

# EFFECT OF BRAIN ASYMMETRY ON LEARNING AND FEEDING IN CHICKENS

LESLEY J. ROGERS

## SUMMARY

This paper suggests that asymmetry of brain function may have important implications for display patterns and social organisation in chickens. The functions known to be asymmetrically organised in the chicken brain are discussed together with the techniques which have been used to reveal these asymmetries. Hemispheric and eye-eye asymmetries have been demonstrated. The latter are manifest in behaviour of the whole animal, such that attack and copulation responses are more likely to be elicited by stimuli in the left visual field, and the right eye is better in performing visual discrimination learning to feed. Suggestions are made for management relating to the use of polypeepers and position of feeders in the cage. The effects of domestication, incubation conditions and hormonal treatment on asymmetry are discussed.

## I. INTRODUCTION

The left and right hemispheres of the chicken brain have been shown to have different functions in the control of many behaviours. Such asymmetry of brain function has now been reported for a number of species (Harnard et al. 1977; Denenberg 1981), but in avian species it has special relevance to the behaviour of the whole animal. The reason for this is that the optic nerve fibres decussate completely in birds, and birds have no major interhemispheric connecting system such as the corpus callosum of mammals. Thus information received by one eye is processed largely by contralateral side of the brain (Rogers 1985). In other words, information processing by the left-eye-system, LES, differs from that of the right-eye-system, RES, and therefore the left and right eyes look at different worlds and direct different behavioural sequences. That is, in birds, asymmetry of brain function becomes manifest at the perceptual level and, for the visual system at least, it becomes an asymmetrical template imposed upon the space surrounding the animal. As a consequence of this, asymmetry of brain function may have become manifest in social behaviour, and so play a role in the management of commercial chicken flocks.

## II. ASYMMETRY IN THE CHICKEN BRAIN

Asymmetry of function in the chicken brain (australorp x leghorn) was first demonstrated by unilateral administration of cycloheximide (CXM), an inhibitor of ribosomal protein synthesis, into either the right or left forebrain hemisphere on day 2 of post-hatching life (Rogers and Anson 1979). Treatment of both hemispheres or of the left hemisphere alone was found to retard learning of a visual discrimination task, in which the chicken has to search for grains of food mash scattered on a background of small pebbles (Rogers et al. 1974). Treatment of the right hemisphere with CXM was found to have no effect on this learning performance; these birds learnt as well as saline-treated controls. The learning deficit which follows treatment of the left hemisphere can be detected long after the CXM has ceased to inhibit protein synthesis. Learning performance is usually measured in the second

week of life, but the deficits have been found to persist up to 20 weeks at least (Rogers et al. 1974). The CXM treatment in early life must disrupt brain development such that subsequent information processing is impaired. This disruption is now known to occur, not directly by CXM's inhibition of protein synthesis, but indirectly by its effect in causing the temporary accumulation of the amino acids glutamate and aspartate in brain amino acid pools (Hambley and Rogers 1979). These amino acids, which are neuronal excitotoxins, cause the same effects as CXM when they are administered alone to the left hemisphere (Rogers and Hambley 1982).

As retardation of visual discrimination learning occurs after treatment of the left hemisphere irrespective of whether the right hemisphere has been treated or not, the simplest hypothesis to explain these results is that the pathways involved in learning to discriminate grain from pebbles are located in the left hemisphere.

This asymmetry can also be demonstrated by testing untreated chicks monocularly on the same task. If untreated male chickens in their second week of life are tested monocularly on the visual discrimination task, those with occlusion of the left eye, and therefore using their right eye and left hemisphere (RES), learn significantly more slowly than those with occlusion of the right eye, and therefore using their left eye and right hemisphere (LES) (Andrew et al. 1982; Rogers 1985). This asymmetry is consistent with that revealed by intracranial administration of drugs. However, while it is present in monocularly tested males, females chickens tested similarly in the second week of life show no eye-eye asymmetry for this task (Rogers 1985; Andrew and Brennan 1984). Given that females do show the asymmetry revealed by unilateral drug treatment of the hemispheres, this suggests sex differences in the organisation of visual pathways from eye to brain in the chicken.

