COMPARATIVE VERTEBRATE LATERALIZATION

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The Nature of Lateralization in Tetrapods

RICHARD J. ANDREW AND LESLEY J. ROGERS

3.1. Introduction

The hypothesis that all vertebrate groups inherit a common basic pattern of lateralization from a common chordate ancestor was advanced in Chapter 2. Here we examine the evidence available from tetrapods to see how far this hypothesis can be sustained. We consider mainly tetrapods other than primates, as primates are examined in other chapters. Nevertheless, since so much more is known of human lateralization than that of any other vertebrate, a final test of each aspect of the hypothesis is how far it is consistent with evidence of lateralization in humans.

The evidence available so far supports our view that there is a common basic pattern of lateralization in all vertebrates. It is, of course, possible that there has been loss or reorganization of the basic pattern of lateralization in some species, but there is no certain example of this as yet. The absence of asymmetry in one or a few tests on a particular species is not strong evidence of its absence, as is clearly exemplified by the work of Hamilton and Vermeire (1983, 1988), who, after providing a large body of negative findings for the rhesus monkey, went on to produce an impressive body of evidence for brain lateralization in that species. Their findings are now corroborated by other studies (see Chapter 12 by Hopkins and Carriba).

In this context, and before beginning a comparative review of evidence for lateralization in tetrapods, some comment is needed on lateralization in rats and mice. The focus of much work on the choice of paw, and on the direction of rotational bias in free locomotion, has led to a common (but far from universal) belief that, in rats and mice, lateralization is clear only at the individual level, and is expressed chiefly or entirely in individual motor biases. In other words, since half of the individuals use the right paw or circle clockwise and the other half use the left paw or circle anticlockwise, there is no bias in the population (Glick and Cox, 1978; Collins, 1985). Collins (1985) even extended this view as applying to animals in general. It thus should be stressed that the same researchers who have supplied most of the evidence on which this position is based have also made it clear that, on other criteria, rodents are very consistently lateralized at the population level.

A few examples will suffice to demonstrate lateralization at the population level in rodents (for more examples, see Bradshaw and Rogers, 1993; Denenberg, 1981). The degree of consistency of these results in demonstrating a population bias is shown by the fact that significant population bias is commonly revealed with group sizes of 10–20 subjects. The examples are as follows:

1. Ablation of the right hemisphere (RHem) of rats elevates their activity levels in open field tests to a greater extent than does ablation of the left hemisphere (LHem) (Denenberg et al., 1978).
2. Greater activity in the left prefrontal region of the cortex is shown by uptake of 2-deoxyglucose (Ross and Glick, 1981) and this is accompanied by larger size of the left prefrontal region, both during periods of development and in adults, coupled with higher dopamine levels (van Eden, Uylings and van Pelt, 1984).
3. Cortical lesions in the RHem, especially anteriorly, lead to a drop in norepinephrine levels on both sides of the brain, and to a rise in open field activity, whilst corresponding LHem lesions have no such effects (Robinson, 1985).
4. Rats, trained to find a hidden escape platform in the Morris water maze and then tested monocularly are able to find the platform, using spatial information, when they use the left eye (RHem) but not when they use the right eye (LHem) (Cowell, Waters and Denenberg, 1997).

The significance of these findings is considered further below; they are mentioned at this point to show that rodents do not contradict the thesis that consistent lateralization at the population level is a general property of vertebrates.

The basic pattern of lateralization in tetrapods may be summarized as follows, and is dealt with more fully later.

1. *Attention, perceptual processing and control of motor response.* All of these aspects of lateralization are closely linked. An example of this can be seen, in a simple form, when an animal approaches a target, which it can see and for which it has a planned response (see also Chapter 2 by Andrew). Both fish and birds (discussed below) use the right eye (RE) to fixate a manipulandum as they approach in order to grasp it with the mouth or

bill. Such use of the RE implies use of the LHem, since the main projection of visual input from each eye is to its contralateral hemisphere (discussed further in Chapter 6 by Deng and Rogers). The use of the RE can be shown to be associated with maintenance of the readiness to manipulate: attention is clearly locked onto the target during such approach. In an approach under identical conditions, but with no target of response visible until the food dish is reached, the left eye (LE) is used.

A complementary set of specializations is shown when the RHem and the LE are in use. Here there is much better use of topographical cues to identify position in space, an ability that requires the animal to use diffuse attention. Spatial context and the detailed properties of objects are attended to, and recorded, more fully than when the RE is in use. This facilitates the detection of novelty and establishment of identity.

The resemblance to human dichotomies of hemispheric function is obvious. The RHem shows diffuse or global attention, spatial analysis and no special involvement in control of response. The LHem shows focused attention, recording of local cues and control of response.

2. *Emotion and inhibition of response.* The best example of a simple behavioural situation, which calls for inhibition of response, is examination of a strange and strongly motivating object from a distance. When examining a potentially dangerous object, escape must be inhibited whilst the object is assessed. In fact, the need for such inhibition is not confined to situations where escape is likely. When a naive chick is deciding whether to approach an attractive object or sound, on which it might imprint, and which it now encounters for the first time (i.e. an attractive but unknown stimulus), approach has to be inhibited while a decision to approach or not is made. At such times the RE or right ear is turned towards the stimulus, indicating LHem control (Miklósi, Andrew and Dharmaretnam, 1996; McKenzie, Andrew and Jones, 1998).

Conversely, there is extensive evidence (discussed below) that responses such as escape, attack and sexual behaviour are evoked more vigorously when the RHem is controlling. This is clearly what would be expected when LHem inhibition is absent. Although direct evidence is lacking, it would be advantageous for the topographical abilities of the RHem to be freely available during the uninhibited performance of such responses. It is necessary for obstacles to be avoided during escape or pursuit, and the position of refuges needs to be used to guide locomotion, despite the dominance of brainstem motivational mechanisms. It is interesting in this context that in goldfish, sudden escape, which is mediated by Mauthner cells, has directional bias determined by visual (and no doubt other perceptual) information about the layout of the environment (Eaton and Emberley, 1991). In toads, the position of escape routes is updated at each bodily movement and guides startle-induced escape leaps (Ingle and Hoff, 1990). As we will discuss later, toads display lateralization of escape leaping and are more responsive to a simulated predator seen on their left side (Lippolis et al., 2001).

