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LATERALITY IN ANIMALS

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We now know that laterality in various forms is a characteristic of a wide range of species, and that it apparently developed very early in evolution. Yet, some hundred years had to elapse after the discovery that there was lateralization, or asymmetry, for control of speech in the human brain, before any earnest attempts were made to discover or recognise the presence of laterality in nonhuman species (see Robinson, Becker & Camp, 1983). The reason for this delay appears to have been the belief that lateralization of brain function was a characteristic unique to the human species, placing our species above all other species.

This belief had been preceded by a well-developed mythology surrounding the sinistral-dextral dichotomy of handedness in humans (Corballis, 1983, pp. 1-9), and the belief that dextrality was also a uniquely human characteristic. It has been argued that shared tool use by humans caused laterality of limb use and, in turn, specialization of the left hemisphere for language (Frost, 1980; Bradshaw & Nettleton, 1982).

Thus, the population bias in handedness in humans was seen to be intimately related to our superior ability to use tools, and the population bias in lateralization of function in the cerebral hemispheres was seen to be the basis of our superior ability for language. Not surprisingly, these unique attributes afforded to the human species were reluctantly relinquished by many psychologists, some (e.g. Levy, 1974, 1979) clinging to them well after lateralization of function in the nervous system had been clearly demonstrated in more than one nonhuman species, in particular for control of singing in song-birds (Nottebohm, 1971; see later).

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LATERALITY OF LIMB USE

When in the 1950s and 1960s psychologists first set about looking for laterality* in nonhuman species, their aim was to see if they could find evolutionary evidence for asymmetry in humans. It is therefore not surprising that they chose to look for evidence of handedness in primates. The overall conclusion drawn from a large number of studies was that nonhuman primates do not have handedness like that of humans (e.g. Warren, 1958; Brookshire & Warren, 1962; or summarised in Corballis, 1983, pp. 113-116; Walker, 1980, pp. 348-351 and Warren, 1980, pp. 535-554). Although individual primates were found to show a preference for using one hand, in contrast to the human species, there was no overall bias in handedness at the population level, and it was generally considered that the individual lateralities in hand use were artifacts of the methods used to test the animals (Warren, 1980).

This view that nonhuman species lacked a population bias in laterality of limb use was reinforced by Collins' (1975) report that mice tested in a task requiring them to reach into a tube to obtain a food reward showed paw preferences as individuals but, as reported for nonhuman primates, there was no population bias of "pawedness". Moreover, raising the mice in right- or left-biased worlds was found to influence the distribution of paw preferences in the expected direction, confirming that experience is a factor influencing preference for limb use.

A recent report by MacNeilage, Studdert-Kennedy and Lindblom (1987) has, however, taken issue with the earlier reports of lack of handedness in nonhuman primates and, on re-examination of the data, the authors have reached the conclusion that there is more than simply suggestive evidence indicating that a number of species of macaques have a left-hand preference (see Ward, 1989, for a summary of reports of left-hand bias in prosimians). For primates in general, the authors propose that there is a left-hand preference for visually guided reaching movements and a right-hand preference for manipulation of objects. The remnants of this division of labour between hands may still be evident in humans despite our right-handedness, as there is some evidence that dextrals performing a task re-

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*It should be noted that the terms laterality and asymmetry are used interchangeably when referring to functional differences between the left and right sides, but asymmetry is the term used for structural differences between the sides. This article will keep to the use of the term laterality unless there is a clear left-right structural difference involved.

quiring fast reaching for a visual target are more accurate than when using the left-hand (Guiard, Diaz & Beaubaton, 1983).

It is not my aim to discuss the relative merits of this particular theory. The data for handedness in primates are still a matter of controversy (see the peer review section following MacNeilage et al., 1987). If the earlier researchers had been able to move further away from the human species and look for laterality of limb use in birds, their search would have been more fruitful, and just as shattering for the belief that laterality of limb use at the population level was unique to humans and possibly caused by shared tool use. In a number of species of parrots and cockatoos there is a population bias in "footedness", as strong as that of handedness in humans.

Friedman and Davis (1938) reported left-footedness for manipulating food objects in several species of African parrots. Even though the sample sizes in this study were very small, it is important to note that this report was overlooked by those researchers looking for laterality in nonhuman species and focussing on primates. Australian cockatoos and parrots also have footedness for manipulating food objects (Rogers, 1981; and see Table 1). A strong bias for left-footedness was found in eight of the nine species scored. The exception was *Platycercus elegans*, the crimson rosella, which showed right-footedness.

