed a significantly higher mean level of this substance in the striatum contralateral to the preferred direction of turn in the T-maze.

Side preferences ('position habits') are ubiquitous and usually an annoyance to be eliminated whenever animals are required to make spatial choices ; but it is unlikely that nigrostriatal asymmetry is the only variable involved. For instance, rats allowed to press either a lever to the left of water location or a lever to the right to produce intermittent water rewards established strong preferences for the right or left lever; but videotape observation revealed that while about 75 per cent of the animals pressed the right lever with their right paw, or the left with their left, a quarter of them tried to press the right lever with the left paw or the left lever with the right paw. This makes assignment of laterality problematical (Glick, 1973 ; Glick & Jerussi, 1974). In these experiments, amphetamine (which, on the basis of the rotation results, increases nigrostriatal asymmetry) tended to shift lever preference towards paw preference (for example, right-pawed rats initially preferring to press the left lever shifted their preference to the right lever when injected with amphetamine). This probably means that paw choice is more closely tied to nigrostriatal factors than lever choice and that position habits for lever pressing are influenced by other variables.

It is at present a matter for conjecture, but these pharmacological and anatomical variables investigated initially in the context of rotation may eventually add substance to the claim of Collins (1977) and others that individual rodents are constitutionally left- or right-handed.

It is also useful to emphasize that motor asymmetries are not necessarily tied to *manipulation*. Asymmetries in locomotion, or in other species-specific activities, may be more interesting in some contexts (for instance, in relation to genetic control) than food reaching. Some species of Baleen whales, though lacking the skeletal distortions of the other suborder, may have skewed distributions of side preferences. Whales often swim on their sides near the bottom, or when feeding, and asymmetries of colouring (Fin whales) or in acquired barnacle encrustations (Gray whales), as well as direct observation, suggest that a large majority of individuals in some species swim more often with the right side down (Mathews, 1978). It used to be thought that there was a spiral component in whale tail movements, and Thompson (1942) believed that counter-torque at the head, during growth, produced Cetacean skull asymmetries in general, and the rifling of the Narwhal's tusk in particular, but this theory has not been supported by subsequent observations (Mathews, 1978).

It seems generally agreed that in another large mammalian species, the African elephant, particular animals have a preference for one of the tusks, which is consequently known as the 'servant' tusk (Sikes, 1971), but reports that the right tusk is generally more worn than the left (e.g. Shortridge, 1934) are probably not reliable. The use of asymmetrical gaits by horses is well known, as is the preference of some individual racehorses for turns in one direction. The use of asymmetrical gaits is extremely widespread in mammals (and also occurs in

amphibians and reptiles), but individuals typically switch from right-lead to left-lead versions as circumstances require. Very little is known about the frequency of individual preferences, or the distribution of such preferences within or between species (see Hildebrand, 1977, for a review).

Apart from locomotion, another category of behaviour where some species asymmetries are known, although information is sparse, is courtship and mating. Genital asymmetries are not uncommon in insects (Neville, 1976) and in the cephalopods, molluscs which may be counted honorary vertebrates on the grounds of brain development, mating is usually dextral. In the common octopus, for instance, the third arm on the right is modified as a sperm-transferring organ in the male (Wells, 1978). In the vertebrates, a similar degree of anatomically unambiguous asymmetry in copulation is probably confined to fish, but lopsided behaviour may be found in reptiles and mammals. One of the most celebrated vertebrate asymmetries occurs in the four-eyed fish (*Anableps anableps*) in which the large intromittent organ of the male is angled either to the right or to the left, and so is the female's genital opening, so that dextral males must mate with sinistral females, and so on. Garman (1896) claimed that there was a small preponderance of dextral males and sinistral females in his sample, so that the remaining (40 per cent) sinistral males and dextral females would have been at a disadvantage, but his observations do not seem to have been repeated. A related genus (Jenynsiids) has dextral and sinistral forms for both sexes, and a different order (Phallostethiformes) with another sort of copulatory organ has dextral and sinistral males, but bilaterally symmetrical females (Breder & Rosen, 1966). However, even more interesting in terms of genetic and non-genetic theories of asymmetries are species in which all or most individuals have the same laterality. The family of live-bearers (Poeciliidae — in the same order as *Anableps*) includes many such species, and a detailed anatomical survey of this family has been provided by Rosen & Bailey (1963). In the main subfamily, 136 species were grouped in 19 genera, with species-wide asymmetries of the male sexual organ characteristic of five genera. Of these five, two genera contain only sinistral species ; one genus is composed of dextral species ; in one genus species are either dextral or sinistral ; and in the last genus species may be either sinistral, dextral or symmetrical. Rosen & Tucker (1961) observed sexual behaviour in species from 13 of the genera. (The family is of small fish, 'suited to the aquarium one of the symmetrical genera includes the guppy.) Not surprisingly, they found that 100 per cent of the erections seen in an anatomically sinistral species were angled to the left. However, it was also found that a species with only slight physical sinistrality had 90 per cent of its erections to the left side, and a symmetrical species had most erections pointing to one side or the other, in equal numbers over the species, but with individuals showing right or left biases, confirming the report by Aronson & Clark (1952). This emphasizes that anatomical bilateral symmetry by no means precludes unilateral behaviours, although in this case no species-wide behavioural asymmetries were observed in physically symmetrical species. Another general point is that side-to-side pairings are inherently asymmetrical: although left or right choices will probably be made at random in the vast majority of species, it is conceivable that behavioural sinistrality or dextrality occurs in species of fish without the anatomical predestination which takes place in these South American live-bearers.

Several thousand species of lower vertebrates have a similar kind of unilateral choice. In sharks and rays, and lizards and snakes, the male is equipped with two intromittant organs, both left and right, although the female possesses only one relevant orifice. Very little indeed is known about the deployment of the sexual anatomy in any of these species (Breder & Rosen, 1966; Carpenter & Ferguson, 1977), but in general it is clear that individual copulations must be either dextral or sinistral, although some species of shark are reputed to accomplish simultaneous insertion of both 'claspers'. It may be that the anatomical

duplication invariably indicates an adaptation for the purpose of individual ambidexterity at a sideways task, but the possibility of unilateral preferences, in reptiles at least, is suggested by the peculiar behaviour of the Virginia opossum. This animal is a marsupial mammal considered not far removed from its reptilian ancestry. (It is sometimes called a 'living fossil', but should not be regarded as necessarily representative of any larger group — Clemens, 1977. It is *not* closely related to the brush-tailed opossum.) Some authorities have claimed that the Virginia opossum can conceive only while lying on its right side (e.g. Reynolds, 1952). A more considered view is that 'It is obvious that the right side is the preferred one for the species and left-side copulation could reduce the probability of fertilization' (Hunsaker & Shupe, 1977, p. 288). Left-sided matings have been observed, but the more frequent practice appears to be for the male opossum to mount the female from the rear, whereupon the pair falls to the right and intromission then takes place. In all marsupials (except kangaroos), semen must traverse the left and/or right lateral vaginas of the female, and the penis of the male is bifurcated (Sharman, 1970). Some anatomical advantage for the right-side channel, which would not be inconsistent with the individual variations observed by Ratcliffe (1941), might render asymmetrical behaviours worthwhile in the Virginia opossum and close relatives. In general, reproductive behaviour in mammals is bilaterally symmetrical. The urogenital system of vertebrates, like other internal organs, may frequently be asymmetrical, without leading to overt biases in behaviour. Although birds and lower vertebrates have more pronounced reproductive asymmetries than mammals (only the left oviduct is usually functional in birds) slight genital inequalities also occur in mammals. Implantation in only the right horn of the uterus occurs in some species of ungulates and rodents as well as in several species of bat (Adsell, 1966). There is a curious asymmetry in the reproductive organs of domestic even-toed ungulates, especially pigs and cattle, in that the penis shows a pronounced spiral deviation, like that of a left-handed corkscrew, with corresponding spiral ridges in the cervix of the female. Semen is ejected to the left and there are various asymmetries within the penis (Ashdown *et al.*, 1968; Hafez, 1974).

It is extremely unlikely that these reproductive asymmetries are directly related to human handedness, but they are important to consider in the light of genetic and embryological theories of animal asymmetry in biology as a whole (Corballis & Morgan, 1978). In the cases of live-bearing fish and the Virginia opossum, it is possible that behavioural preferences would be reflected by differential effects of left- and right-hemispheric lesions on reproductive activity. Corballis & Morgan (1978) put forward the hypothesis that there is a universal vertebrate tendency for the left side of the body to develop faster than the right, which needs numerous modifications to account for the lack of consistency, between and within species, in manifestations of the universal tendency. Variations in direction of lateralization in the reproductive system, between both unrelated and closely related vertebrate species, suggest that any universal left-leading tendency allows equally well for sinistral, dextral and bilateral structures.

#### *Forepaw preferences in cats*

Domestic cats often use the forepaws one at a time — to pat a ball of paper in play, or to make a strike in more serious hunting — and pieces of food 'transfixed on one paw may be taken directly into the mouth. Experimental assessment of paw preferences in cats has been performed with methods similar to those used with other animals — variations on the theme of reaching for static items of food. Cole (1955) observed 60 cats reaching for food placed in a transparent tube fixed on the floor of the cage. Using a criterion of 75/100 reaches with the same paw, only 20 per cent were right-handed, 38.3 per cent were left-handed and 41.7 per cent were ambidextrous. The preponderance of left-handers has not been confirmed by others (Forward *et al.*, 1962; Warren *et al.*, 1967) but the high proportion of ambidextrous cats appears to be a reliable finding: Warren *et al.* (1967) tested 34 young cats and of these 48 per

cent were ambidextrous using the 75 per cent criterion. This is for reaching out of a 'handedness box' through a 2 in gap between the floor and the bottom edge of a glass front. There was no difference between the preference scores of animals given over 1000 trials in the box between 2 and 5 months of age, and animals tested for the first time at 5 months, which suggests that early learning was not a factor. The same 34 cats were given five more reaching tests by Warren *et al.* (1967) immediately after the handedness box test. These involved reaching through vertical bars at the front of a large cage for a piece of meat which was either in a food well, or covered by a wooden block which could be pushed aside, or in a trough, or in a glass tube, or under a large block that had to be pushed away. Seventeen of the 34 cats preferred the same paw in all the reaching tasks (50 per cent) and, of these, 15 had consistent significant preferences (44 per cent).

It seems reasonable to say that about half the cats had paw preferences, whereas the other half did not. This would make cats considerably more ambidextrous than the rats, mice or Australian opossums discussed above. There is no reason why cats should not differ from rodents or marsupials on degree of laterality of food reaching. Although the apparent differences may be partly a matter of treatment of data, 62 per cent of the mice studied by Collins (1977) made at least 96 per cent of their reaches with the same limb, while only 38 per cent of Warren *et al.*'s kittens reached a similar criterion in the handedness box.