Here we note the existence of comparable evidence (discussed later) in humans for association of intense emotion with RHem control, and inhibited emotion with LHem control. In fact, there is also clear evidence for two species of primate (rhesus monkey and common marmoset) that the RHem is used for the expression of intense emotion: this is manifested as greater movement of the mouth and other facial features on the left side of the face (controlled by the RHem) in expressing fear (Hauser, 1993; Hook-Costigan and Rogers, 1998; discussed also in Chapter 13 by Weiss et al.).

3.2. Left Hemisphere: Attention, Perceptual Processing and Control of Motor Response

The use of the RE to control placement of, and manipulation by, the mouth has been recorded in fish, amphibia and birds. In the zebrafish, the RE is used to fixate a target that the fish intends to bite, but not when biting does not follow, even if the target is identical (Miklósi and Andrew, 1999). Toads (*Bufo bufo* and *Bufo viridis)* are more likely to strike at prey items when these are seen in the right visual hemifield (Vallortigara et al., 1998; see Figure 3.1). The same study showed that toads (*Bufo marinus*) were more likely to deliver aggressive tongue-strikes at conspecifics in their left visual hemifield (discussed in more detail below). Here again control using the RE is specific to taking a target into the mouth, whilst an 'emotional' response of similar form, but not involving seizing a target, is not.

Use of the RE to control approach to grasp a manipulandum has been demonstrated in the domestic chick. The study used three different manipulations, all requiring the displacement of a light paper lid to allow access to food in a dish (Andrew, Tommasi and Ford, 2000). In one test the chick displaced the (square) lid by grasping either its left or right protruding corner; in another the bill had to be inserted into a notch placed at the front of the lid, which was circular like the dish and difficult to grasp in any other way; in the last test, a short string protruding vertically up from the centre of the lid had to be pulled. In all cases, irrespective of whether the manipulandum was medially placed or not, RE fixation was used during approach with striking consistency. In the same apparatus, but in the absence of the lid, the LE was used with equal consistency during approach to the food dish.

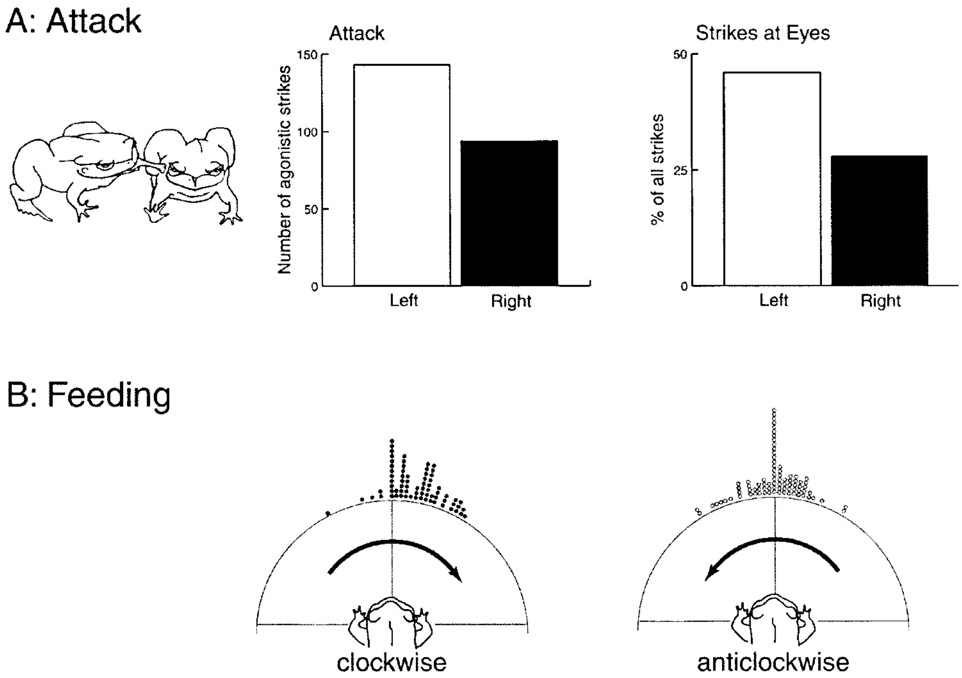

Figure 3.1. Summary of the complementary specialization of the left and right visual hemifields of toads for attack and feeding responses. (A) Attack: *Bufo marinus* toads were tested in a group and were competing for prey (crickets). Significantly more of their agonistic strikes at each other were directed to the left (open bar) than to the right (black bar) visual hemifield. In addition, striking at the eye of a conspecific was avoided to a greater extent in the right hemifield than in the left hemifield. (B) Feeding: strikes at at prey were also lateralized but here the preference was to strike at prey on the right side. *Bufo viridis* toads were tested by placing them, one at a time, inside a glass cylinder and then rotating a prey (insect larva) around the toad and outside the cylinder. Strikes at the prey were recorded by videotaping. Each dot represents a strike. Note that when the prey was rotated clockwise (from the toad's left to right) strikes (black dots) were directed to it when it was in the right visual hemifield. When the prey was rotated anticlockwise, the strikes (open circles) were distributed more evenly around the midline but there was still a tendency for more strikes in the right hemifield. Lateralization is shown by the fact that the pattern of strikes is not simply reversed for the clockwise versus anticlockwise presentations. Data from Robins et al. (1998) and Vallortigara et al. (1998).