Footedness appears to occur only in those avian species which use their feet in feeding. Pigeons do not manipulate food objects with their feet, and Güntürkün, Kesch and Delius (1988) have recently reported the absence of footedness in pigeons tested by sticking a piece of tape on the tip of the beak and scoring the foot used in the first attempt to remove it (see Table 1). They found no bias in foot use at either the population or individual level. This lack of footedness in pigeons is species rather than task specific: they tested a small number of parrots on the same task and found the preferred foot used to remove the tape was consistent with their footedness for manipulation of food objects. Ducker, Luscher and Schulz (1986) have observed right-footedness (100%) in gold finches, *Carduelis carduelis*, tested on a task requiring the birds to open doors and catches using the beak and a foot in order to obtain a food reward. These data support the general hypothesis that limb use preferences occur only in species which use their limbs for manipulative activities (Walker, 1980).

We therefore decided to test this hypothesis using a species of parrot which does not manipulate objects with its feet. Budgerigars were tested for foot use in removal of a piece of sticky tape from the beak (Workman & Rogers, in preparation; see Table 1). Nine individuals were scored for a mean of 20 trials each. They showed no footedness either at the population level or as individuals. This supports the

TABLE 1
Footedness in Birds.

	Species	*Percentage left-footedness*	*Number of observations*
A	Galah (*Cacatua roseicapilla*)	89	68
	Sulphur crested cockatoo (*Cacatua galerita*)	87	113
	Little corella (*Cacatua sanguinea*)	93	15
	Long-billed corella (*Cacatua tenuirostis*)	89	19
	Pink cockatoo (*Cacatua leadbeateri*)	100	24
	Yellow-tailed black cockatoo (*Calptorhynchus funereus*)	100	7
	Gang-gang (*Callocephalon fimbriatum*)	100	38
	Crimson rosella (*Platycercus elegans*)	23	90
	Yellow rosella (*Platycercus f. flaveolus*)	100	6
B	Chicken (*Gallus gallus*)	32 (±3)	240 (6 animals)
C	Budgerigar (*Melopsittacus undulatus*)	* 53 (±9)	180 (9 animals)
	Chicken (*Gallus gallus*)	* 16	37 (37 animals)
	Pigeon (*Columbia livia*)	* 53	250 (50 animals)

Foot use in feeding or in attempting to remove a piece of sticky tape from the beak (the latter scores being marked by asterisks). For the first nine species listed under A, the percentage of left-footedness refers to the percentage of animals using the left foot to manipulate food objects, the animals being observed either in captivity or in their natural environment. All of these species show significant footedness (data quoted from Rogers, 1981). Additional data (not included here) of repeated observations of foot use by single individuals indicate that individuals have a consistent foot preference. The results listed under B are for the foot used to initiate a scratching bout during feeding. There were 40 such scores for a total of 6 animals, and the data are given as a mean and standard error (in brackets). Note the right-footed bias. The result for chickens listed under C is the percentage of animals using the left foot to remove a piece of sticky tape from the beak (one observation, of the first movement made, per bird). Again, note the right-footed bias. Also listed under C are mean scores, with standard errors, for repeated attempts of budgerigars or pigeons to remove a piece of sticky tape from the beak. There is no footedness in these species. The data for pigeons are quoted from Güntürkün, Kesch and Delius (1988). Means and standard errors (in brackets) are given where it was possible to make repeated measures on given individuals.

hypothesis that laterality in limb use occurs only when the feet are used to manipulate objects.

Yet, contrary to this hypothesis we have recently found footedness in a species which does not use its feet to manipulate objects. Chickens (*Gallus gallus*) do not use their feet to pick up and manipulate food or other objects, but they frequently scratch the ground when searching for food. Workman and Rogers (in preparation) scored the first foot used to rake the ground at the beginning of a bout of ground scratching. Six animals were scored for 40 scratching bouts each. Though both feet are used in this behaviour, there was a significant tendency to initiate a bout of ground scratching by using the right foot (68 ± .03% right-footedness, mean and standard error; $p < .05$). When 10-day old chicks were tested on the task requiring removal of sticky tape from the beak a stronger right-foot bias was found (84%; $p < .01$; the first foot chosen to scratch the tape was scored, thus giving one score per individual, $n = 37$). Apparently, it is not manipulative ability alone which confers footedness on avian species, but also active use of the feet in feeding or searching for food.

The fact that chickens show right footedness in searching for food is not insignificant as they have dominance of the right eye in tasks requiring them to search for food and to perform visual discrimination learning. By testing chickens monocularly on a task requiring search for food grains Andrew, Mench and Rainey (1982) and Zappia and Rogers (1987) have shown that the right eye learns to discriminate grains from small pebbles more rapidly than does the left eye. Also chickens trained binocularly on a visual discrimination task have dominance of the right eye for recall of the task (Gaston & Gaston, 1984). Given this dominance of the right eye in searching for food and the fact that chickens have laterally placed eyes with only a small area of binocular overlap, it makes logical sense that chickens have right footedness for initiating scratching of the ground to expose grains of food.