#### *Hand preferences in primates*

Use of the forelimbs for gathering and inspection of food and for bringing it to the mouth is typical of primates from bush-babies to man (Jolly, 1972), although all species also make some use of the hands in locomotion. Small and primitive primates such as the bush-baby normally use their hands for catching insects (a task requiring a considerable degree of accuracy and speed), while the anthropoid apes have a well-developed precision grip between the side of the thumb and index finger (Napier, 1961). However, data on handedness in non-human primates is extremely limited and consists largely of studies of food reaching in the rhesus monkey.

Much of the work on food reaching in rhesus monkeys is due to Warren (Warren, 1953, 1958, 1977; Warren *et al.*, 1967). The view expressed by Warren *et al.* (1967) was that 'rhesus monkeys have lateral preferences that are relatively strong, moderately stable over many months, and rather resistant to change by training', with the implication that the preferences were homologous to human handedness. More recently, Warren (1977) has explicitly recanted this implication and emphasized the dissimilarities between monkey hand-preferences and human handedness.

The character of the evidence for lateral preferences in monkeys is relatively straightforward, if the theoretical implications are not: food-reaching hand preferences in rhesus monkeys are roughly similar to those observed in rodents. The 'method for assessing handedness is also similar, except that monkeys pick up small items of food with one hand under more varied conditions. .

Warren *et al.* (1967) and Warren (1977) discuss the results from a number of variations of the food-reaching test using a Wisconsin General Test Apparatus (Harlow, 1949). A peanut or raisin was presented, either on the surface of the food tray in front of the monkey's cage, or at the end of a wooden trough extended away from the animal, or in a horizontal tube, or in a vertical tube. In an additional test, cereal rings were presented on horizontal wires in order to observe lateral movements — but the monkeys usually just broke the food off the wire.

Typical performance in the WGTA requires object displacement — the pushing away of a card or block which covers a food-well. Usually monkeys push the covering object with one hand and pick up the peanut with the other, and therefore the object displacement qualifies as a bimanual task. The Warren studies employed three object-displacement tests (with a tin, a

card and a wooden block as food covers), and two further bimanual tests: pulling in a raisin on the end of a light chain and dragging towards the cage (by a handle) a small wooden box placed far enough away to make this necessary if the animal was to get at the reward contained in it.

Fourteen monkeys were tested on the entire series of tasks 200 trials on each test) and were retested twice 2 years later. Taking mean preference scores across all tests, the monkeys ranged evenly from strongly left-handed to strongly right-handed, and there was a significant correlation between the overall preference scores obtained 2 years apart ( $\rho = 0.85$ ). This was the basis for the conclusion of Warren *et al.* (1967) that stable and consistent hand preferences were observed, although, as with other animals, there was no indication of right- or left-handedness in the sample as a whole. The misgivings expressed by Warren (1977) arose from more detailed analysis of the same data, which showed that the consistency of the total preference scores was not characteristic of each individual test. There appeared to be three categories of test. The object displacement tests (requiring the pushing away of a tin, card or block from the food-well) not surprisingly correlated with each other very well at all stages. Four of the food-reaching tests (from the surface, vertical tube, trough, or box) were initially not inter-correlated, but at the two retests were correlated with each other and the object displacement tasks. Finally, reaching for food from the wire or horizontal tube, or from the end of the chain, and pulling at the chain or box, did not correlate well with each other or with the other tasks at any stage.

Warren (1977) interprets this variability between tasks as meaning that hand preferences in monkeys is task-specific, and strongly affected by experience and practice, and therefore not revealing of organismic or constitutional asymmetries, and not homologous to human handedness. Another study of 171 rhesus monkeys' simple food reaching from the home cage found that consistency and strength of hand preference increased considerably over only 3 days of testing (with 100 reaches twice each day — Lehman, 1978). An aspect of task specificity in Warren's data is that the bimanual object displacement tasks gave more consistent preference scores than the unimanual reaching response. Beck & Barton (1972) also found that a much higher proportion of monkeys (in this case, stump-tail macaques) had stronger preferences for bimanual than for single-handed tasks. In their experiments the bimanual tasks were more demanding than object displacement they included holding open a spring-loaded drawer with one hand while taking out a raisin with the other, and undoing a series of latches in order to open a box. Task difficulty in general, or complementary asymmetrical use of both hands in particular, may increase the degree of hand preference exhibited by non-human primates.

There are few systematic data on hand preferences in apes, but it is unlikely that handedness is any more significant in the behaviour of wild apes than it is in monkeys — neither the observations of Schaller (1963) of gorillas in their natural habitat, nor those of Goodall (1965) on chimpanzees, revealed strong hand preferences for food reaching in groups or in individuals. Goodall (1965) states that in the much cited chimpanzee tool-using behaviour — 'fishing' for termites with a piece of grass — either hand may be used. Schaller reported that of 72 male gorillas observed chest-beating, 59 (82 per cent) began with their right hands, but does not report strong limb preferences for the associated unilateral displays of leg kicking and vegetation throwing.

#### *Relation to human handedness*

One extremely clear generalization emerges from the data on lateralization of motor performance in animals, and it is as well to assert it before considering other aspects of the data which are not at all clear. None of the mammalian species in which forepaw preferences have been systematically studied shows a species-wide preference for one or other forelimb. If there is an innate preference for use of the right forelimb in the human species, it does not

seem to be foreshadowed in other mammals, with the possible exception of gorillas. Since it is the species preference for the right which seems to be of most interest in human handedness, further discussion may be superfluous. However, the suggestion by Annett (1970) that human hand preferences should be considered as a distribution skewed to the right gives some point to the question of whether mammalian handedness differs from human handedness only in the greater mammalian proportion of left-handers.

Rats, mice, brush-tailed opossums and macaque monkeys, as individuals, may have strong and consistent hand preferences for at least one motor response that of reaching for food ; and in monkeys the same hand may be preferred for several forms of object manipulation. At a superficial level these individuals show lateralization of forelimb ‘, control — the difficult questions concern what is responsible for ‘these paw preferences and for human hand preferences. The data suggest that such forepaw preferences as do arise in rodents are caused by constitutional factors rather than chance reinforcements. The work of Glick *et al.* (1977) suggests that physical asymmetries between the two sides of the extra-pyramidal motor system may account for some of the behavioural variance. The usual assumption is that asymmetries of the motor cortex, or pyramidal pathway from it (Cole, 1955), are responsible for behavioural asymmetries in higher mammals, but it has yet to be shown that either rodent or human handedness is caused by constitutional asymmetries in motor pathway anatomy.

It is unlikely that manual preferences will be explained purely in terms of anatomical asymmetries, even in animals, because when more than one task is observed in rats (Peterson, 1934) or in monkeys (Warren, 1977) direction of preference and its strength and consistency is seen to vary with the task. Warren seems to think that this makes the preferences non-human. This would be so if human hand preferences were entirely consistent from task to task, and immune to practice effects. But we know, if we do not always acknowledge, that human hand preferences are not typically consistent from task to task (Annett, 1970, 1972). We know less about how practice affects hand preference in human skills, but all skills considered for a human adult are likely to be over practised by comparison with all specific animal tests, with handwriting the most practised of all.

In order to make more accurate comparisons between human and animal hand preferences, it would be useful to have different kinds of data in both cases. For humans more data would be helpful on food reaching responses for adults as well as infants (reaching for a biscuit, eating an apple, or drinking a cup of tea may very well be less strongly lateralized, on initial testing, than tool-using skills). More valuable would be data for animals on any other task apart from food reaching. If a monkey (or a rat) is taught a difficult asymmetrical task, and given considerable overtraining on it, how well does the task transfer if laterally reversed? Pressing a lever to within fine limits of angular displacement with one limb would be a straightforward test, and more elaborate tasks such as those used by Beck & Barton (1972) might be revealing. There seems to be little discussion of how well humans may transfer one-handed skills when forced to do so, but one would expect some transfer effects, visible for instance in the relearning of handwriting by adult amputees.

At present no firm conclusions can be drawn, apart from the truism that both constitutional and environmental factors probably affect hand preferences in animals and man. Perhaps the most salutary implication that could be drawn from the study of animal limb preferences is that hand or paw preference in a particular task should not be taken as an indubitable sign that hemispheric dominance is being manifested.

### 3.2 Vocalization

Although vocalization in man undoubtedly serves higher purposes than it does in other animals, the human vocal apparatus (lung, larynx, tongue, and so on) shares many features, including the forms of muscular control and innervation, with other mammals, and some general features with birds. While cerebral dominance for language may have occurred because of the special nature of human vocalization, alternative hypotheses (for instance, that species-specific vocalizations are controlled by only one side of the brain in all vertebrates) need to be eliminated, if lateralization of control of human language is to have a unique status.

There is in fact very little evidence appropriate for deciding whether species-specific vocalization is under bilateral or unilateral control in species other than man ; but it is possible to make a claim, in the cause of provocation if not strict accuracy, that production or reception of species-specific vocalizations is controlled by the left, but not the right, cerebral hemisphere, in all vertebrate species for which appropriate evidence is available. These include, unfortunately, only three species: the canary, the Japanese macaque monkey, and man. Left-hemisphere control of human speech has been discussed in a previous section, and it therefore remains to consider only the data for the other two species.

#### *Left-hemisphere dominance of song in the canary*

Singing by male canaries is severely disrupted by lesions to some areas of the left cerebral hemisphere, but much less affected by lesions to the same parts of the right hemisphere (Nottebohm *et al.*, 1976; Nottebohm, 1977). Domesticated strains of the canary have been selectively bred for elaborate and reliable singing (by the males only), so that individual birds produce as many as 30 or 40 separate 'syllables', identifiable as distinct patterns on a sound spectrogram. Although the basic pattern of canary song emerges in a bird never allowed to hear another canary, infant birds normally imitate adults if they can hear them and make use of auditory feedback from their own efforts (Waser & Marler, 1977). The terminal auditory projection in birds, analogous to primary auditory cortex in mammals, occurs in a particular area of the neostriatal layer of the hemispheres. Nottebohm *et al.* (1976) found that the most severe disruptions of song occurred in canaries lesioned just above and behind this auditory projection, in a region of the hyperstriatum ventrale (although unilateral lesions of the auditory area itself had no immediate effects on singing). There appears to be hemispheric dominance of song control in the canary, since lesions of this 'song control centre' in only the left hemisphere reduced singing vocabulary from an average of 24 syllables to an average of less than one syllable in the second week after the operation, while similar lesions of the right hemisphere allowed retention of more than half (13) of the pre-lesion average (24 again) of syllables. This result was obtained using four birds with left-hemisphere lesions, and five birds with right-hemisphere lesions, and needs replication, but other evidence for left-sided lateralization of song control comes from more peripheral interruption of the song-control pathways.