It should be noted that RE use is also shown when a target food item can be seen. During free search over an arena floor, chicks showed a preference to take food grains that had been located with the RE, although both eyes were used freely in searching (Andrew, Tommasi and Ford, 2000). The key factor determining eye use in the chick is thus visual guidance of the bill to the target that is to be grasped. When no target can be seen during approach to the dish, the LE is used, despite the fact that feeding is certainly the reason for approach, just as in the lid condition.

Hunt (2000) has provided evidence that the tropical crow *Corvus moneduloides* cuts its tools (hooked strips of Pandanus leaves used to obtain food) from the left edge of these large leaves. Hunt shows that the method of working along the edge away from the trunk means that such removal will normally require the bird to turn its head to view its work with the RE, and argues that this reflects 'specialization of the right-eye system for object-related tasks'. This fascinating finding is clearly consistent with the RE control of manipulation described above for the chick.

Control of response by the RE is likely to explain special involvement of the LHem in learning based on the association of the consequences of response with the stimulus to which the response was directed. At its simplest, in animals with independent eye movements, it will sometimes be only the RE that sees what is to be recorded. The recording of selected cues associated with the (successful) outcome of response is suggested by the more rapid acquisition by right-eyed chicks than by left-eyed chicks of a discrimination between familiar food grains and unfamiliar inedible distractors (Zappia and Rogers, 1987). The chicks tested monocularly had to search for grains of chick-mash scattered on a floor to which small pebbles had been adhered. The distractors (pebbles) roughly matched the food grains in size and hue, so that it was necessary to select appropriate cues to make a successful discrimination. The experiments showed that young chicks could inhibit pecking at pebbles and choose grain, provided that they used the RE in monocular tests, and provided that the LHem was fully functional; treatment of the LHem with cycloheximide or glutamate impaired the chick's ability to choose grain over pebbles, but treatment of the RHem had no such effect (Rogers and Anson, 1979; Howard, Rogers and Boura, 1980). Recent experiments using localized placement of glutamate injections in various regions of the hemispheres have shown that it is only the visual Wulst region of the LHem that controls the shift from pecking randomly at grains and pebbles to pecking predominantly at grain (Deng and Rogers, 1997; see also Chapter 6 by Deng and Rogers).

The use of shift strategies to choose potential feeding sites occurs when the LHem, but not the RHem, is controlling (see Chapter 15 by Andrew); again this result suggests LHem involvement in recording the outcome of response (here the consumption of food at the previous visit). Vallortigara and Regolin (Chapter 11) present evidence showing that the chick can shift the food type chosen following a devaluation procedure (with training and devaluation carried out with both eyes in use); such shifts take place only when the RE is in use during testing (Cozzutti and Vallortigara, 2001).

Very much the same pattern of lateralization is shown by marsh tits during recovery of hoarded food items, when the birds are tested with one or other eye covered (Clayton and Krebs, 1994). When the RE (LHem) is in use, retrieval just after hoarding makes use of the local cues that were associated with the hole into which the tit had previously inserted the food item. When the LE (RHem) is in use, spatial position relative to the test room is used instead. Recording local cues suggests once again that the LHem is more likely to record consequences of the response (successful hoarding) that is associated with the perception of these cues.

Any consideration of mammalian evidence must start with the consensus that the human LHem typically controls purposive movements (see review in Kimura, 1982). This is strikingly true of multiple movements, whether of hand or mouth (Kimura, 1982). However, it also holds for the selection of one out of a number of (arbitrary) motor responses, when this learned response has to be the one appropriate to the presented stimulus (Rushworth et al., 1998). The resemblance of this result to the bird condition is close enough to suggest that, underlying the complications of LHem control of spoken sequences, and of skilled manipulation by the right hand in human beings, is the basic vertebrate pattern assigning the LHem to control a planned response to a perceived stimulus.

This specialization of the LHem may also underlie its apparent greater activation in the marmoset during the emission of close-range, social contact calls (twitters) that signal intent to approach a conspecific (or human). These calls are accompanied by more vigorous contraction of facial muscles on the right side, thereby opening the mouth wider on the right side (Hook-Costigan and Rogers, 1998). This contrasts with the role of the RHem in producing, and responding to, mobbing and fear calls that require more diffuse attention and unplanned outcomes. Such calls are accompanied by greater muscular contraction on the left side of the face (Hauser, 1993; Hook-Costigan and Rogers, 1998). It is argued in Chapter 10 by Andrew and Watkins that the lateralization of control of species-specific vocalizations, the discovery of which by Nottebohm (1970) was largely responsible for the return of interest in cerebral lateralization in vertebrates in general, can also be understood as originating from control of response to a stimulus (here, a conspecific call). The responses of importance include approach (or avoidance), as well as reply by calling.

The next question is how far can a comparable condition be shown to hold for mammals other than primates. The rodents provide an excellent test case because they have been separate from the primate line since the Cretaceous (Archibald, 1996); resemblances between them and primates would thus probably be derived from the common ancestor of Eutherian mammals. Such evidence has been provided by Bianki and his collaborators in studies using rats, which began in the 1960s, but which were initially little quoted, no doubt because they were published in Russian. The full corpus of work is summarized and discussed by Bianki (1988) in English.

The usual approach was to use spreading depression of the cortex achieved by the application of potassium chloride to inactivate one or other hemisphere. A striking variety of studies using this technique show the same shift in hemispheric control during the elaboration of conditioned reflexes. Early in acquisition, RHem inactivation disturbs the conditioned response (CR) more than LHem inactivation but, when the CR is fully elaborated, it is LHem inactivation that disturbs performance. In this second phase of elaboration, not only does LHem control allow more correct responses but also they are emitted significantly more quickly. The studies used both active avoidance and food reinforcement, and so effects of hemispheric involvement in behaviour like escape are unlikely to be responsible for the shift. Instead, the involvement of the rat LHem in performance of an established CR is better compared with the human use of the LHem to select the learned response appropriate to the stimulus presented (as discussed previously). The RHem dominance early in acquisition can be understood as appropriate to a phase when the rat is not quite clear what is the signal, nor when to respond. As a result, diffuse general attention and attempts to process all detected stimuli would be appropriate.