The pigeon has the same lateralization of eye use in visual discrimination learning as does the chicken (Güntürkün, 1985), but it does not have footedness and it does not use the feet to scratch the ground while feeding. This suggests that footedness (in both feeding and non-feeding tasks) in avian species may have developed secondarily to lateralization of visual functions at the perceptual level, and only in species which actively use their feet in feeding, either to manipulate the food or to uncover it by scratching the ground.

In other words, if the feet are used in feeding, laterality of foot use may occur as a *result* of the constraints placed upon it by lateralization in perceptual or cognitive processes linked to either eye.

If one tentatively considers extending this hypothesis to mammalian species, it may be argued that handedness followed on from the presence of laterality at the cognitive or perceptual level of brain organisation, rather than it being an antecedent of the latter, as implied by McNeilage et al. (1987) and as stated by Kimura (1979) and Frost (1980) (see later for evidence of lateralization of cognition in mammalian species).

Unfortunately, we know nothing as yet of lateralization of function in the forebrain of parrots or cockatoos, except that *Amazona amazonica*, which is 75% left-footed (Friedman & Davis, 1938), does not have lateralization of control of vocalisation (Nottebohm, 1976b). Nevertheless, it is highly likely that parrots and cockatoos do have laterality for other forebrain functions. Zebra finches, for example, have no, or possibly only slight, laterality for control of their vocalisations (Nottebohm, personal communication) but they show strong functional laterality for copulation responses: the male views the female with his right eye when performing courtship behaviour (Workman & Andrew, 1986). The right footedness of *Platycerus elegans* may indicate a different, if not inverted, laterality at higher levels of central processing in this species.

With the development of greater manipulative ability (e.g. with the evolution of the opposable thumb in primates) laterality of limb use, though perhaps originally developed for feeding, would become manifest in a range of activities, including tool use. As primates became more able to adopt an upright posture they needed to use the originally non-specialised (right) fore-limb less often for supporting the body. MacNeilage et al. (1987) argue that this may have altered the evolutionary course of handedness, as the right hand could now take over and specialise for manipulation while the left remained specialised for visually guided reaching. In birds there is no possibility for simultaneous use of both limbs to "handle" an object as one limb is always needed to support the body. Thus, in birds the foot first specialised to hold food may be retained for all manipulative functions. So saying, one must recognise that the question as to why some species are left-footed and others right-footed remains open. It may perhaps depend on the particular direction of laterality in the perceptual processes used in feeding behaviour in the given species or, indeed, in the given individual. Alternatively, it may depend on the type of searching strategy which the particular species utilises in feeding. Andrew, Mench and Rainey (1982) have found that the left eye of the chicken is specialised for analysis of the spatial position of objects, whereas the right eye is specialised for discriminating and categorising objects, particularly food versus non-food, irrespective of their position in space. Left-footedness may occur in species in which foraging involves greater use of spatial cues rather than detailed discrimination of food objects from the background, and *vice versa* for right-footed species.

LATERALITY OF COGNITIVE FUNCTION

It is in perceptual and cognitive functioning that we find the clearest examples of laterality in animals at the population level. In Japanese macaques the left hemisphere is specialised for processing their species-specific vocalisations (Peterson, Beecher, Zoloth, Moody & Stebbins, 1979). Denenberg (1981) has shown that rats have lateralization of "affective behaviour", measured in terms of taste aversion and muricide. The data suggest that the right hemisphere is more fearful than the left, and that the left hemisphere can inhibit this aspect of functioning in the right (Denenberg & Yutzey, 1985). Denenberg's extensive studies on laterality in rats have led him to conclude that the right hemisphere of this species is specialised for "strong emotional" behaviours and some spatial processes (Denenberg, 1984b).

In a series of experiments testing rats in operant conditioning tasks Bianki (1983, 1988) has demonstrated that the left hemisphere is specialised for processing sequentially presented visual stimuli while the right is specialised for processing simultaneously presented visual stimuli. Bianki's findings are strikingly reminiscent of the lateralized organisation present in humans.

These lateralities of hemispheric functions in rats are correlated with asymmetries in the structure of the cortex and in the cellular densities. In male Long-Evans rats most areas of the cortex are thicker on the right side than the left (Diamond, 1984), and this greater thickness results from having a higher number of both neuronal and glial cells (McShane et al., 1988), although it is not known whether, or how, these structural differences pertain to functional lateralization.

It should be noted again that this population bias in cortical laterality in rats is not manifest in "pawedness" at the population level, although there is at least one motor output pattern which shows a population bias. Rats handled in early life show a left side bias in the direction in which they make their first move when placed in the open field (Sherman, Garbanati, Rosen, Yutzey & Denenberg, 1980). Intact, non-handled rats show no spatial bias, but ablation of the left hemisphere generates a left-side bias while ablation of the right generates a less marked right-side bias. Hence, Sherman et al. (1980) deduced that handling in early life produces a right hemispheric dominance, and so unmasks population laterality in the direction of moving off in the open field.