Many of the details of the acoustics of how birds produce sounds remain to be settled, but the relevant point here is that, although the larynx is used to control air flow, birds use ( a specialized sound source, the syrinx, which is positioned at the junction of the two bronchial passages at the bottom of the trachea. In the canary, the muscles on the left side of the syrinx are larger than those on the right (Nottebohm & Nottebohm, 1976). The main innervation of the syrinx is via branches of the hypoglossal (XII) cranial nerve (the left and right tracheosyringealis nerves). The motor control of the syrinx appears to be by an entirely ipsilateral pathway: from the left hyperstriatal centre to another telencephalic structure (in the archistriatum) and from there to an ipsilateral brain-stem nucleus and the hypoglossal nerve, and then to the left side syringeal muscles. When the left hypoglossal connection to the syrinx is severed, canaries can produce no complete syllables. . The birds go through the motions of singing, but only faint and hoarse clicks or subsyllabic elements emerge. On the other hand,

severing the right hypoglossal innervation of the syrinx may leave song entirely unaffected, and on average only a tenth of the song-syllables are modified or eliminated. This left hypoglossal dominance has been observed without any exceptions in a large number of canaries, and in chaffinches (Nottebohm, 1971) and in a species of sparrow (Lemon, 1973). It is, therefore, quite possible that left hypoglossal dominance occurs in large numbers (if not all) of passerine species, and left hemispheric dominance may be similarly widespread, although it has been directly tested only in the canary.

It is certain, however, that not all bird species exhibit left hypoglossal dominance. In at least one species of parrot each hypoglossal innervates both halves of the syrinx (Nottebohm, 1976). Cutting either left or right hypoglossal connections to the syrinx produces only very minor changes in vocalization because both sides of the syrinx are adequately served by the remaining innervation. This does not necessarily preclude hemispheric dominance: unilateral damage to the nerves controlling the human larynx produces the same degree of hoarseness whether it is on the left or right side, and the remaining innervation will allow good recovery (Greene, 1964).

The lateralization of vocal control as it apparently occurs in the canary is more thoroughgoing than the lateralization of human speech, in that, in the canary, the left hemisphere seems to control only the left effectors, while in man, each hemisphere projects bilaterally to the brainstem nuclei of most of the cranial nerves, including those governing the larynx and tongue (Espir & Rose, 1970). Is it the case that left-hemisphere control of vocalization in the canary is firmly built in and unalterable? Two aspects of Nottebohm's experiments suggest that the right hemisphere may take over control of vocalization after early left-hemisphere damage. The birds which received left-hemisphere lesions which severely impaired song did so when they were 12 months old, when ontogenetic development of song was virtually complete. After the immediate post-operative loss of song, a considerable degree of song recovery took place, so that by 7 months after the operation some of the birds had almost as many syllables as before the operation. Now they were subjected to sectioning of the right hypoglossal connection to the syrinx, and lost most or all of the 'recovered' syllables. This implies that the right hemisphere, rather than remaining tissue in the left hemisphere, had been responsible for song recovery (Nottebohm *et al.*, 1976). It is also likely that a right-hemisphere takeover of song can be induced by neonatal damage to the left hypoglossal, since if this nerve is cut in 2-week-old birds, left-hemisphere lesions in the same birds when an adult has a reduced effect (Nottebohm, 1977).

The canary thus seems to share with man a left-hemisphere dominance of vocalization combined with a right-hemisphere capacity for vocal control usually revealed only when the left hemisphere is damaged. Children without the use of the left hemisphere show reasonable competence for language (Lenneberg, 1967) and Kinsbourne (1971) found that adult left-hemisphere stroke patients who recovered from aphasia lost their recovered ability if the right hemisphere was disabled by sodium amytal injections. Some restitution of speech has been observed in adult patients after excision of the entire left hemisphere (Smith, 1978).

#### *Left-hemisphere dominance of species-specific cry reception in the Japanese macaque monkey*

It is claimed in a recent report that 'Japanese macaques engage left-hemisphere processors for the analysis of communicatively significant sounds that are analogous to the lateralized mechanisms used by humans listening to speech' (Peterson *et al.*, 1978, p. 324). If this claim is correct it provides something of a landmark in the search for subhuman cerebral dominance. The evidence for it is as follows.

Japanese macaques make a number of 'coo' sounds in the context of friendly social behaviour. Field recordings of two of these subtypes of vocal signal were the stimuli tested in the Petersen *et al.* (1978) investigation. Functionally, one type of 'coo' is used by females



when soliciting males for sexual purposes, and the other type seems to be a more general contact-seeking call. Acoustically, the soliciting 'coo' has a smooth late peak, and the general 'coo' a smooth early peak ; both types occur with a range of fundamental frequencies. Discrimination of recordings of eight late-peak and seven early-peak calls, presented via headphones to either the left or right ear, was the experimental technique used to assess cerebral dominance. The animals were required to squeeze a tube to initiate a series of late-peak calls, played into either the left or the right ear in a randomly alternating sequence. The task was to hold the tube until the series of late-peak calls was interrupted by an early-peak call — if the monkey released the tube at this point it received a food reward.

The performance of five Japanese macaques, and five other Old World monkeys, was assessed to see if the early-peak stimuli were detected more successfully with one ear than with the other. The number of exemplars of each call-type included per session was gradually increased during the training of individual monkeys until the animal could successfully discriminate when all 15 stimuli were included on the same day. For each training session, each of the early-peak signals that had been included could be classified as showing left-ear advantage, right-ear advantage, or no advantage, on the basis of percentage correct scores achieved after reception at the individual ears. At the end of training, particular monkeys could be assessed according to the proportion of right-ear advantage instances thus accumulated. All five of the Japanese macaques had higher proportions of right-ear advantages than should have occurred by chance, although the superiority was not overwhelming — on average only 60 per cent of the individual signal tests showed better detection by the right ear. However, only one of the other five monkeys demonstrated a significant right-ear advantage. Two of these others and two of the Japanese macaques were then trained to sort the same field-recorded signals by pitch. The task was to detect a high-pitched call, irrespective of its functional type, in a series of low-pitched calls. Both the Japanese animals showed a reduced right-ear effect, in one case amounting to a significant proportion of left-ear successes, and the other two animals again did better with the left ear as often as with the right. Although samples of this size are hardly conclusive, it would be expected that any left-hemisphere dominance effect should occur with complex and socially significant discrimination sounds rather than pitch.

What may be concluded from the differences in performance which resulted from playing the early peak 'coo' into the right, rather than the left ear of these five Japanese monkeys? An analogous finding would almost certainly be interpreted as demonstrating left-hemisphere dominance, in human subjects. An argument may be made that, in the monkeys, the left-hemisphere was exclusively responsible for detecting early peak 'coos'. For roughly 60 per cent of the samples, when the right ear was better than the left, it would be assumed that the right ear had better access to the left hemisphere than the left ear. This is in accordance with the anatomical and electrophysiological data. On 40 per cent of the samples, when the left ear was performing more accurately than the right, one would have to assume that attentional factors had temporarily overcome the built-in right ear ease of access of the left hemisphere. Since sounds were randomly alternated between left and right ears, this is not implausible.

Catlin *et al.* (1976) performed a rather similar experiment to that of Peterson *et al.* (1978) but used human subjects, and found a very small right-ear advantage in reaction time to a target speech sound: differences between the ears when sounds are presented monaurally are usually marginal, and dichotic presentation of certain kinds of stimuli is needed to obtain a more reliable right-ear advantage (Darwin, 1974). Dichotic presentation was not used by Peterson *et al.* as their research program was not primarily concerned with ear differences. Thus although the magnitude of the effects obtained in their experiments was not great, it is

entirely consistent with a left dominance of conspecific call reception, of the same order as that observed in man.

#### *Left-hemisphere dominance of animal vocalization: Conclusions*

Direct evidence for a greater involvement of the left hemisphere in production or reception of vocalization in a non-human species is limited to data on singing in four left-hemisphere-lesioned canaries (Nottebohm, 1977, 1979). Further experiments comparing the effect of left- and right-hemisphere lesions on singing in canaries are needed to confirm Nottebohm's results, and since there is as yet no evidence of this sort for hemispheric dominance of song in avian species other than the canary (Nottebohm, 1979), it is too early to say whether its occurrence in this bird is an isolated peculiarity, a result of selective breeding, or an example of a widespread avian (or vertebrate) phenomenon.

It seems likely, however, that a peripheral asymmetry in vocalization as assessed by the differential effects of left and right denervation of the syrinx is characteristic of several seed-eating song-birds. It is conceivable therefore that hemispheric dominance, which is associated with left syringeal dominance in the canary, occurs in a number of other passerine species. Both the syringeal and the cerebral dominance effects have been measured exclusively for song production, rather than song reception, or response to vocal signals and calls more generally. In order to make further comparisons of cerebral dominance in birds and man it would be useful to discover whether there is any dominance for song *reception*. There are several ways to assess species-specific responses to song: for instance, captive female cowbirds will adopt certain postures on hearing recordings of male songs, and this is quantifiable (King & West, 1977; West *et al.*, 1979). If it is confirmed that the left hemisphere is dominant for the production of male canary song, it would be interesting to know whether or not the female canary's left hemisphere is dominant for receiving it. Apart from examining possible cerebral dominance via species-specific responses to species-specific acoustic signals, more conventional laboratory techniques for discrimination learning might be used one wonders whether the procedure utilized by Petersen *et al.* (1978) would reveal a right-ear advantage for detecting complex sounds in the canary. Conversely, one may ask if Japanese monkeys have left-hemisphere dominance of vocal *production*. If Petersen *et al.* (1978) are correct in inferring from their data that their monkeys' receptive mechanisms were lateralized in a manner analogous to those used by humans to analyse speech, the strength of the analogy must be tested by whether or not unilateral lesions of frontal cortex can be found to reveal left dominance of vocal production. Techniques for such experiments are difficult, but impairment of vocalization by bilateral lesions of frontal limbic regions has been demonstrated (Sutton *et al.*, 1974). Only bilateral removal of the cingulate and subcallosal gyrus was tested in two animals. Neither unilateral nor bilateral lesions to frontal or parietal areas selected as homologs to human speech areas had any effect on the vocalization tested, but this was a prolonged call emitted by a restrained and isolated animal for automatic food rewards. Evaluation of the social vocabulary after unilateral lesions would be preferable. In man, left dominance of vocal production appears to be stronger than dominance of comprehension, but, on the other hand, left dominance may be less strong or even reversed for emotional and instinctive cries (Gardner, 1977). However, it would be expected that unilateral left-hemisphere rather than right-hemisphere lesions of secondary auditory cortex would produce pronounced impairment of the call-type discrimination tested in Petersen *et al.*'s ear-advantage experiment. No such difference was observed in the experiment of Hupfer *et al.* (1977) but only two animals appear to have been given appreciable unilateral lesions on the left.

Until more evidence is available, cerebral dominance of animal vocalization remains an interesting possibility rather than a confirmed fact. However, data on dominance and vocalization as it stands are qualitatively different from those for handedness in animals.

Animal hand preferences are equitably distributed in the species — giving roughly equal numbers of left- and right-handers. It might have been expected, therefore, that any asymmetry in cerebral control of animal vocalization would follow the same pattern, with equal numbers of animals showing right dominance and left dominance. It appears that this is not the case — the dominance of the left part of the syrinx in canaries is almost without exception, and the small sample of Japanese macaques all have right ear advantages (i.e. left-hemisphere dominance). It is slightly absurd to make inductions from only three species, but if left dominance holds across these species, explanations of why it is the left rather than the right hemisphere which dominates speech in man may need a more general framework.