A second finding by Bianki is consistent with special LHem involvement in recording the consequences of response, such as appears to be present in birds (see above). When the probability of food reinforcement associated with different stimuli was varied, LHem control allowed emission of responses with likelihoods proportional to the frequency with which each stimulus had been rewarded, whereas RHem control was associated with equal probabilities for all stimuli.

LHem recording of the outcome of recent responses may also explain the finding that LHem control was necessary to allow efficient rapid visiting of all the arms in a radial maze, without returns to arms that had already been visited (Bianki, 1988). In other words, rats using their LHem adopted an efficient, sequential searching strategy in the radial-arm maze, whereas rats using the RHem were unable to do so. A comparable result for the effects of unilateral removal of right whiskers on performance in a radial maze is discussed in Chapter 10 by Andrew and Watkins.

Finally, a very marked asymmetry was found for timing of responses. When the time approached at which a CS was expected to occur, normal rats, and rats in which the LHem was controlling, showed a substantial rise in responses, whilst RHem rats distributed responses with little reference to time. Somewhat comparable results were obtained by Mittleman, Whishaw and Robbins (1988), who tested rats with intact hemispheres in a task using stimuli presented sequentially. The rats were trained to hold their snouts in a central hole of a test chamber after a light had been illuminated inside the hole. A cue light was then presented to the left or right side of the hole. This signalled the rat to move its head to the left or right and, in doing so, to intercept the beam of a photocell that would lead to the delivery of a reward. The response was more rapid when the rat moved to its right side than to its left side. In other words, the LHem was better able to respond quickly to the relevant stimulus than was the RHem.

Bianki (1988) argued that the abilities of the rat LHem for sequential analysis resemble the LHem advantage seen also in humans for the analysis of sequences in time. It may also be interpreted as due to LHem control of response, with the LHem again being especially concerned with recording the circumstances under which a successful response was performed, and then using the record to control future responses.

Bianki (1982) also suggested that the LHem of the rat analyses abstract characteristics of stimuli, compared to the RHem, which processes and records concrete or absolute characteristics. One of the examples, on which he based this conclusion, was the rat's ability to discriminate between the areas of unfamiliar geometrical shapes. The rat had to respond, in an operant task, to the key that displayed shapes with a larger total area. When using the LHem only (RHem inactivated), rats could perform this task well, but they were less able to perform the task when using the RHem only. Bianki (1983a) noted that the same separate specializations of the hemispheres as seen in the rat (summarized in Bradshaw and Rogers, 1993) are found also in humans, and this is, perhaps, best exemplified by the LHem's specialization for abstraction.

Such an ability to analyse the abstract characteristics of stimuli would allow the LHem to categorize stimuli and, indeed, this ability of the LHem is present in both the chick and the pigeon. Chicks using the LHem are able to categorize grain from pebbles (discussed earlier; see also Figure 3.2) and also to respond to 'chicks' as a category. The latter was demonstrated by Vallortigara and Andrew (1991) by testing chicks with a choice of a familiar cage-mate and a stranger (a chick that the test chick had not seen previously). When tested monocularly using the LE, the test chick approached its cage-

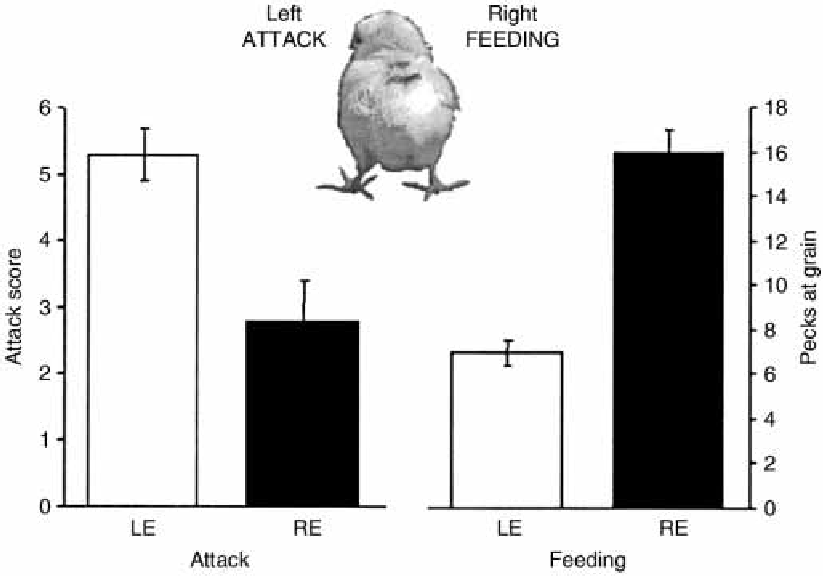

Figure 3.2. Complementary specialization of the left and right eyes of the chick for attack and feeding responses. The white bars represent means (with standard errors indicated) of groups of chicks (approximately 10 in a group) tested using the left eye (LE) and the black bars represent the same for chicks tested using the right eye (RE). Attack scores were obtained by testing testosterone-treated chicks using a standard hand-thrust test, in which the tester's hand is used to simulate an attacking chick. The responses of the chick are ranked according to intensity of attack. Attack is elevated when the chick uses its left eye, but not when it uses its right eye. Feeding scores were obtained by testing chicks on a search task of grain scattered on a background of small pebbles. The chicks could avoid pecking at pebbles when they were tested using their right eye but not when using their left eye. The scores plotted are number of pecks at grain in a block of 20 pecks, pecks 41–60 after the first peck given in the test. Adapted from Rogers, Zappia & Bullock (1985) and Rogers (1997).

mate in preference to the stranger but, when using its RE, the chick approached either, or both of the chicks. It seems, therefore, that the LHem attends to a chick as a category matched by all, or most, chicks, whereas the RHem records more specific and detailed information.