The direction of the first move made in the open field is not related to turning behaviour in rats, as studied by Glick (see Glick, 1983, and Glick & Shapira, 1985). Glick has looked at turning or circling behaviour which occurs in a preferred direction in the individual either spontaneously at night or after treatment with drugs such as amphetamine or apomorphine. Examination of a group of over 600 rats revealed that 54.8% circled to the right and this was calculated to be a significant population bias (Glick 1983, p. 18), although it is by no means an impressively sized bias. Ross, Glick and Meibach (1981) and Denenberg et al. (1982) have shown a similarly sized significant population bias in the direction in which neonatal rats hold their tails, the actual direction of the bias depending on both the sex and strain of the rats.

The direction of circling in an individual correlates with the relative concentrations of dopamine in the striata on the left and right sides of the brain: the rats rotate contralaterally to the side with the higher dopamine level. Moreover, tail posture in neonates predicts both the rotational bias and dopamine asymmetry (Rosen, Finklestein, Stoll, Yutzey & Denenberg, 1984). Pawedness can be generated at the individual level by conditioning, and there is some suggestion that in this case it correlates with laterality in dopamine levels (Schwarting, Nagel & Huston, 1987). Dopamine levels are higher in the amygdalae ipsilateral to the paw used in the task. It would be interesting to know how this relates to the direction of turning. That is, whether the direction of rotation is also changed by this conditioning process.

Thus, in rats there are individual lateralities at one level of brain organisation (in the striata and amygdalae) and a population bias at another level of organisation (cortex). Different types, degrees, and directions of asymmetry occur in different regions of the brain. There is, however, no obvious hierarchical organisation as to which form of laterality occurs at the various levels of complexity in processing because, like the cortex, the hypothalamus also displays laterality of functioning at the population level. Implantation of oestradiol into either the left or right side of the hypothalamus of neonatal female rats causes different effects on sexual behaviour in adulthood (Nordeen & Yahr, 1982). Implanting oestradiol into the ventromedial nucleus on the left side of the hypothalamus was found to suppress lordosis by a mean of approximately 35%, while implants in the right ventromedial nucleus had no effect on this behaviour. Implants of oestradiol into the preoptic area on the right side of the hypothalamus elevated mounting by a two-fold factor, while implanting the equivalent region on the left side had no effect.

The hypothalamus of the rat also has laterality for control of hormonal output from the pituitary (Bakalkin et al. 1984). In Wistar rats, the right side of the hypothalamus has a higher concentration of luteinizing hormone releasing factor; in an albino rat strain it is the other way around.

Many of the earlier concepts of lateralized brain function incorporated the idea that it was present only in the cortex and required a corpus callosum to interconnect the two hemispheres so that one hemisphere (the left in most cases) could suppress the other (see Gazzaniga, 1974; Denenberg, 1981). Gazzaniga and Le Doux (1978) postulated that evolution of the corpus callosum was essential for the appearance of laterality in the brain. They based their argument on empirical evidence that lateralization of language in humans does not develop until the fibres in the corpus callosum are fully myelinated (Gazzaniga, 1974). It is not difficult to see that their general hypothesis for the presence or absence of laterality is human-centred and based on the original premise that laterality is unique to humans and their capacity for language. Denenberg (1981) extrapolated this idea to include all mammalian brains and developed a model to explain his data for laterality in rats (see earlier), involving suppression of the right hemisphere by the left via the corpus callosum. Berrebi et al. (1988) have now found evidence that handling increases the size of the corpus callosum in male rats aged 110 days, which certainly supports a role for the corpus callosum in functional laterality at the level of the cortex since, as discussed previously, handling unmasks laterality in the direction of moving off in the open field. Nevertheless, laterality in the hypothalamus cannot easily be tied to the corpus callosum unless the laterality in the hypothalamus is conferred upon it by higher centres in the cortex.

Evidence of laterality in the avian brain conclusively shows that the corpus callosum is not necessary for asymmetry to occur, as there is no corpus callosum in the avian brain. Pathways do cross from left to right in the avian brain in the supra-optic decussation and the tectal posterior and anterior commissures but these are small pathways. Also the supra-optic decussation does not connect homologous regions of the brain, the latter being the essential property of the corpus callosum and its chief attribute thought to be used by one side to inhibit the other and so generate functional lateralization.