Apart from the right or left question, a general explanation will be needed if many species show dominance of vocalization by either hemisphere, whether it is the left or the right, or if individuals within species have dominance by one or other hemisphere. A division of labour between hemispheres may be as advantageous to small-brained species as it is to ourselves, but if cerebral dominance of species-specific vocalization occurs with any regularity at all in non-human species, and even if it occurs only in canaries and macaques, then the ‘doubling of cognitive capacity’ consideration (Levy, 1977) will be less apt.

Even the present hints that cerebral dominance in production and reception of sounds may not be a unique human characteristic prompt one to ask why bilateral control of sound production should be retained if it is not strictly necessary. A factor which distinguishes the organs of vocal production in most vertebrates from, for instance, the limbs, is that it is not particularly useful to control each half of the vocal organs independently — the two sides of the body might just as well be operated in parallel for vocal functions, although this would certainly not be true for locomotion. Should we be surprised, then, if any vertebrate species accomplishes vocalization with one hemisphere active and the other lazy? The same argument might of course apply to other oral movements apart from those connected with vocalization: left-hemisphere dominance for non-verbal oral movements may occur in man (Mateer, 1978), and there is certainly left-side dominant innervation of the oral region in the lancelet (*Amphioxus*) sometimes considered as a vertebrate prototype (Kappers *et al.*, 1936), but little is known of possible asymmetries of oral control in other vertebrate species in between. In the light of the ‘immense left-sided larval mouth’ of *Amphioxus* (Young, 1962, p. 45) and the left-sided respiration of the very earliest chordates (ancestors of vertebrates — Jeffries, 1975), left-sided dominance of speech may be one of the most conservative of human features.

### *3.3 Perception*

#### *Hearing*

A ‘least effort’ hypothesis may be applied to the reception of sounds. Because of the organization of the auditory pathways, the same auditory information can be analysed twice — once in each hemisphere. It would be odd for either hemisphere to ignore fundamental characteristics of auditory input such as pitch and intensity — but analysis of complex sounds, especially involving integration and comparisons over time, could reasonably become optional, with only one of the hemispheres organized to do it.

It might be the case that hemispheric differences occur for the reception of species-specific cries, as discussed in the last section, in the absence of more general asymmetries in audition. On the other hand, somewhat broader categories of function, such as auditory short-term memory, or sequential analysis of complex sounds, rather than simply recognition of a collection of innately programmed signals, may characterize a hemisphere advantage. Two sorts of experiment in which differential effects of left- and right-hemisphere lesions on auditory performance seem to have been found may be quoted:

experiments testing short-term memory for audio-visual associations in monkeys ; and testing of sound localization in cats.

Dewson (1977) argues that the left hemisphere of rhesus monkeys is more important than the right for some forms of non-vocal auditory processing, referring to differential effects on performance after lesions of auditory cortex in the left and right hemispheres. The task which revealed these effects involved memory for sounds and/or colours. Monkeys heard a 1kHz tone or a burst of white noise when they pressed a panel. After a delay period of up to 20 seconds, two lower panels were lit up, one red and the other green, with the position of the colours unpredictable. The monkeys had to remember to select red after the tone and green after the white noise. Before brain operations they did this with few errors over delays of 1 or 2 seconds, but made more and more errors as the delay was increased during a test session, declining to chance levels of accuracy at delays of between 10 and 20 seconds. Left-hemisphere lesions, aimed at removing the cortex from a limited area of the superior temporal gyrus, produced a long-lasting drop in accuracy of performance with delays of more than a second. Similar lesions in the right hemisphere, however, seemed not to affect the ability to remember at all.

This seems to be a clear demonstration of left-hemisphere dominance with an area of the cortex linked to the auditory modality (Dewson *et al.*, 1969). The main reservation is that only five monkeys provided the data. Two were given right-hemisphere lesions and showed no deficit, and three received left-hemisphere damage after which their performance suffered. One of the right-lesioned animals was subsequently given the operation on the left side as well, whereupon the deficit appeared. This is all consistent with the possibility that the delay test taps exclusively left-hemisphere processes, but not sufficient to exclude a statistical null hypothesis. An additional peculiarity of the monkeys employed was that, except for one of the left-hemisphere animals, they had previously been deafened in one ear by cochlear destruction, but the side of the deafening varied and had no observed influence on the results. Thus a left-hemisphere monkey showed a deficit and a right-hemisphere monkey did not when deaf in the ear on either the same side or opposite side.

If we were to assume that, in any non-human mammal, left-hemisphere auditory cortex alone is required for some aspects of sound recognition or short-term storage of sound-linked information, we would ask whether there might be a corresponding specialization of right-hemisphere hearing. A possible candidate would be sound-localization of some sort. It would provide a nice simple theory if mammalian hearing assigned ‘what is it?’ and ‘where is it?’ questions to the left and right hemispheres respectively. Such a clean disjunction does not occur, but there is almost as much evidence, in terms of numbers of subjects, for differential right-lesion effects on sound localization in cats as for left-lesion influence on recent sound memory in monkeys. There have been several reports of deficits in learned responses to localized sounds in cats with unilateral ablations of auditory cortex (Cranford *et al.*, 1971 ; Whitfield *et al.*, 1972; Whitfield *et al.*, 1978). Cats in these experiments run a Y-maze for food reward, which side is correct being signalled by tones from speakers behind the goal boxes. Simply running to the source of the only sound is a fairly rudimentary type of localization test, but accuracy at this task is severely impaired after bilateral lesions of auditory cortex, though not after unilateral damage (Neff *et al.*, 1956). A slightly more difficult discrimination is to go left to a tone on the left, but right when there are tones on left and right at the same time. On this ‘one versus two’ test, both left and right unilateral lesions have an effect, but only when the task requires running to the side contralateral to the lesion, in response to sound from both sources (Whitfield *et al.*, 1978). An extra test given when ‘one versus two’ training had already taken place, involved the ‘precedence effect’ — the tendency of sounds from both left and right to be perceived as one sound, coming from the

location of the first, if one precedes the other by about 5 ms. (Whitfield *et al.*, 1972; Whitfield *et al.*, 1978).

In the initial reports, comparison of the behaviour of left- and right-lesioned animals 'revealed a very definite asymmetry' (Whitfield *et al.*, 1972, p. 26), with left-lesioned animals performing better than the right-lesioned cats on the one-versus-two discrimination, and especially on the precedence tests. However, most, if not all, of this difference is attributable to the asymmetry in training rather than the site of the lesion. Whitfield *et al.* (1978) attribute any difference between left and right lesions to the direction of the training test, and individual variation. They characterize the basic deficit following unilateral lesions of auditory cortex as the lack of normal response to a compound stimulus localized on the contralateral side. This interpretation was roughly consistent with the performance of two surviving right-lesioned cats but not applicable to the performance of two of the three left-lesioned animals whose results are reported in the Whitfield *et al.* (1978) paper. It seems generally the case that there are extremely marked individual differences after unilateral brain lesions of auditory cortex. Cranford & Oberhoitzer (1976) found that two out of five cats with left-hemisphere lesions, and one out of four cats with right-hemisphere lesions, seemed to show improvement in the precedence effects, while the others showed marked impairment. Individual animals, perhaps in response to physical hemispheric asymmetries such as those reported by Webster (1977), may favour one or other of the hemispheres for some sorts of binaural comparison, even if there is no species-characteristic left or right dominance. It can only be said, then, that possibility of hemispheric differences in the spatial aspects of hearing in cats has not been completely ruled out. The four right-lesioned animals in the Whitfield *et al.* (1972) paper seem to have done rather badly, and this remains worthy of further investigation. The attraction, of course, is the supposed pre-eminence of the human right hemisphere in spatial matters. Although there is no agreement that the human right hemisphere is especially involved in the localization of sounds, a comparison of 78 human patients in all by Shankweiler (1961) suggested that right temporal damage impaired pointing to a sound location more than similar damage on the left.

It must be concluded that evidence for hemispheric differences in hearing in mammals, not involving species-specific communication, is at present extremely slight, but not slight enough to demonstrate the absence of such differences. As there is already evidence for lateralization of singing in song-birds, and as there are anatomical asymmetries in the external ears of some nocturnal species of owl, possible hemispheric specializations in avian hearing need pursuing. It has recently been shown that pigeons can localize brief sounds by binaural disparities of time and intensity, in a manner analogous, if not homologous, to that of mammals (Jenkins & Masterton, 1979), and techniques are therefore available for determining whether there is any hemispheric dominance in these tasks. A more difficult undertaking would be the assessment of possible hemispheric differences in the echo-locating skills of porpoises and other Odontocete whales, but since the cranial asymmetries in these animals (referred to above) include dramatic differences in the size of the left and right jawbones, which are assumed by Erulkar (1972) to be the primary pathway for conduction of high-frequency sounds to the inner ears, speculation along these lines is not entirely groundless.

### *Vision*

Since each hemisphere receives inputs from both ears via the ascending pathways and can thus independently survey the entire auditory field, specialization of one hemisphere for a demanding aspect of the analysis of auditory signals seems a plausible evolutionary development for any higher vertebrate species. Hemispheric specializations in other sensory modalities would be rather more surprising, as one would expect to find distinct asymmetries in performance. If, for example, we consider the consequences of a pigeon or rat developing a

dominance for visual recognition of predators in the right hemisphere, we would be led to hypothesize a species peculiarly vulnerable to attack from its minor (right) visual field. No indications are to hand that such species exist, or that non-human vertebrate species with symmetrical bodies show obvious asymmetries in the effectiveness of perception for left and right sensory fields.

However, in investigating the effects of unilateral brain stimulation on the emotional reactions displayed by doves to test stimuli, Vowles & Beazley (1974) report experimentally induced asymmetry of reaction: while receiving electrical stimulation of a site on one side of the forebrain, some doves would give fearful responses to a toy spider presented in the contralateral visual field, but aggressive responses when the identical stimulus appeared on the same side as the stimulation. Since birds have rather meagre connections between their cerebral hemispheres, and since each eye feeds most directly only to the contralateral visual centres, it is almost as if there must be separate control of emotional reactions to the information received by individual eyes. A similar sort of visual field effect has been observed in split-brained monkeys by Barrett (1969). Various midbrain and forebrain cross-connections ensure a degree of interaction between hemispheres, but Stevens & Klopfer (1977) have shown that some classically conditioned emotional responses to visual stimuli remained one-sided in experimental tests of interocular transfer in gulls, pigeons and chickens. For example, pigeons with one eye occluded, shown a distinctive cap-pistol before it was fired a few feet away, rapidly acquired the response of moving away from the pistol on sight, but showed no signs of recognizing it when only the previously occluded eye was available. The implication of such a finding is merely that the hemispheres may act independently, not that they have any built-in functional asymmetry; indeed, the greater the independence of the left and right visual fields the less opportunity there is for functional specializations.