The ability of the pigeon's LHem to categorize stimuli was demonstrated clearly by von Fersen and Güntürkün (1990) by training pigeons in an operant situation to discriminate several abstract visual shapes from a large collection of similar shapes; the pigeon could do so only when using its RE.

We can conclude for these findings that rats, birds and humans all use the LHem for sequential analysis, and for abstracting characteristics of the stimuli to which planned responses will be directed. Comparable arguments are advanced in Chapter 10 by Andrew and Watkins for hearing. It is likely that the earliest use of hearing in tetrapods included the performance of appropriate responses to conspecific calls. In the most complicated use of vocalizations other than that by humans, namely that shown by passerine birds, it has been shown (Cynx, Williams and Nottebohm, 1992), for at least one songbird, that LHem use facilitates learning to associate reinforcement with familiar categories of (complex) conspecific sounds, whilst RHem use facilitates detection and response to small and unexpected changes of detail. The LHem specializations for control of response and associated erection of categories of stimuli, to each of which there is an appropriate response, may thus have affected the evolution of the lateralization of hearing as well as of vision (see also Chapter 10 by Andrew and Watkins).

3.3. Right Hemisphere: Diffuse Attention and Perceptual Processing

There is clear evidence for RHem advantage in the use of environmental layout to guide locomotion to a target site (i.e. to use spatial or topographical information). In the chick, Rashid and Andrew (1989) showed that, after binocular training, LE use allowed chicks to use both distant and local features to guide locomotion, whereas RE use led to almost complete failure to use distant features. Tommasi, Vallortigara and Zanforlin (1997) showed that, once chicks had learned to search in the centre of an arena, they went to the geometrical centre of distorted versions of the arena when using their LE. However, chicks used a much simpler rule when using the RE. They searched in a strip around the arena that was at about the distance from the wall that the centre of the training arena had been; in other words, they followed a rule that allowed them to find the centre in the unmodified arena (see Chapter 11 by Vallortigara and Regolin; also see Tommasi and Vallortigara, 2001). When a local landmark, which had identified the centre during training, was moved, LE birds used position in the arena whilst RE birds followed the local cue. As has already been noted, exactly the same pattern (position in space when the LE is used, local cues when the RE is used) is shown by marsh tits when retrieving a recently hoarded food item.

In the chick, RHem advantage is also shown in other tasks that involve spatial patterns but are not topographical. LE chicks respond to changes in the spatial context of a stimulus that are ignored in the RE condition. This is illustrated by the finding that chicks using the RE retain habituation of pecking at a coloured bead mounted on the end of a rod, even though the angle at which it is introduced to their home-cage is changed. In contrast, chicks using the LE respond to a change in the angle of introduction (spatial cue) by loss of habituation (Andrew, 1983, 1991). Further, LE chicks respond to moderate transformations in the appearance of model social partners (Vallortigara and Andrew, 1991) or partner chicks (Vallortigara and Andrew, 1994), which are ignored by RE chicks.

The same specialization of the RHem and LHem is shown by spontaneous patterns of eye use in chicks. Preferential use of one eye over the other can be measured by observing from overhead which lateral visual field is used by the chick to view the stimulus (i.e. by scoring head turning and visual fixation). Once chicks have attached to a model social partner, they use the LE when approaching it, whereas when deciding whether to approach at the first encounter they use the RE (McKenzie et al., 1998). Note that novelty detection or establishment of identity requires the use of detailed records of past appearance, which (it is here argued) is the responsibility of the RHem. The use of the LE when faced with a familiar stimulus or environment will usually confirm identity and so is the appropriate default condition; equally, unexpected novelty will be identified.

Once again, the human evidence is in agreement. Indeed, there appears to be no dissent from the proposition that the human RHem has advantage for spatial analysis, and that it shows global attention rather than focused (e.g. Posner and Petersen, 1990). Naturally enough, analysis has been pushed much further in work on humans; thus Kosslyn et al. (1992) have shown, using simple dot stimuli, that the RHem excels in judgements of position as measured by X-Y coordinates, whilst the LHem is as good or better at 'categorical' judgements, like above or below a reference position. They also show that the differences could be generated if field sizes of visual units were larger in visual analysis by the RHem.

Some evidence suggests that the RHem is specialized for processing spatial information in primates too. For example, capuchins (*Cebus apella*) show a stronger left-hand preference on haptic and haptic-visual tasks than they do on simple reaching tasks (Lacreuse and Fragaszy, 1999). As the researchers suggest, this may result because the right hemisphere is specialized to integrate the spatial processing and sensorimotor components of the actions demanded by the haptic tasks. Also, gorillas and baboons have been found to display left-hand preferences on spatial tasks, requiring them to align transparent doors in order to obtain food (Fagot and Vauclair, 1988a, 1988b). Other experiments have shown RHem advantage in primates for global processing, an ability that may be associated with spatial processing by that hemisphere: Deruelle and Fagot (1997) tested baboons (*Papio papio*) in an operant task in which they had to respond to a letter of the alphabet made up of smaller letters, which could be the same as, or different from, the larger letter. Attention to the larger letter was interpreted as 'global precedence' and this was associated with use of the RHem. Attention to the smaller letters indicated local attention and was associated with use of the LHem. Also, chimpanzees have a RHem advantage for locating a short line contained within a geometric figure, which suggests specialization of the RHem for spatial processing (Hopkins and Morris, 1989).