The avian forebrain has some fine examples of laterality. In a number of species of song-birds, singing is controlled by the left hemisphere (in chaffinches, Nottebohm, 1971; in crowned sparrows, Nottebohm, 1976a; and in canaries, Nottebohm, 1977). Lesions of the hyperstriatum ventrale, pars caudalis (HVc) on the left side eliminate singing, whereas lesions of the right HVc have no effect. This striking finding has been widely quoted in terms of its analogy to the human condition with language on the left side, particularly given the parallels which have been drawn between the "syntactical" structure of bird song and human language. Yet, there is a distinct difference between the two systems. There are anatomical asymmetries associated with the functional lateralization of language/speech in humans, but no structural asymmetries are present in the centres controlling singing in the song-birds.

In humans the region involved in speech comprehension (Wernicke's area) is larger on the left side (Geschwind and Levitsky, 1968), and damage to this area in adults leads to aphasia with the right side being unable to take over to produce speech. In contrast, birds have the full complement of structures which control singing on both sides of the brain. If the left HVc of canaries is lesioned in one reproductive season no singing will occur in that season, but in the next season the right HVc takes over and the full song repertoire is regained. It is not known how much, if any, of the previous season's song is retained. The function of the right HVc in an intact brain is not known. Perhaps it is used in analysis and comprehension of the songs of other birds, or in storing a memory of the individual's own song. Given the absence of a corpus callosum interconnecting homologous regions in the forebrain, one wonders how the left HVc suppresses the right HVc in the intact brain. Also why does the right HVc remain suppressed for the rest of the singing season when the left is lesioned? In other words, when the left HVc has been lesioned, why is there a delay until after the sex steroid hormone levels have subsided and re-elevated before the right HVc can take over and control singing? Elevated testosterone levels permit neurogenesis in the adult canary brain (Nottebohm, 1987, 1989), and this neural plasticity is clearly necessary for the right HVc to assume control of singing after lesioning the left. Possibly rising levels of testosterone at the beginning of the reproductive season are essential to trigger the combined processes of song production and neural plasticity. There are many interesting questions yet to be answered. It should be noted that in chaffinches, which unlike canaries do not embellish their song repertoire each season, the right HVc does not take over the control of song after the left HVc is lesioned (Nottebohm, 1987). Canaries are, according to Nottebohm, "open-ended learners" which retain neural and functional plasticity in adulthood, while chaffinches are "critical-period learners" which lose and never regain the ability to add to their repertoire.

As mentioned briefly before, the chicken (*Gallus gallus*) brain has laterality for a number of functions. Our original studies revealed laterality by injecting the protein synthesis inhibitor, cycloheximide (CXM) into either the left or right forebrain hemisphere in early life. Treatment of the left produced a permanent deficit in the ability to learn a task requiring the chick to discriminate between grains of food and small pebbles adhered to the floor (the 'pebble floor task') and retarded habituation to both visual and auditory stimuli (Rogers & Anson, 1979). Treatment of the right hemisphere did not affect these behaviours. These results were subsequently confirmed by testing uninjected chicks monocularly. The avian nervous system has an anatomical feature which makes it admirably suited to studying laterality; viz. the optic nerves decussate completely so that the primary visual connections go only to the contralateral side of the brain (Cowan, Adamson & Powell, 1961). Thus monocular testing achieves the same unilateral input to the brain as does the complicated tachistoscopic presentation to humans of stimuli placed in the extreme peripheral fields of vision. In this respect, the bird brain may be considered as a "split-chiasma" mammalian brain.

When tested monocularly on the 'pebble floor' visual discrimination task, young male chicks using the right eye learn as well as binocularly tested controls, but in those tested using the left eye learning is retarded (Mench & Andrew, 1986; Zappia & Rogers, 1987). By the age of 23 days post-hatching this laterality in performing the pebble floor task has disappeared as both eyes now learn well (Rogers, 1990b).

The presence of this functional lateralization for visual discrimination learning in young male chicks correlates with a structural asymmetry in the visual projections from the thalamus to the visual Wulst, or hyperstriatum, of the forebrain (Boxer & Stanford, 1985; Rogers & Sink, 1988). The left side of the thalamus, which receives input from the right eye only, sends projections to hyperstriata on both sides of the forebrain. The right side of the thalamus, which receives input from the left eye only, projects to the right hyperstriatum but very few projections cross over to go the hyperstriatum on the left side. This better connectivity of the right eye to both sides of the hyperstriatum may well explain its superior performance in visual discrimination learning. By the beginning of the third week of life post-hatching the projections from the right side of the thalamus to the left hyperstriatum have developed and there is no longer any asymmetry in the organisation of these thalamofugal visual pathways. The loss of this structural asymmetry parallels the loss of functional laterality in visual learning ability on the pebble floor, suggesting a direct connection between the two.