In order to obtain measures of the independent visual activities of the hemispheres in mammals the cerebral commissures and/or the optic chiasma may be sectioned. The performance of human patients after such operations has, of course, been one of the main sources of evidence for human hemispheric differentiation. 'Split-brain' cats and monkeys, tested on visual discrimination learning tasks, have shown very few signs of imbalance in the learning abilities of the left and right parts of the visual system (Webster, 1977; Hamilton, 1977). In one experiment when a relatively abstract perceptual task was used (Robinson & Voneida, 1973), there was evidence of unequal hemispheric abilities in individual cats, but the same number of animals (three) was inferred to have right-hemisphere dominance as left.

#### *Spatial and tactile learning*

Orientation in space, in such forms as maze learning by rats, or homing by pigeons, might be expected to reveal sensitivity to right-hemisphere lesions if anything akin to human minor hemisphere functions is lateralized in these species. There is a finding which connects right-hemisphere damage to peculiarities of movement in a novel environment for rats (Denenberg *et al.*, 1978) but it is not straightforward and is considered to indicate an effect on emotionality if anything (see below).

Tactile information may be part of the human right-hemisphere specialization observable in split-brain patients (Ledoux *et al.*, 1977). Although split-brain monkeys have not manifested asymmetries for the learning of tactile discriminations (Ebner & Myers, 1962b) it appears that a test more similar to those used with patients (feeling three-dimensional shapes) is sensitive to unilateral lesions of parts of somato-sensory cortex (SII which is a bilateral projection), when the unilateral lesions are made in a monkey's 'major' hemisphere, determined by its hand preference (Garcha & Etlinger, 1978). The number of animals involved (three) does not allow any estimate of whether this effect is due to lateralization or whether it is a task for which both hemispheres are required. However, any

bilateral learning deficit produced by a unilateral lesion in animals is unusual, and is open to interpretation as a sign of lateralization until it is clear that the side of the lesion is irrelevant.

It should be noted that there are data from electro-encephalographic assessments of hemispheric activity in mammals. Nelson *et al.* (1977) using rabbits, Webster (1977) using cats, and Stamm *et al.* (1977) using stump-tail monkeys, have all observed differences in the electrical activity of the two hemispheres: during sleep (in the rabbits and cats), and also during visual discrimination learning (the cats and monkeys) and a simple auditory discrimination (in the rabbits). In no case, however, was there a systematic difference favouring the left or right side for a particular species. There are technical and theoretical problems of inference from electrical activity measures (such as movement artifacts): it has recently been suggested that the electrical activity of the human hemispheres does not differ significantly during the performance of cognitive tasks when all stimulus and response artifacts are removed (Gevins *et al.*, 1979).

In the areas of perception and cognition in animals therefore — in so far as these correspond to the limited range of conditioning and discrimination learning tests that are employed — the only signs of a species-characteristic dominance of one hemisphere over the other have occurred when macaque monkeys have been given a relatively difficult task involving the processing of auditory information. It has been reported that Japanese macaques may have right-ear advantage for the reception of species-specific calls (Petersen *et al.*, 1978) and that rhesus monkeys are affected by left-hemisphere, but not right-hemisphere, lesions in tests of recent auditory memory for an audio-visual association (Dewson, 1977). Further investigation of the differential effects of unilateral lesions to auditory projection areas in the left and right hemispheres of mammals and birds appears warranted.

### 3.4 *Emotionality*

Perception and production of facial emotional expression, or emotionality more generally, has been assigned to the human right hemisphere. While facial expressions like our own may be observed in primates (Jolly, 1972), but not in other orders, the brain mechanisms associated with emotionality are not so restricted, and if either left or right halves of the limbic system had a special effect on motivation and emotion in any vertebrate, this should be readily observable. In general, it seems that either half of limbic structures is sufficient to control behaviour, and bilateral lesions are therefore necessary to produce behavioural impairments. Systematic assessment of hemispheric asymmetries in the control of emotional behaviour in animals is, however, rare. It is arguable that specific ratings of, for instance, aggressive behaviours, sexual responses and reaction to novel objects would be preferable to an overall index of emotionality. Gibson & Gazzaniga (1972), for instance, suggest there is a hemispheric difference for eating raisins in split-brain monkeys. But, for convenience, 'emotionality' in rats has frequently been measured by placing the animal for the first time in a shallow box a yard or so square, and counting the amount of movement (and sometimes amount of defecation) in a given number of minutes. Animals which move very little and defecate a lot are said to be most emotional (see Gray, 1979).

A carefully planned study employing measurement of amount of movement in this 'open field' test has indicated that the right hemisphere may affect emotionality more than the left in rats (Denenberg *et al.*, 1978). The absolute size of the mean difference was considerable, but so was variability within the groups of animals tested and the right/left hemisphere differences appear only under certain conditions of laboratory housing. Rats were handled daily for the first 3 weeks of life, or not so handled, then further divided into groups reared together in large and interesting enclosures, and animals living in pairs in bare laboratory cages, for a further month. After these differences in treatment during the first few weeks of

life the rats were all caged singly until they were 4 months old, when brain operations were performed, followed by the behavioural test. Either the left or the right hemisphere was partially removed by suction, or a sham operation was performed.

In general, the enriched-environment rearing increased open field activity a little, as did postnatal handling. The handling was crucial, however, in determining reaction to brain damage. Unhandled animals increased activity as a consequence of either left- or right-hemisphere ablations. Handled rats were made either very active, or virtually immobile by right-hemisphere damage, and affected very little by the left-hemisphere operation. It was the handled and then group-reared animals who were immobilized, and the handled, cage-reared rats who were extremely active (Denenberg *et al.*, 1978). Without special handling, Robinson (1979) found that damage to the right hemisphere, but not to the left, made rats more active both in the open field and in a running wheel.

In similar experiments Sherman *et al.* (1979) have obtained a slightly more direct effect of right-hemisphere ablations on an aggressive response. Male rats were handled or not handled as neonates, as in the Denenberg *et al.* (1978) procedure, and tested for mouse killing, when adults, by the introduction of a mouse into their individual home cages. There was no difference between left- and right-hemisphere ablations for the unhandled rats. But with the handled animals, the group with right-neocortex lesions took about 2 days to kill the intruder, while the rats with left-hemisphere damage usually dispatched the mouse within the first 24 hours. This could be taken to indicate a greater involvement of the right hemisphere in aggression, or emotional reactions more generally in handled laboratory rats.

It is odd that a functional asymmetry should appear only in rats subjected to disturbance in the first weeks of life. However, the research of Diamond *et al.* (1975) indicates that this may be a period when physical asymmetries in favour of the right hemisphere are at a maximum (see above).

It would be unwise to conclude anything from these strange results (Denenberg *et al.*, 1978; Sherman *et al.*, 1979) before replication. But effects such as these would be remarkable, if they are genuine, in that a species-characteristic left/right difference of any kind would be a major addition to the present rather flimsy collection of functional hemispheric asymmetries in animals other than man.

#### **4. Conclusions**

On the basis of the reports of hemispheric asymmetries in non-human species reviewed here, it is difficult to reject the null hypothesis that the vertebrate nervous system is an entirely symmetrical device, with the possible exceptions of the brains of humans and canaries. In only these two species is there strong evidence that damage to one side of the brain has behavioural effects different from those which result when the other side suffers similar injuries. In many species individuals have reliable motor preferences for one side of the body, but only in man is the distribution of manual preferences non-random. Do the comparative data therefore support the proposition that functional lateralization of the brain is a uniquely human phenomenon, or the more specific contention that human cognitive abilities depend on, or are significantly assisted by, functional lateralization? Even if only the results which indicate that vocalization in male canaries is controlled by the left hemisphere are accepted, there are implications for theories of human cognition. The possession of fully human cognitive abilities cannot now be said to be a necessary condition for the appearance of hemispheric lateralization in the vertebrate brain. An alternative hypothesis is that emphasis on vocalization is associated with lateralization of function. An account of this phenomenon could be given by appealing to an ontogenetic and phylogenetic 'law of least effort': hemispheric space is not used if it can be managed without, and vocalization unlike,



for instance, locomotion does not require the left-right differentiation usually achieved by the symmetrical employment of both sides of the brain.

Of all the modalities, hearing is the one for which a single hemisphere is most generously supplied with direct access to inputs from the entire sensory field, and thus is the modality where similar hemispheric economies could most easily be applied to perception. The possibility that macaque monkeys show preferential use of the left hemisphere for some aspects of hearing gives support to this idea. If signs of left dominance for vocal production or reception in non-humans is rare, behavioural data to suggest alternative specializations in the animal minor hemisphere are even rarer, but the possibility remains that some (or many) vertebrate species may favour the right hemisphere for emotionality and spatial knowledge. Marked physical asymmetries in the limbic system of lower vertebrates with very small brains, and in the cranial bones of some marine mammals with very large brains, provide a basis for the speculation that asymmetries of forebrain function may be widespread in vertebrates.

These few bits of evidence seem negligible when set against the volume of reports concerning human handedness, and lateralization of cognitive processes. However, if there is any form to the comparative evidence at all, it is that human asymmetries in vocalization and hearing may have evolutionary precedents, if not primate beginnings; whereas human right-handedness lacks any obvious animal precursors. If it becomes necessary to provide independent accounts of left-brain dominance of vocalization (as a vertebrate or primate tactic) and right-handedness (as a peculiarly human characteristic), then human tool-using is sufficiently different from that of other species to have supplied an entirely new selection pressure. More theoretical parsimony would be achieved by assuming that handedness is secondary to language — in other words that right-handedness arose only when vocalization, already lateralized, became associated with manual skills.

### Acknowledgements

I should like to thank Max Coltheart for his careful reading of earlier versions of this paper, and V. H. Denenberg, F. Nottebohm and I. C. Whitfield for prompt replies to queries about their work.

### References

- ABLER, W. L. (1976). Asymmetry in the skulls of fossil man: Evidence of lateralized brain function? *Brain Behavior and Evolution*, 13, 111—115.
- ADAMS, R. D. & VICTOR, M. (1977). *Principles of Neurology*. New York: McGraw-Hill.
- ADSELL, S. A. (1966). Evolutionary trends in reproduction. *Symposia of the Zoological Society of London*, 15, 1-43.
- AITKEN, L. M. & WEBSTER, W. R. (1972). Medial geniculate body of the cat: Organisation and responses to tonal stimuli of the ventral division. *Journal of Neurophysiology*, 35, 365-380.
- ANNETT, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology*, 61, 303-321.
- ANNETT, M. (1972). The distribution of manual asymmetry. *British Journal of Psychology*, 63, 343—348.
- ANNETT, M. (1975). Hand preference and the laterality of cerebral speech. *Cortex*, 11, 305—328.
- ARONSON, L. R. & CLARK, E. (1952). Evidence of ambidexterity and laterality in the sexual behaviour of certain poeciliid fishes. *American Naturalist*, 86, 161—171.