Once again, the rodent evidence is crucial in deciding whether mammalian lateralization resembles that of other vertebrates. Adelstein and Crowne (1991) found right, but not left, parietal lesions to impair the use of allocentric cues, during navigation in a water maze. King and Corwin (1992) present similar findings and, as mentioned previously, rats are able to rely on spatial memory to find the escape platform in a Morris swim maze when they use the LE (RHem), but not when they use the RE (Cowell et al., 1997). Bianki (1988) presents evidence from a number of tests that show marked resemblance between the RHem advantage for spatial analysis, present in both rats and humans. There is RHem advantage for discriminations based on texture and on dot location. In discriminations based on arrays of three stimuli, RHem performance is better when matching has to be on arrangement in space (ordered in a linear array), whilst LHem performance is better when it is necessary to ignore spatial order and match on stimulus properties. This latter finding is true, both when the training stimuli are presented in a different order, and when only one of them is presented. LHem analysis thus is of separate stimuli, and does not stress arrangement or even the presence of the full set. RHem analysis includes the spatial arrangement of the full array, as well as the properties of individual stimuli.

Similar differences between the hemispheres probably underlie the results obtained in tasks testing generalization to transformations of the training stimuli (Bianki, 1988). In tests requiring the rat to choose between the original and a transformed stimulus, RHem analysis produces matching on absolute size, whereas LHem analysis tends to use the relative difference present in training (e.g. take the larger). However, this property of LHem analysis does not mean that absolute size cannot be used by the LHem. When only one stimulus is presented, so that the decision is whether to respond or not to a transformed stimulus, it is the LHem which tends to withhold responses after large changes in size (especially reduction) but no change in shape. As we have already mentioned, it is likely that categorization by the LHem determines the outcome, setting limits to the tolerable degree of transformation of the key stimulus dimensions. The RHem apparently continues to assess the transformed stimulus as being to some degree similar to the positive pattern.

Finally, when the positive pattern has a complex outline, and changes involve progressive stylization (i.e. loss of detail in the outline), it is the LHem that accepts greater change of the original, training stimulus (Bianki, 1983b). Here, it seems, the presence of some change in almost all features results in an estimate of very large change by the RHem, whereas the LHem relies on assessment of selected properties, in particular overall match in general outline. Again, this may depend on the ability of the LHem to attend to features defining a category, and so to accept major changes in the stimulus configuration.

This impressive body of work goes beyond establishing resemblance between rodent and human: it begins to extend our understanding of the general principles of vertebrate lateralization. In the rat, free from the complications introduced by LHem verbal abilities, it is possible to see more clearly that the LHem functions by categorizing objects using selected stimulus dimensions, such as size and general outline. The RHem tends to analyse in terms of all the properties of an object.

Recent studies in the chick (C. Jones, pers. comm.) have shown that when generalization along a single dimension (degree of rotation of a bar, in relation to the vertical) is studied, use of the LHem results in clear boundary values at which choice is concentrated, which shift progressively with experience, but remain sharp. It is likely that these are the current values by which the LHem defines a category. By contrast, use of the RHem results in choice, showing generalization that gradually decreases as the degree of transformation is increased.

3.4. Lateralized Control of Emotional Behaviour

3.4.1. Intense Emotion and RHem

Once again the chick makes a convenient starting point for this discussion. The use of the LE (and so of the RHem) of the chick facilitates attack, copulation and fear responses.

Following treatment of the young chick with testosterone, levels of attack and copulation are elevated, provided that the chick is tested either binocularly or monocularly using its LE. No effect of the testosterone treatment is evident when the same chicks are tested using the RE only (Rogers, Zappia and Bullock, 1985; Figure 3.2). Normal levels of these responses in chicks treated with testosterone are depressed by RE use. Thus, the LHem suppresses the attack and copulation response. Tests of agonistic behaviour in adult, untreated hens indicated the same role of the LHem in suppressing attack (Rogers, 1991).

RHem facilitation of fear behaviour is shown by the fact that lesioning of the right archistriatum reduces distress calling in an unfamiliar environment far more than corresponding left lesions (Phillips and Youngren, 1986). The archistriatum contains the homologue of the amygdala, the involvement of which in both fear and fear conditioning is well established for mammals (Maren, 1999). Adamec and Morgan (1994) have shown that kindling (i.e. chronic activation) of the right amygdala facilitates fear in the rat in a way which LHem kindling does not.

In humans, RHem control has been variously associated with intense emotions, or negative emotions or withdrawal (Davidson, 1995). Thus Dimond, Farrington and Johnson (1976) showed that the use of the left visual field to view film material resulted in a much more negative assessment than did right visual field viewing. Frontal and anterior regions of the RHem are selectively activated in withdrawn emotional states involving fear and disgust and, consistent with this, PET scans have revealed elevated activation of the RHem, during resting in panic-prone subjects (Davidson, 1995). Also, schizotypy with social and emotional withdrawal is associated with RHem dominance, seen in terms of scoring better memory of faces than words and poverty of speech (Gruzelier and Doig, 1996). Damage to the frontal region of the LHem, presumably forcing the equivalent region of the RHem to take control, leads to decreased interaction with other people and difficulty in initiating voluntary action (Davidson, 1995). Moreover, patients with injury to the left hemisphere resulting from stroke are significantly more depressed than those with equivalent injury to the right hemisphere (Robinson and Price, 1982; Robinson et al., 1984). RHem involvement in human emotion would, therefore, seem to be associated with negative and intense states, as well as with social withdrawal.

In contrast, the LHem has been assigned the opposite associations (i.e. positive emotions: Ahern and Schwartz, 1979, 1985; Davidson, 1992, 1995). Schizotypy with positive mood valence and eccentricity is associated with better memory of words than faces, indicating LHem dominance (Gruzelier and Doig, 1996). The inhibition of emotions by the LHem is sometimes suggested (e.g. Nestor and Safer, 1990). Clearly, this last position has much in common with the general vertebrate condition for which we argue here: that the LHem tends to inhibit responses like escape, attack and sexual behaviour. In fact, there is some evidence indicating that in humans the LHem also inhibits aggressive behaviour: subjects with epileptic seizures focused in the left temporal lobe (and so impaired LHem function) have higher than average levels of hostile feelings (Devinsky et al., 1994). Also, reduced activity in posterior regions of the LHem has been associated with suicidal and aggressive behaviour (Graae et al., 1996).