Newly hatched female chicks have no asymmetry in the organisation of their visual projections from thalamus to hyperstriatum (Adret & Rogers, 1989) and no difference in visual learning ability between the left and right eyes (Zappia & Rogers, 1987). It is possible that the visual pathways develop over a different time-course in females and that they do have asymmetry in them at an age not yet sampled, possibly before hatching.

In young male chicks the left eye is more responsive to novel stimuli and shows more fear responses to a purple coloured bead (Andrew & Brennan, 1983). This form of laterality is also transient, disappearing by the second week of life, which is earlier than the loss of asymmetry in the thalamofugal visual projections.

Young female chicks do not have laterality in their fear responses: both eyes of the female respond the same as the right eye of the male (Andrew & Brennan, 1984). Both eyes of the female and the right eye of the male have their full complement of contralateral visual projections from each side of the thalamus to the hyperstriatum, while the left eye of the young male is deficient in contralateral projections from thalamus to hyperstriatum (Adret & Rogers, 1989), which suggests at least some link between organisation of the visual pathways and fear responses to a bead.

Phillips and Youngren (1986) have found that unilateral injection of kainic acid into the right archistriatum of 5 day-old chicks reduces fear responses in the open field, whereas injection of the left archistriatum does not. It is, as yet, unclear how these results may link to lateralities in fear responses scored in monocular testing.

Interestingly, there is no sex difference in the effect of unilateral treatment of the forebrain with glutamate or cycloheximide. Treatment of either the left or right hemisphere reveals the same lateralization for visual discrimination learning in both males and females even though females tested monocularly on this task show no laterality (Rogers, 1986). The unilateral administration of drugs, therefore, reveals that females have laterality at deeper levels of brain processing (i.e. further removed from the level of perceptual input).

Chickens therefore exhibit laterality at several levels of neural organisation and there are sex differences at the perceptual level. The left and right eyes of male chickens perceive entirely different visual worlds, and there is asymmetry in the visual pathways which carry information from the mid-brain to the forebrain. Females have no asymmetry at the perceptual input level but, similar to males, they have functional asymmetry at higher levels of processing in the forebrain.

The left eye of the chicken is used for control of attack and copulation responses (Howard, Rogers & Boura, 1980; Bullock & Rogers, 1986; Rogers, Zappia & Bullock, 1985). For example, chicks treated with testosterone (or oestrogen) show elevated copulation scores when they are tested binocularly on standard hand-thrust tests, and also when they are tested with the right eye occluded (i.e. using the left eye only). In contrast, when they are tested with the left eye occluded (i.e. using the right eye only), they show no evidence of having been treated with the hormone; their scores for attack and copulation are not elevated above control levels.

Recently, we have shown that asymmetry for attack, at least, persists into adulthood. Adult hens with the left binocular area of the visual field occluded by "monocular polypeepers" have a low level of agonistic behaviour, equivalent to that of hens wearing "binocular polypeepers". Those with occlusion of the right binocular field have a high level of agonistic behaviour, equivalent to that of controls not wearing polypeepers (Rogers & Workman, in preparation). Since this form of laterality is present in adults and in females, it is unlikely to depend directly on differential input to the forebrain caused by asymmetry in the visual projections. Alternatively, if asymmetry in the visual projections exists at some time during the early development of the female, this may confer a functional laterality on the forebrain which persists after the asymmetry in visual pathways has disappeared. For example, asymmetry in visual inputs to the hyperstriatum may establish an initial laterality in perceptual analysis and memory formation, which lays the foundations for subsequent differentiation of processing between the hemispheres.

DOMINANCE VERSUS DIFFERENTIAL USE OF THE HEMISPHERES

Laterality of brain function may involve complete dominance of one hemisphere over the other so that all of a given sort of analysis occurs on one side only, it may be a matter of relative degrees of involvement of the hemispheres in a given form of processing, or it may involve simultaneous but differential use of the hemispheres in performing a given function. The latter occurs in imprinting in the chicken.

The intermediate and medial parts of the hyperstriatum ventrale (IMHV) on the left and right sides of the forebrain are differentially involved in imprinting (Cipolla-Neto, Horn & McCabe, 1982; and see Horn, 1985, pp. 129-150). The memory of imprinting is stored in both the left IMHV and right IMHV for approximately the first 3 hours after training, but by some 15 hours later the right IMHV no longer retains its store of the memory while the left does. On the right side the memory store is shunted to some other region of the hemisphere. Horn and his colleagues demonstrated this by placing sequential lesions in the left and right IMHV regions after imprinting. In one group of chicks the right IMHV region was lesioned 3 hours after imprinting on day 1 of life (the memory of imprinting was retained by these animals), and then the left IMHV was lesioned some 23 hours later. After this sequence of lesions no memory of the imprinting was retained. In another group of chickens the left IMHV was lesioned 3 hours after imprinting (memory being unaffected by this), and then 23 hours later the right IMHV was lesioned. Subsequently, these chicks were found to have memory of the imprinting stimulus. Thus, the long-term memory of imprinting is consolidated in different regions of the left and right hemispheres. This differential use of the hemispheres may possibly be the reason why imprinting forms a strong and stable memory trace (Rogers, 1986).