- ASHDOWN, R. R., RICKETIS, S. W. & WARDLEY, R. C. (1968). The fibrous architecture of the integumentary coverings of the bovine penis. *Journal of Anatomy*, 103, 567—572.
- BARRETT, T. W. (1969). Studies of the function of the amygdaloid complex in *M. mulatta*. *Neuropsychologia*, 7, 1—12.
- BASSER, L. S. (1962). Hemiplegia of early onset and the faculty of speech with special reference to the effects of hemispherectomy. *Brain*, 85, 427—460.
- BECK, C. H. M. & BARTON, R. L. (1972). Deviation and laterality of hand preference in monkeys. *Cortex*, 8, 339—363.
- BERLIN, C. I. (1977). Hemispheric asymmetry in auditory tasks. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- BOGEN, J. E. & BOGEN, G. M. (1976). Wernicke's region — Where is it? *Annals of the New York Academy of Sciences*, 280, 834—843.
- BOORD, R. L. (1968). Ascending projections of the primary cochlear nuclei and nucleus laminaris in the pigeon. *Journal of Comparative Neurology*, 133, 523—542.
- BRAITENBERG, V. & KEMALI, M. (1970). Exceptions to bilateral symmetry in the epithalamus of lower vertebrates. *Journal of Comparative Neurology*, 138, 137—146.
- BREder, C. M., JR & ROSEN, D. E. (1966). *Modes of Reproduction in Fishes*. Jersey City: TFH Publications.
- CAIN, D. P. & WADA, E. A. (1979). An anatomical asymmetry in the baboon brain. *Brain, Behaviour and Evolution*, 16, 222—226.
- CAMPAIN, R. & MINCKLER, J. (1976). A note of the gross configurations of the human auditory cortex. *Brain & Language*, 3, 318—323.
- CAMPBELL, R. (1978). Asymmetries in interpreting and expressing a posed facial expression. *Cortex*, 14, 327—342.
- CARPENTER, C. C. & FERGUSON, G. W. (1977). Variation and evolution of stereotyped behaviour in reptiles. In C. Gans & D. W. Tickle (eds), *Biology of the Reptilia*. London: Academic Press.
- CATLIN, J., VANDERVEER, N. J. & TEICHER, K. D. (1976). Monaural right-ear advantage in a target identification task. *Brain and Language*, 3, 470—481.
- CHI, J.G., DOOLING, E.C. & GILES, F. H. (1977). Gyral development of the human brain. *Annals of Neurology*, 1, 86—93.
- CHRISTIE, J. E. & CROW, T.J. (1971). Turning behaviour as an index of the action of amphetamine and ephedrine on central dopamine-containing neurons. *British Journal of Pharmacology*, 43, 658—667.
- CLEMENS, W. A. (1977). Phylogeny of the marsupials. In B. Stonehouse & D. Gilmore (eds), *The Biology of Marsupials*. London: Macmillan.
- COBB, S., (1964). A Comparison of the size of an auditory nucleus (*n. mesencephalicus lateralis, pars dorsalis*) with the size of the optic lobe in twenty-seven species of birds. *Journal of Comparative Neurology*, 122, 271—280.
- COLBOURN, C. J. (1978). Can laterality be measured? *Neuropsychologia*, 16, 283—289.
- COLE, J. (1955). Paw preference in cats related to hand preference in animals and men. *Journal of Comparative and Physiological Psychology*, 48, 137—140.
- COLLINS, R. L. (1968). On the inheritance of handedness. I. Laterality in inbred mice. *Journal of Heredity*, 59, 9—12.

- COLLINS, R. L. (1969). On the inheritance of handedness. 11. Selection for sinistrality in mice. *Journal of Heredity*, 60, 117—119.
- COLLINS, R. L. (1975). When left-handed mice live in right-handed worlds. *Science*, 187, 181—189.
- COLLINS, R. L. (1977). Towards an admissible genetic model for the inheritance of the degree and direction of asymmetry. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- COLTHEART, M. (1979). Deep dyslexia: A right hemisphere hypothesis. In M. Coltheart, K. Patterson & J. C. Marshall (eds), *Deep Dyslexia*. London: Routledge.
- CORBALLIS, M. C. & BEALE, I. L. (1970). Bilateral symmetry and behaviour. *Psychological Review*, 77, 451—464.
- CORBALLIS, M. C. & BEALE, I. L. (1976). *The Psychology of Left and Right*. Hillsdale, NJ: Lawrence Erlbaum.
- CORBALLIS, M. C. & MORGAN, M. J. (1978). On the biological basis of human laterality. *The Behavioural and Brain Sciences*, 2, 261—336.
- COUGHLAN, A. K. & WARRINOTON, E. K. (1978). Word comprehension and word retrieval in patients with localized cerebral lesions. *Brain*, 101, 163—185.
- CRANFORD, J. L. & OBERHOLTZER, M. (1976). Role of neocortex in binaural hearing in the cat. II. The precedence effect in sound localization. *Brain Research*, 111, 225—239.
- CRANFORD, J., RAVIZZA, R., DIAMOND, J. T. & WHITFIELD, I. C. (1971). Unilateral ablation of the auditory cortex in the cat impairs complex sound localization. *Science*, 172, 256—288.
- CROW, T. J. (1971). The relation between lesion site, dopamine neurons, and turning behaviour in the rat. *Experimental Neurology*, 32, 247—255.
- CUENOD, M. (1974). Commissural pathways in interhemispheric transfer of visual information in the pigeon. In F. O. Schmitt & F. G. Worden (eds), *The Neurosciences: Third Study Program*. Cambridge, Mass. & London: MIT Press.
- CUNNINGHAM, D. F. (1892). *Contribution to the Surface Anatomy of the Cerebral Hemispheres*. Dublin: Royal Irish Academy.
- DARWIN, C. J. (1974). Ear differences and hemispheric specialization. In F. O. Schmitt & F. G. Worden (eds), *The Neurosciences. Third Study Program*. Cambridge Mass. & London: MIT Press.
- DENENBERG, V. H., GARBANATI, J., SHERMAN, G., YUTZEV, D. A. & KAPLAN, R. (1978). Infantile stimulation induces brain lateralization in rats. *Science*, 201, 1150—1152.
- DENNIS, M. & WHITAKER, H. A. (1976). Language acquisition following hemidecortication: Linguistic superiority of the left over the right hemisphere. *Brain and Language*, 3, 404—433.
- DEWSON, J. H. (1977). Preliminary evidence of hemispheric asymmetry of auditory function in monkeys. In S. Harnad, R. W. Doty, J. Jaynes, L. Goldstein & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- DEWSON, J. H., PRIBRAM, K. H. & LYNCH, J. C. (1969). Effects of ablations of temporal cortex upon speech sound discrimination in the monkey. *Experimental Neurology*, 24, 579—591.

- DIAMOND, M. C., JOHNSON, R. E. & INGHAM, C. A. (1975). Morphological changes in the young, adult and aging rat cerebral cortex, hippocampus and diencephalon. *Behavioral Biology*, 14, 163—174.
- DIMOND, S. J. (1972). *The Double Brain*. London: Churchill Livingstone.
- EBBESSON, S. O. E. (1970). On the organisation of the central visual pathways in vertebrates. *Brain, Behavior and Evolution*, 3, 178—194.
- EBNER, F. F. (1967). Afferent connections to the neocortex in the opossum (*Didelphis virginiana*). *Journal of Comparative Neurology*, 129, 241—268.
- EBNER, F. F. (1969). A comparison of primitive forebrain organization in metatherian and eutherian mammals. *Annals of the New York Academy of Sciences*, 167, 241—257.
- EBNER, F. F. & MYERS, R. E. (1962a). Commissural connections in the neocortex of monkey. *Anatomical Record*, 149, 229.
- EBNER, F. F. & MYERS, R. E. (1962b). Corpus callosum and the interhemispheric transfer of tactual learning. *Journal of Neurophysiology*, 25, 380—391.
- EBNER, F. F. & MYERS, R. E. (1965). Distribution of corpus callosum and anterior commissure in cat and racoon. *Journal of Comparative Neurology*, 124, 353—365.
- ERULKAR, S. D. (1972). Comparative aspects of spatial localization of sound. *Physiological Reviews*, 52, 237—360.
- ESPIR, M. L. E. & ROSE, F. C. (1970). *The Basic Neurology of Speech*. Oxford: Blackwells.
- FORWARD, E., WARREN, J. M. & HARA, K. (1962). The effects of unilateral lesions in sensory motor cortex on manipulation by cats. *Journal of Comparative and Physiological Psychology*, 55, 1130—1135.
- FOSTER, R. E. & HALL, W. C. (1978). The organization of central auditory pathways in a reptile, *Iguana iguana*. *Journal of Comparative Neurology*, 178, 783—831.
- FOX, R., LEHMKUHLE, S. W. & BUSH, R. C. (1977). Stereopsis in the falcon. *Science*, 197, 79—81.
- FRIEDMAN, H. & DAVIS, M. (1938). Left-handedness in parrots. *Auk*, 55, 478—480.
- GAINOTTI, G. (1972). Emotional behaviour and hemispheric side of lesion. *Cortex*, 8, 41—55.
- GALABURDA, A. M., LEMAY, M., KEMPER, T. L. & GESCHWIND, N. (1978). Right-left asymmetries in the brain. *Science*, 199, 852—856.
- GARCHA, H. S. & ETLINGER, G. (1978). The effect of unilateral or bilateral removals of the second somato-sensory cortex (SII): A profound tactile disorder in monkeys. *Cortex*, 14, 319—326.
- GARDNER, H. (1977). *The Shattered Mind*. London: Routledge & Kegan Paul.
- GARMAN, S. (1896). Cross fertilization and sexual rights and lefts among vertebrates. *American Naturalist*, 30, 232.
- GAZZANIGA, M. S. (1975). Brain mechanisms and behavior. In M.S. Gazzaniga (ed.), *Handbook of Psychobiology*. London: Academic Press.
- GAZZANIGA, M. S. (ed.) (1979). *Handbook of Behavioral Neurobiology*. Vol. 2. *Neuropsychology*. New York & London: Plenum Press.
- GESCHWIND, N. (1974). The anatomical basis of hemispheric differentiation. In S. J. Diamond & J. G. Beaumont (eds), *Hemisphere Function in the Human Brain*. New York: Wiley.