It is recognized in the human literature that there is an unresolved issue here: are all intense emotions, or only negative ones, associated with RHem control? The chick evidence suggests one way of resolving the issue: does RHem control go with facilitation of sexual behaviour in humans, as it does in the chick? Sexual behaviour is unlikely to be classified as involving 'negative' emotion in humans. There is extensive evidence that this is so in humans (review: Tucker and Frederick, 1989). Disturbed and exaggerated sexual behaviour is associated with RHem-related mania. RHem stroke is more likely to depress sexual function than LHem stroke. Sexual arousal is accompanied by central or posterior greater electroencephalogram (EEG) desynchronization in the RHem than in the LHem. Flor-Henry (1980) cites other evidence (e.g. RHem involvement in rapid eye movement sleep, and the typical accompaniment of such sleep by penile erection).

Evidence from other tetrapods is also consistent with RHem involvement in all intense (i.e uninhibited) emotional behaviour, rather than solely in negative emotional behaviour. For example, in *Bufo marinus* toads, aggressive tongue-strikes at conspecifics are more likely to occur when the conspecific is seen in the left visual hemifield than when it is seen with the right visual hemifield, indicating less inhibition, or activation, of aggressive responses by the RHem (Robins et al., 1998; Figure 3.1). In addition, those attack strikes that do occur to conspecifics on the toad's right side are aimed to avoid the recipient's eye (see Figure 3.1; more strikes at the eye occur to the left compared to the right). This bias may result from the LHem's ability to inhibit strikes directed at eyes on the right side, whereas the RHem is not able to do this.

In lizards, attack is again more likely when the conspecific is seen with the LE (Deckel, 1995). Since reptiles have much the same organization of the visual projections from the eyes to the brain as do birds, use of the LE means use of the RHem. Thus, in *Anolis,* aggression is initiated preferentially by the LE/RHem, but this aggression can be inhibited by the LHem in conditions that are mildly disturbing, and so call for such inhibition (Deckel, 1998).

The LE/RHem control of attack responses in the domestic fowl (both soon after hatching and in adulthood), which has already been described, is also revealed by differences between responses to conspecifics seen in the left or right monocular visual fields. Recently, Vallortigara et al. (2001) have shown that, when a young chick is temporarily paired with another that it has not seen before, in most cases the chick views the stranger using its left lateral field before pecking.

The preferential involvement of the right hemisphere in aggressive responses appears to have been conserved in a broad range of species, including primates. Gelada baboons (*Theropithecus gelada*) direct more agonistic responses to conspecifics on their left side than on the right (Casperd and Dunbar, 1996). In line with this finding, at least in terms of the presence of lateralization if not its direction, Drews (1996) found that carcasses of wild baboons (*Papio cynocephalus*) are marked by more injuries on the right side of the head region than on the left side. This finding is reminiscent of Jarman's (1972) earlier report of more scars on the right side of the pelts of impalas than on the left. Of course, lateralized occurrence of scars may depend on lateralized responding of the attacker or the one attacked but, comparing the results from these widely divergent species, the finding is suggestive of lateralization of aggressive responses.

The greater role of the RHem in initiating fear responses to novel stimuli has also been demonstrated in toads. Lippolis et al. (2001) tested fear responses of three species of toad (*Bufo bufo*, *Bufo viridis* and *Bufo marinus*) by introducing a simulated predator (a snake model) into the left or right lateral field. The toads were more reactive when the stimulus entered the left field than when it entered the right.

In rats, Robinson (1979, 1985) has shown that RHem lesions (infarcts, cortical undercuts and direct depression of noradrenergic activity) elevate activity in the open field, whereas corresponding LHem lesions have no effect. A rise in locomotion in the open field is likely to represent reduced immobility (freezing); a more general disinhibition is suggested by the fact that running wheel activity is also elevated. Robinson and Downhill (1995) compare these effects of RHem infarcts in rats, with effects of RHem insult in humans, such as general anxiety, without depression and secondary mania.

Finally, the association of RHem control with behaviour such as fear, aggression and sexual behaviour is paralleled by the fact that the RHem sympathetic outflow is the more effective, whereas parasympathetic outflow is under LHem control (Wittling, 1997). In humans (Hugdahl, 1995), whereas LHem controls the parasympathetic (vagal) outflow to the sinoatrial node (the heart 'pacemaker'), there is greater effectiveness of the sympathetic outflow from the RHem to the heart (via the stellate ganglia). In fact, the latter has been described for dogs, cats and humans (Lane and Jennings, 1995; Wittling, 1995). The stress hormone system (i.e. the hypothalamic–pituitary–adrenocortical axis) is, it appears, also under greater control by the RHem than the LHem (Wittling, 1997). Clearly, it is functionally appropriate for feed-forward preparations for exertion to accompany disinhibition of intense response.

It will be obvious that this preponderant involvement of the RHem in descending sympathetic outflow is paralleled by its own greater input of noradrenergic fibres. This is provided by neurones in the *locus coeruleus,* which in the rat are activated by startling and painful stimuli, but by little else (Aston-Jones et al., 1986). The RHem thus is affected more than the LHem by startling stimuli, as well as by the cognitive detection of novelty.