Both hemispheres are also used differentially when young chicks learn a passive avoidance task which involves pecking of a bead coated with the noxious tasting substance, methyl anthranylate. There is laterality in the time course of memory events occurring in each hemisphere. The right eye shows a brief period of improved recall 30 to 32 minutes after training, while the left does so at 25 minutes after training (Andrew & Brennan, 1985).

In the same task Rose & Csillag (1985) have shown laterality in neuronal metabolism using the radioactive 2-deoxyglucose technique. This is an example of 'metabolic' dominance. One can say 'dominance' since the chicks were tested using both eyes, the bead was held in the binocular field of vision and competition between the hemispheres could occur. It is possible to make inferences about laterality from tasks in which birds are tested monocularly, but dominance can be determined only by testing them binocularly. The latter requires competition and one side "winning" over the other.

Subcellular structural components in the IMHV, such as synaptic apposition length, also change asymmetrically after training on the passive avoidance bead task (see Stewart, Rose, King, Gabbott & Bourne, 1984), some of the changes being greater on the left side, others on the right.

Finally, it is worth mentioning that birds spend a considerable amount of their sleeping time with one hemisphere asleep while the other is awake. This is monocular sleep in which only the hemisphere contralateral to the closed eye shows a lateralized sleep pattern of electrical activity (Ball, Amlaner, Shaffery & Opp, 1988). The laterality in brain function generated thus is only transient, but it may be essential to behaviour and possibly memory formation. It is possible that a bird sleeping in its left hemisphere only would be more responsive to novel stimuli, and subsequently show a greater likelihood of attacking, compared to one sleeping in its right hemisphere only. We do not yet know whether one hemisphere sleeps more than the other, or whether performing certain sorts of behaviour may trigger more sleep on one side than the other.

LATERALIZATION IN INDIVIDUALS AND IN POPULATIONS

Up until now, there has been a tendency to underestimate the importance of laterality at the individual level, and to focus only on laterality in the population as a whole. This has resulted from an emphasis on looking for genetic/evolutionary explanations for laterality in humans, but, if a brain needs to be lateralized to function efficiently, it may not matter on which side it conducts one set of functions versus the other, only that laterality is present in one direction or the other.

At least, this would be the case at the level of the individual. Nevertheless, if lateralization of brain function has a role in social behaviour, whether or not most (or even all) individuals in the social group are lateralized in the same direction may be influential. Indeed, in groups of young chickens the presence or absence of lateralization at the population level has been shown to alter the stability of the social hierarchy (Rogers & Workman, 1989). Chicks hatched from eggs exposed to light during incubation all have their brains lateralization in the same direction (see later); they have lateralization at both the individual and the population levels. Those hatched from eggs incubated in darkness have lateralization at the individual level, but not at the population level (Rogers, 1982; see later); half of the individuals have lateralization in one direction and half in the other. The social groups of chicks exposed to light during incubation form a more stable and rigid hierarchy, as measured in terms of their competition for access to a food source. The group structure of chicks hatched from eggs incubated in darkness was more variable from day to day, possibly because there was less predictability from individual to individual within the social group.

To summarise, for solitary behavioural performance the direction of lateralization for perception, cognition, footedness or handedness may not matter. However, the presence of a population bias in lateralization may well have some influence on social interaction and group structure. It is, of course, the latter situation which has concerned anthropologists with respect to handedness in the human population and shared tool use.

FACTORS AFFECTING THE DEVELOPMENT OF ASYMMETRY

In the chicken the direction of brain laterality is determined by differing amounts of light input received by the left and right eyes of the embryo (Rogers, 1982; Rogers 1986). During the last three or so days of incubation the chick embryo is oriented in the egg such that its left eye is occluded by its body and the right eye is exposed to receive light input entering the egg through the shell and membranes. The greater amount of light received by the right eye during the sensitive period just prior to hatching stimulates the growth of visual pathways from that eye in advance of those from the left eye.

If the embryo's head is withdrawn from the egg on day 19 or 20 of incubation, the right eye occluded and the left eye exposed to light, there is a reversal of both structural and functional laterality in the brain. The asymmetry in the visual projections from thalamus to forebrain in male chicks is reversed (Rogers & Sink, 1988), and the functional lateralization for attack and copulation behaviour is reversed (Rogers, 1990a). Chicks hatched from eggs incubated in darkness show no population laterality for attack and copulation, but appear to retain laterality at the individual level (Zappia & Rogers, 1983). Thus, lateralized light input before hatching aligns the direction of laterality in the population, but it does not actually generate the asymmetry. (Only 2 hours of light is sufficient to do this; Rogers, 1982.) Compare the effects of handling in rats in which the early experience unmasks or generates a laterality not present in non-handled animals (Sherman et al., 1980; see earlier).