- GESCHWIND, N. & LEVITSKY, W. (1968). Human brain: Left—right asymmetries in temporal speech region. *Science*, 161, 186—187.
- GEVINS, A. S., ZEITLIN, G. M., DOYLE, J. C., YINGLING, C. D., SCHAFFEL R. E., CALLAWAY, E. & YEAGER, C. L. (1979). Electroencephalogram correlates of higher cortical functions. *Science*, 203, 665—668.
- GIBSON, A. R. & GAZZANIGA, M. S. (1972). Hemispheric differences in eating behaviour in split-brain monkeys. *Physiologist*, 14, 150.
- GLICK, S. D. (1973). Enhancement of spatial preferences by d-amphetamine. *Neuropharmacology*, 12, 43—47.
- GLICK, S. D. & JERUSSI, T. P. (1974). Spatial and paw preferences in rats: Their relation to rate-dependent effects of d-amphetamine. *Journal of Pharmacology and Experimental Therapeutics*, 188, 714—725.
- GLICK, S. D., JERUSSI, T. P. & ZIMMERBERG, B. (1977). Behavioural and neuropharmacological correlates of nigrostriatal asymmetry in rats. In S. Harnad, R.W. Doty, L. Goldstein, J. Jaynes & G.Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- GOLDSTEIN, K. (1948). *Language and Language Disturbances*. New York: Grune & Stratton.
- GOODALL, J. (1965). Chimpanzees of the Gombe Stream Reserve. In I. DeVore (ed.), *Primate Behaviour*. New York: Molt, Rinehart & Winston.
- GRAY, J. A. (1979). Emotionality in male and female rodents: A reply to Archer. *British Journal of Psychology*, 70, 425—440.
- GREENE, M. C. L. (1964). *The Voice and its Disorders*. London: Pitman Medical.
- HAFEZ, E. S. E. (ed.) (1974). *Reproduction in Farm Animals*. Philadelphia: Lea & Febiger.
- HAIGHT, J. R. & NEYLON, L. (1978). Morphological variation in the brain of the marsupial brush-tailed possum, *Trichosurus vulpecula*. *Brain, Behavior and Evolution*, 15, 415—445.
- HAMILTON, C. R. (1977). Investigations of perceptual and mnemonic lateralization in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G.Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- HARDYCK, C. (1977). A model of individual differences in hemisphere functioning. In H. Whitaker & H. A. Whitaker (eds), *Studies in Neurolinguistics*, vol. 3. New York: Academic Press.
- HARDYCK, C. & PETRINOVICH, L. F. (1977). Left-handedness. *Psychological Bulletin*, 84, 385—404.
- HARDYCK, C., PETRINOVICH, L. & GOLDMAN, R. (1976). Left-handedness and cognitive deficit. *Cortex*, 12, 266—278.
- HARLOW, H. F. (1949). The formation of learning sets. *Psychological Review*, 56, 51—65.
- HILDEBRAND, M. (1977). Analysis of asymmetrical gaits. *Journal of Mammology*, 58, 131—156.
- HUNSAKER, D. & SHUPE, D. (1977). Behaviour of New World Marsupials. In D. Hunsaker (ed.), *The Biology of Marsupials*. New York: Academic Press.
- HUPFER, K., JURGENS, U. & PLOOG, D. (1977). The effect of superior temporal lesions on the recognition of species-specific calls in the squirrel monkey. *Experimental Brain Research*, 30, 75—87.
- INGLE, D. & CAMPBELL, A. (1977). Interocular transfer of visual discriminations in goldfish after selective commissure lesions. *Journal of Comparative and Physiological Psychology*, 91, 327—335.

- IORDANSKY, N. N. (1973). The skull of the crocodilia. In C. Gans & J. S. Parsons (eds), *The Biology of the Reptilia*, vol. 4. London & New York: Academic Press.
- JEFFRIES, R. P. S. (1975). Fossil evidence concerning the origin of the chordates. *Symposia of the Zoological Society of London*, 36, 253—318.
- JENKINS, W. M. & MASTERTON, R. B. (1979). Sound localization in the pigeon (*Columba livia*). *Journal of Comparative and Physiological Psychology*, 93, 403—413.
- JOHNSON, J. H. & MICHELS, K. M. (1958). Learning sets and object size effects in visual discrimination learning by raccoons. *Journal of Comparative and Physiological Psychology*, 51, 376—379.
- JOLLY, A. (1972). *The Evolution of Primate Behavior*. New York: Macmillan.
- KAPPERS, C. U. A., HUBER, G. L. & CROSBY, E. C. (1936). *The Comparative Anatomy of the Nervous System of Vertebrates, including Man*. New York: Macmillan.
- KING, A. P. & WEST, M. J. (1977). Species identification in the North American cowbird: Appropriate responses to abnormal song. *Science*, 195, 1002—1004.
- KINSBOURNE, M. (1971). The minor cerebral hemisphere as a source of aphasic speech. *Archives of Neurology*, 25, 302—306.
- LEDOUX, J. E., WILSON, D. H. & GAZZANIGA, M. S. (1977). Manipulospacial aspects of cerebral lateralization: Clues for the origin of lateralization. *Neuropsychologia*, 15, 743—750.
- LEHMAN, R. A. W. (1978). The handedness of Rhesus monkeys: I. *Neuropsychologia*, 16, 33—42.
- LEMAY, M. (1976). Morphological cerebral asymmetries of modern man, fossil man and non-human primates. *Annals of the New York Academy of Sciences*, 280, 349—366.
- LEMAY, M. & GESCHWIND, N. (1975). Hemispheric differences in the brains of Great Apes. *Brain, Behavior and Evolution*, 11, 48-52.
- LEMON, R. E. (1973). Nervous control of the syrinx in white-throated sparrows (*Zonotrichia albicollis*). *Journal of Zoology, London*, 71, 131—140.
- LENNEBERG, E. (1967). *Biological Foundations of Language*. New York: Wiley.
- LEVY, J. (1969). Possible basis for the evolution of lateral specialization of the human brain. *Nature*, 224, 614—615.
- LEVY, J. (1977). The mammalian brain and the adaptive advantage of cerebral asymmetry. *Annals of the New York Academy of Sciences*, 299, 264-272.
- MACCOBY, E. E. & JACKLIN, L. N. (1975). *The Psychology of Sex Differences*. London: Oxford University Press.
- MATEER, C. (1978). Impairments of nonverbal oral movements after left hemisphere damage: A follow-up analysis of errors. *Brain and Language*, 6, 334—341.
- MATHEWS, L. H. (1978). *The Natural History of the Whale*. London: Weidenfeld & Nicholson.
- MCGLONE, J. (1977). Sex differences in the cerebral organization of verbal functions in patients with unilateral brain lesions. *Brain*, 100, 775—793.
- MEGIRIAN, D., BURESOVA, O., BURES, S. & DIAMOND, S. (1974). Electrophysiological correlates of discrete forelimb movements in rats. *Electroencephalography and Clinical Neurophysiology*, 36, 131—139.
- MEGIRIAN, D., WELLER, L., MARTIN, O. H. & WATSON, C. R. R. (1977). Aspects of laterality in the marsupial *Trichosurus vulpecula* (Brush-tailed possum). *Annals of the New York Academy of Sciences*, 299, 197—212.

- MICHELIS, K. M., PUSTER, J. J. & JOHNSON, J. H. (1961). The solution of patterned string problems by raccoons. *Journal of Comparative and Physiological Psychology*, 54, 439—441.
- MILLER, E. (1971). Handedness and the pattern of human ability. *British Journal of Psychology*, 62, 111—112.
- MILNER, B. (1974). Hemispheric specialization: Scope and limits. In F. O. Schmitt & F. G. Worden (eds), *The Neurosciences — Third Study Program*. Cambridge, Mass. & London: MIT Press.
- MORGAN, M. J. (1977). Embryology and inheritance of asymmetry. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- MORGAN, M. J., O'DONNELL, J. & OLIVER, P. F. (1973). Development of habenular asymmetry in the Habenular nuclei of *Rana temporaria*. *Journal of Comparative Neurology*, 149, 203—214.
- MORGAN, P. J. & JACOBS, M. S. (1972). Comparative anatomy of the cetacean nervous system. In R. J. Harrison (ed.), *Functional Anatomy of Marine Mammals*. London & New York: Academic Press.
- NAPIER, J. R. (1961). Prehensility and opposability in the hands of primates. *Symposia of the zoological Society of London*, 5, 115-132.
- NEBES, R. D. (1971). Superiority of the minor hemisphere in commissurotomized man for the perception of part-whole relation. *Cortex*, 7, 333—349.
- NEBES, R. D. (1974). Hemispheric specialization in commissurotomized man. *Psychological Bulletin*, 81, 1—14.
- NEFF, W. D., FISHER, J. F., DIAMOND, I. T. & YELA, M. (1956). Role of auditory cortex in discrimination requiring localization of sound in space. *Journal of Neurophysiology*, 19, 500—512.
- NELSON, J. M., PILLIIS, R. & GOLDSTEIN, L. (1977). Interhemispheric EEG laterality relationships following psychoactive agents and during operant performance in rabbits. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- NESS, A. R. (1967). A measure of asymmetry of the skulls of odontocete whales. *Journal of Zoology (London)*, 153, 209—221.
- NEVILLE, A. C. (1976). *Animal Asymmetry*. London: Edward Arnold.
- NOTTEBOHM, F. (1971). Neural lateralization of vocal control in a passerine bird. I. Song. *Journal of Experimental Zoology*, 177, 229—262.
- NOTTEBOHM, F. (1976). Phonation in the orange-winged amazon parrot. *Amazona amazonica*. *Journal of Comparative Physiology, Series A*, 108, 157—170.
- NOTTEBOHM, F. (1977). Asymmetries in neural control of vocalization in the canary. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- NOTTEBOHM, F. (1979). Origins and mechanisms in the establishment of cerebral dominance. In M. S. Gazzaniga (ed.), *Handbook of Behavioral Neurobiology* vol. 2. *Neuropsychology*. New York & London: Plenum Press.
- NOTTEBOHM, F. & NOTTEBOHM, M. E. (1976). Left hypoglossal dominance in the control of canary and white-crowned sparrow song. *Journal of Comparative Physiology*, 108, 171—192.
- NOTTEBOHM, F., STOKES, M. M. Q. & LEONARD, C. M. (1976). Central control of song in the canary, *Sennus canaria*. *Journal of Comparative Neurology*, 165, 457—486.