3.4.2. Inhibition of Emotional Behaviour by the LHem

It is argued here that LHem mechanisms provide inhibitory influences on behaviour such as fear and attack, and that the LHem is used when there is a need to assess the situation before taking a decision. Inhibition by the LHem of particular responses should be distinguished from states of general inhibition associated with fear and depression. Depression in humans, and immobility in fear (freezing) in the rat, are both actively organized (and probably comparable) conditions. It is known, in the rat, that they have direct dependence on a specific midbrain system, the ventrolateral periaqueductal gray (Bandler and Shipley, 1994). The inhibition of intense emotion can thus result in the removal of inhibition (e.g. of locomotion) at a lower level, as has already been noted for the effects of RHem lesions on locomotion in the rat.

However, such complications in the interpretation of findings obtained from studies of rats were avoided by a study of Adamec and Morgan (1994), in which unilateral kindling of the amygdala resulted in appropriate shifts in the amount of locomotion in open and covered parts of an elevated maze. Anxiety is known to increase the relative time spent under cover: RHem activation had this effect (suggesting that such activation increased fear), whereas LHem activation produced the opposite shift from control levels, indicating reduced fear.

Further evidence of inhibition of intense response by the LHem in the rat is provided by mouse killing, which is substantially elevated by LHem lesions, but not RHem lesions (Denenberg, 1984). Note that the tested rats were not experienced killers, and so they were faced with a stimulus that both presented strong releasers for the behaviour and was sufficiently unusual as to call for careful assessment with concomitant inhibition of response.

Asymmetries of facial expression provide further relevant evidence. Hauser (1993) reports more vigorous development of facial expressions on the left side of the face in rhesus monkeys, as mentioned earlier (see also Chapter 13 by Weiss et al.). All three of the expressions that showed significant asymmetry were related to fear or threat. It is possible that the left side of the face shows greater intensity of expression only when emotion is intense. Hook-Costigan and Rogers (1998) found that in marmosets there was greater intensity on the left for two fear expressions but on the right for a social contact call (the twitter). This appears to be the first demonstration in a primate other than humans of greater LHem control of production of a vocalization. Since the call is an affiliative social signal, it is likely that the marmoset at the same time inhibits the expression of intense emotion (e.g. withdrawal) in order to make social contact. Control by the LHem is, therefore, entirely consistent with our previous argument for its role in inhibition of intense emotions.

The human evidence is, at least partially, inconsistent with this general pattern. Borod, Koff and Caron (1983) found greater intensity on the left side of the face for expressions that include greeting and clowning, as well as horror, grief and disgust. However, the evidence of association of affiliative behaviour with LHem control is explicable by the hypothesis that is advanced here. Much of the difficulty of comparing human and animal evidence arises from the existence in humans of states of amusement. The discussion may conveniently begin with Gainotti (1972, 1989), who summarized evidence that the diagnosis of LHem insult often evoked (appropriately enough) a 'depressive catastrophic' reaction in the patient: in other words the response was great disturbance and depression. A comparable diagnosis involving RHem lesion tended to be accompanied by 'denial of illness' and joking (Gainotti, 1979). The interpretation of these findings depends on whether it can be safely assumed that the dominant effect of the brain damage was to increase control by the intact hemisphere. This is made almost certain by evidence (see below) from normal subjects, using behavioural or brain activation measures.

The association between LHem control and behaviour accompanied by laughter (humour, social interaction) is strengthened by the fact that pathological activation of the LHem, either by epileptic seizures or by RHem damage, is likely to be accompanied by uncontrolled laughter, whereas corresponding RHem activation is more likely to be accompanied by crying (Sackeim et al., 1982). Evidence from normal subjects is in good agreement: Ahern and Schwartz (1979) found that positive emotional content to questions brought about LHem involvement (as shown by rightward eye movements), whereas negative content involved the RHem. A specific connection of LHem functioning with laughter was revealed by Ahern and Schwartz (1985): when subjects thought about laughing there was LHem EEG activation frontally, whereas thought about fear produced such activation in the RHem.

A remarkable finding is that by repeatedly performing movements of the right or left side of the mouth, or the right or left hand, emotional state can be affected (Schiff and Lamon, 1989, 1994). Left side movement produces sadness (and even weeping), whereas right side produces emotion described as 'sarcastic, cocky, good, smug'.

Finally, there are studies in which stimuli are assessed according to their pleasantness. Painful or near-painful stimuli are judged more unpleasant when applied to structures of the left side (Schiff and Gagliese, 1994); this is true for both chronic (shoulder pain) and acute (hand in ice water) conditions. Ehrlichman (1986) found that odours presented to the right nostril (RHem input) are rated as more unpleasant than when they are presented to the left. This may also be the case in chicks: a chick will shake its head in a disgust response when it detects a noxious odour with its right nostril (left nostril occluded) but not when they use the left nostril (Rogers, Andrew and Burne, 1998). It should be noted here that the neural inputs from the olfactory epithelium of each nostril project to their ipsilateral hemisphere and do not cross over the midline to the contralateral hemisphere, as in the case of other sensory inputs. Thus, use of the right nostril reflects processing of olfactory information in the right RHem.

The subjective sensations described by humans during LHem control are beyond examination in animals. However, a humorous, joking or sarcastic approach allows humans to examine and evaluate stimuli and situations, which under other circumstances they would find too disturbing for rational treatment. Two components of 'humorous' states should be distinguished. Firstly, there is reduced likelihood of terminating examination whilst the state lasts. Secondly, the experience is not remembered as one to be avoided in the future; indeed, it may be subsequently sought after rather than avoided. Both are made likely in humans by positive affect; neither is likely in the absence of the special conditions of amusement.

The first component (i.e. reduced likelihood of terminating examination) is clearly present when animals persistently examine frightening and potentially dangerous objects (when RE and LHem are usually involved). The second (i.e. remembering the experience as being positive) may well also hold, since such viewing is likely to be adaptive; if it were accompanied by negative reinforcement, the animal would presumably learn not to do it again.

Association of laughter with emotional states, arising when a potentially disturbing experience is assessed as amusing or unimportant, is no doubt one mechanism for minimizing social disruption in humans by means of the effect