The hormone testosterone can also influence the development of laterality in male chicks (Zappia & Rogers, 1987). Treatment with testosterone on day 2 causes a reversal in the laterality of eye differences in performance on the visual discrimination, pebble floor task. Contrary to expectations, treatment of females with testosterone does not generate lateralized differences between the eyes; that is, it does not “masculinize” their brains.

Diamond (1985) has reported asymmetries in the thickness of various regions of the cortex of the rat. In males on the whole the right cerebral cortex is larger than the left, and the reverse is generally true in females. Ovariectomising females leads them to have the male-type pattern. Yet hormones are not the only variables determining thickness of the cortex as it is also affected by age and experience in enriched and impoverished environments. These latter factors also influence the degree of asymmetry between the left and right sides. Consistent with this, Berrebi et al. (1988) have shown effects of sex, early experience and age on various regions of the corpus callosum.

There are sex differences in the lateralized bias in tail posture adopted by neonatal rats, the exact nature depending on the strain (see Denenberg, 1984a), and Rosen, Berrebi, Yutzey & Denenberg (1983) have shown that this can be influenced by administering androgens prenatally. Females responded to treatment with testosterone showing a reversal in the bias of their tail posture but the treatment did not make them the same as males. There was no effect of testosterone treatment on the males.

Geschwind and Behan (1982) have postulated that testosterone may have a role in the development of laterality in the human brain and so account for at least some of the differences in behaviour between the sexes. Theirs is a rather unitary hypothesis giving testosterone a major, or even sole, role in determining laterality in the human brain. As the studies using the chicken brain as a model demonstrate, testosterone and environmental experience (light input) can both influence laterality, and these must both interact with genetic factors (which are likely to determine the orientation of the embryo in the egg) to produce a final result in a given brain. No single factor can be separated out as the major or sole determinant in its own right.

Geschwind & Behan (1982) proposed that testosterone acts on the left hemisphere to retard its development, and thus high levels of testosterone in the foetus may cause an increased incidence of left-handedness and mental retardation, both occurring more frequently in males. High levels of testosterone also, apparently, alter the efficiency of the immune system and a number of other physiological processes. Hence, they suggested that exposure of the foetus to high levels of testosterone causes a constellation of effects. Geschwind and Galaburda (1987) have also argued that abnormally high levels of testosterone may cause "giftedness", and even that homosexuality results from effects of testosterone on brain lateralization and that is coupled with an immune system more susceptible to AIDS infection. This latter hypothesis is based on several assumptions and a rather convoluted path of reasoning. Firstly they believe, without convincing evidence of support, that male homosexuality depends on lower than normal levels of circulating free testosterone, and also that it results from stress during pregnancy. This stress is said to cause a transient increase in testosterone levels to be followed later by a rebound lowering of testosterone levels. The transient increase in testosterone, they hypothesise, causes increased "nonrighthandedness" in homosexuals and possibly an immunological condition more susceptible to autoimmune disease (pp. 175 of Geschwind and Galaburda, 1987).

There is no evidence from the human species to support these ideas, and the experimental data obtained from animals demonstrate clearly that such complex behaviours cannot be tied to a unitary cause of hormonal action.

CONCLUSIONS

The number of examples of both structural and functional laterality in nonhuman species is growing rapidly, and it is now clear that lateralization of brain structure and function developed very early in the course of evolution. Indeed, functional lateralization may have become an essential aspect of brain function not long after the brain became bilaterally duplicated in structure. It did not arise secondarily to shared tool use and handedness in humans, although these factors may subsequently have influenced the degree and nature of the laterality. Laterality in perceptual and cognitive processes appears to have been an antecedent to laterality of limb use in both birds and primates.

It is timely for psychologists concerned with understanding laterality in the human species to examine the data available in animals, not simply to find evidence for the evolutionary origins of laterality in humans, but also to discover the factors which influence the development of laterality. Experience has been shown to play an important role in the development of laterality in two species so far. The sex hormones also influence the development of asymmetry, but their role does not appear to be straightforward in the way postulated by some psychologists working with humans.

Laterality in the nervous system can occur in a number of different forms: structural and functional, at the population level and the individual level. Functional laterality may even change from 'moment-to-moment' as in the case of lateralized sleep in birds. A static view of laterality may have served a purpose while we were still in the phase of documenting the presence of asymmetries in different species, but laterality is a dynamic phenomenon varying with age, experience and the particular situation in which the animal finds itself. The studies using animals are providing a means to understand these dynamic processes in laterality.

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