- OAKLEY, K. P. (1972). *Man the Toolmaker*. London: Trustees of the British Museum (Natural History).
- OJEMANN, G. A. (1976). Subcortical language mechanisms. In H. Whitaker & H. A. Whitaker (eds), *Studies in Neurolinguistics*, vol. I. New York: Academic Press.
- OJEMANN, G. A. & WHITAKER, H. A. (1978). Language localization and variability. *Brain and Language*, 6, 239—260.
- OLDFIELD, R. C. (1969). Handedness in musicians. *British Journal of Psychology*, 60, 9 1—99.
- ORNSTEIN, R. E. (1972). *The Psychology of Consciousness*. New York: Viking Press.
- PEARSON, R. & PEARSON, L. (1976). *The Vertebrate Brain*. London: Academic Press.
- PETERSON, G. M. (1934). Mechanisms of handedness in the rat. *Comparative Psychology Monographs*, 9, 1—67.
- PETERSON, G. M. (1951). Transfer of handedness in the rat results from forced practice. *Journal of Comparative and Physiological Psychology*, 44, 184-190.
- PETERSEN, M. R., BEECHER, M. D., ZOLOTH, S. R., MOODY, D. & STEBBINS, W. L. (1978). Neural lateralization of species-specific vocalizations by Japanese macaques (*Macaca fuscata*). *Science*, 202, 324—327.
- PETERSON, G. M. & DEVINE, J. V. (1963). Transfer in handedness in the rat, resulting from small cortical lesions after limited forced practice. *Journal of Comparative and Physiological Psychology*, 56, 752—756.
- PETERSON, G. M. & MCGIBONEY, D. R., JR (1951). Re-education of handedness in the rat following cerebral injuries. *Journal of Comparative and Physiological Psychology*, 44, 19 1—196.
- POPPER, K. R. & ECCLES, J. C. (1977). *The Self and Its Brain*. London: Springer International.
- RATCLIFFE, H. L. (1941). A medical vaginal canal and other anomalies of the genital tract of the opossum, *Didelphys Virginiana*. *Anatomical Record*, 80, 203—209.
- RAVIZZA, R. J. & BELMORE, S. M. (1978). Auditory forebrain: evidence from anatomical and behavioural experiments involving human and animal subjects. In R. B. Masterton (ed.), *Handbook of Behavioural Neurobiology*. Vol. 1 . *Sensory Integration*. New York & London: Plenum Press.
- REYNOLDS, H. C. (1952). Studies on reproduction in the opossum (*Didelphys virginiana virginiana*). *University of California Publications in Zoology*, 52, 223—284.
- RICHMAN, D. P., STEWART, R. A., HUTCHINSON, J. W. & CAVINESS, V. S. (1975). Mechanical model of brain convolitional development. *Science*, 189, 18—21.
- RIKLAN, M. & COOPER, I. S. (1977). Thalamic lateralization of psychological functions: Psychometric studies. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- ROBINSON, J. S. & VONEIDA, T. T. (1973). Hemisphere differences in cognitive capacity in the split-brain cat. *Experimental Neurology*, 38, 123—134.
- ROBINSON, R. G. (1979). Differential behavioural and biochemical effects of right and left hemispheric cerebral infarction in the rat. *Science*, 205, 707— 710.



- ROSEN, D. E. & BAILEY, R. M. (1963). The Poeciliid fishes (Cyprinodontiformes), their structure, zoogeography, and systematics. *Bulletin of the American Museum of Natural History*, 126, 1—176.
- ROSEN, D. E. & TUCKER, A. (1961). Evolution of secondary sexual characters and sexual behaviour patterns in a family of viviparous fishes (*Cyprinodontiformes: Poeciliidae*). *Copeia*, 201—212.
- ROYAL COLLEGE OF SURGEONS (1902). *Descriptive and Illustrated Catalogue of Comparative Anatomy*. 2nd ed. London: Taylor & Francis.
- RUBENS, A. B. (1977). Anatomical asymmetries of human cerebral cortex. In S. Harnad, R. W. Doty, J. Jaynes, L. Goldstein & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- RUBENS, A. B., MAHOWALD, M. W. & HUTTON, J. T. (1976). Asymmetry of the lateral sylvian fissures in man. *Neurology*, 26, 620—624.
- SACKEIM, H. H., GUR, R. C. & SAULY, M. C. (1978). Emotions are expressed more intensely on the left side of the face. *Science*, 202, 434—436.
- SARNAT, H. B. & NETSKY, M. O. (1974). *Evolution of the Nervous System*. New York: Oxford University Press.
- SCHALLER, G. B. (1963). *The Mountain Gorilla*. Chicago: University of Chicago Press.
- SEARLEMAN, A. (1977). A review of right-hemisphere linguistic capacities. *Psychological Bulletin*, 84, 503—528.
- SEMMES, J. (1968). Hemispheric specialization: A possible clue to mechanism. *Neuropsychologia*, 6, 11—26.
- SERVIT, Z. & STREJCKOVA, A. (1970). An electrographic epileptic focus in the fish forebrain and pathways of propagation of focal and paroxysmal activity. *Brain Research*, 17, 103—113.
- SHANKWEILER, D. P. (1961). Performance of brain damaged patients on two tests of sound localization. *Journal of Comparative and Physiological Psychology*, 54, 375-381.
- SHARMAN, G. B. (1970). Reproductive physiology of marsupials. *Science*, 167, 1221—1228.
- SHERMAN, G. F., GARBANATI, J. A., HOFMANN, M. J., ROSEN, G. D., YUTZEV, D. A. & DENENBERG, V. H. (1979). Early experience, brain asymmetry, and muricide in the albino rat. *Society for Neuroscience Abstracts*, 5, 120.
- SHORTRIDGE, G. C. (1934). *The Mammals of South-West Africa*, vol. 1. London: Heinemann.
- SIKES, S. K. (1971). *The Natural History of the African Elephant*. London: Weidenfeld & Nicholson.
- SLIJSER, E. T. (1962). *Whales*. London: Hutchinson. SMITH, A. (1978). Lenneberg, Locke, Zangwill and the neuropsychology of language and language disorders. In G. A. Miller & E. Lenneberg (eds). *Psychology and Biology of Language and Thought*. New York: Academic Press.
- SPERRY, R. W. (1968). Hemispheric disconnection and unity in conscious awareness. *American Psychologist* 23, 723—733.
- SPRINGER, S. P. (1977). Tachistoscopic and dichotic listening investigations of laterality in normal human subjects. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.

- STAMM, J. S., ROSEN, S. C. & GADOTTI, A. (1977). Lateralization of functions in the monkey's frontal cortex. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- STEVENS, V. J. & KLOPFER, F. D. (1977). Interocular transfer of conditioning and extinction in birds. *Journal of Comparative and Physiological Psychology*, 91, 1074—1081.
- SUTTON, D., LARSON, C. & LINDEMAN, R. C. (1974). Neocortical and limbic lesion effects on primate phonation. *Brain Research*, 71, 61—75.
- THOMSON, SIR L. A. (1964). *A New Dictionary of Birds*. London: Nelson.
- THOMPSON, SIR D'A. W. (1942). *On Growth and Form*, 2nd ed. Cambridge: Cambridge University Press.
- TOMILIN, A. G. (1967). *Mammals of The USSR and Adjacent Countries*. Vol IX. *Cetacea*. Jerusalem: Israel Program for Scientific Translations.
- TSUNODA, T. (1975). Functional differences between right- and left-cerebral hemispheres detected by the key-tapping method. *Brain & Language*, 2, 152—170.
- VOWLES, D. M. & BEAZLEY, L. D. (1974). The neural substrate of emotional behaviour in birds. In I. J. Goodman & M. W. Schein (eds), *Birds: Brain and Behaviour*. London: Academic Press.
- WADA, J. A., CLARKE, R. & HAMM, A. (1975). Cerebral hemispheric asymmetries in humans: Cortical speech zones in 100 adult and 100 infant brains. *Archives of Neurology*, 32, 239—246.
- WALLS, G. L. (1942). *The Vertebrate Eye*. Bloomfield Hills: Cranbrook Institute of Science.
- WARREN, J. M. (1953). Handedness in the rhesus monkey. *Science*, 118, 622—623.
- WARREN, J. M. (1958). The development of paw preferences in cats and monkeys. *Journal of Genetic Psychology*, 93, 229—236.
- WARREN, J. M. (1977). Handedness and cerebral dominance in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- WARREN, J. M., ABPLANALP, J. M. & WARREN, H. B. (1967). The development of handedness in cats and monkeys. In H. W. Stevenson, E. H. Hess & H. L. Rheingold (eds), *Early Behavior*. New York: Wiley.
- WASER, M. S. & MARLER, P. (1977). Song learning in canaries. *Journal of Comparative and Physiological Psychology*, 91, 1—7.
- WEBSTER, W. G. (1977). Hemispheric asymmetry in cats. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (eds), *Lateralization in the Nervous System*. London: Academic Press.
- WELKER, W. I. & SEIDENSTEIN, S. (1939). Somatic sensory representation in the cerebral cortex of the racoon. *Journal of Comparative Neurology*, 111, 469—501.
- WELLS, M. J. (1978). *Octopus*. London: Chapman & Hall.
- WEST, M. J., KING, A. P., EASTZER, D. H. & STADDON, J. E. R. (1979). A bioassay of isolate cowbird song. *Journal of Comparative and Physiological Psychology*, 93, 124-133.
- WHITAKER, H. A. & OJEMANN, G. A. (1977). Lateralization of higher cortical function: A critique. *Annals of the New York Academy of Sciences*, 229, 459—476.
- WHITFIELD, I. C. (1967). *The Auditory Pathway*. London: Edward Arnold.

- WHITFIELD, I. C., CRANFORD, J., RAVIZZA, R. & DIAMOND, I. T. (1972). Effects of unilateral ablation of auditory cortex on complex sound localization. *Journal of Neurophysiology*, 35, 718—731.
- WHITFIELD, I. C., DIAMOND, I. T., CHINERWALLS, K. & WILLIAMSON, T. G. (1978). Some further observations on the effects of unilateral cortical ablation on sound lateralization in the cat. *Experimental Brain Research*, 31, 221—234.
- WHITNEY, L. F. & UNDERWOOD, A. B. (1952). *The Raccoon*. Orange, Conn.: Practical Science Publishing.
- WITELSON, S. F. (1976). Sex and the single hemisphere: Specialization of the right hemisphere for spatial processing. *Science*, 193, 425—427.
- WITELSON, S. F. & PALLIE, W. (1973). Left-hemisphere specialization for language in the newborn: Neuroanatomical evidence of asymmetry. *Brain*, 96, 641—646.
- YENI-KOMSHIAN, G. & BENSON, D. (1976). Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees and rhesus monkeys. *Science*, 192, 387—389.
- YEO, C. H. & SAVAGE, G. E. (1975). The tectal commissures and interocular transfer of shape discrimination in the goldfish. *Experimental Neurology*, 49, 291—298.
- YOSHIOKA, J. C. (1930). Handedness in rats. *Journal of Genetic Psychology*, 38, 471—474.
- YOUNG, J. Z. (1962). *The Life of Vertebrates* 2nd ed. . New York & Oxford: Oxford University Press.
- ZAIDEL, E. (1978). Lexical organization in the right hemisphere. In P. Buser & A. Rougeul-Buser (eds), *Cerebral Correlates of Conscious Experience*. Amsterdam: Elsevier.
- ZANGWILL, O. L. (1960). *Cerebral dominance and its Relations to Psychological Function*. Edinburgh: Oliver & Boyd.
- ZANGWILL, O. L. (1978). Aphasia and the concept of brain centres. In G. A. Miller & E. Lenneberg (eds), *Psychobiology of Language and Thought*. London: Academic Press.
- ZEIR, H. (1975). Interhemispheric interactions. In P. Wright, P. G. Caryl & D. M. Vowles (eds), *Neural and Endocrine Aspects of Behaviour in Birds*. Amsterdam: Elsevier.
- ZIMMERBERG, B., GLICK, S. D. & JERUSSI, I. P. (1974). Neurochemical correlates of a spatial preference in rats. *Science*, 185, 623—625.

Received 31 October 1979

0007-1269/80/030329—39 \$02.00/0 © 1980 The British Psychological Society