Rogers and Anson (1979) found that, irrespective of whether they learnt to discriminate grain from pebbles in the task, chicks tested using the RES in general pecked more rapidly than those tested using the LES. Consequently, they proposed that the right-eye-left-hemisphere system may drive pecking to feed. In a different task which examined pecking rates at a novel, bead stimulus, Andrew et al. (1982) found that pecking performance of the RES was the same as that of birds tested using their binocular field, but that of the LES was different. This led them to deduce that right-eye mechanisms dominate control of pecking in the binocular field. The RES has also been found to dominate for recall of memory of an operant, visual discrimination task for food reward (Gaston and Gaston 1984). All three of these paradigms implicate the right-eye-left hemisphere system as dominant for control of pecking and feeding behaviour.

Chickens treated with CXM or glutamate in both hemispheres, or the left hemisphere only, also show slowed auditory habituation learning and attentional persistence (Anson and Rogers, 1979; Howard et al. 1980; Rogers, 1985). Treatment of the right hemisphere has no effect on these behaviours. An attentionally persistent animal switches attention from one stimulus type to another less frequently (Andrew and Rogers 1972; Rogers 1985). Attentional persistence has been studied on visual tasks for choice of food grains. Chicks treated with drug in the left hemisphere or both hemispheres switch search from red to yellow coloured food grains less frequently. Since attentional persistence is manifest in the visual system (it may be present in other modalities as well), it is likely to be present as an eye-eye asymmetry with implications for feeding and social behaviour. It should be noted that attentional persistence is distinct from retarded learning, since the two

behaviours can be clearly separated (Rogers and Anson 1978). It is not yet possible to say whether the asymmetries in auditory habituation are likely to be manifest as asymmetries in behaviour of the whole animal, because less is known about the organisation of the auditory pathways from receptor to brain.

The forebrain also plays an asymmetrical role in the control of attack and copulation behaviour in the chicken. Treatment of the left hemisphere of male or female **chicks** with CXM **or** glutamate leads to elevation of attack and copulation scores, just as if the chicken had received treatment with an androgenic steroid (Howard et al., 1980). No such elevation of these behaviours occurs after treatment of both hemispheres or of just the right. Given that treatment of both hemispheres has no effect in this case and elevated scores only occur after treatment of the left, the left hemisphere must know the state of the right, and vice versa. In this respect asymmetry for attack and copulation differs from visual discrimination learning as revealed by treatment on day 2 of life. Asymmetry for control of attack and copulation is present, but it requires interhemispheric coupling.

The asymmetrical control of copulation is also evident as asymmetry between the eyes. If birds treated with testosterone are made monocular from **day 5**, before copulation testing **commences**, those using their LES show elevated scores equivalent to the levels reached by binocularly tested birds, but those using their RES do not (Rogers et al. 1985). This occurs in both male and female chicks, although different steroid doses are needed to reveal the effect in each sex (Bullock 1985). These data suggest that the right hemisphere activates copulation while the left hemisphere suppresses it (Attack could not be accurately investigated in monocular tests since monocular chicks show variable attack scores depending on whether the chicken has caught sight of the stimulus or not. However, the asymmetry for attack was similar to that obtained for copulation.)

Comprehensive accounts of the asymmetry present in the chicken brain have been given in two reviews (Rogers 1980; Rogers 1985). To summarise briefly, the right eye-left hemisphere system contains the pathways necessary for visual discrimination learning, it dominates control of pecking in the binocular field, is involved with switching attention from one stimulus type to another, and it suppresses the performance of attack and copulation. All of the functions of the RES taken together, indicate that it may have a dominant role in feeding behaviour, involving choice of food type and search for food. The left eye-right hemisphere system activates attack and copulation, and, as Andrew and Brennan (1983) have shown, it is also the system which has increased responsiveness to novelty and fear. Andrew (1982) has therefore suggested that the right hemisphere is active during the intense performance of species-specific responses, and he suggests a parallel to the right hemisphere's involvement in emotional responses in humans.

### III. CONSEQUENCES OF ASYMMETRY ON BEHAVIOUR OF THE CHICKEN

As a consequence of the asymmetrical organisation of the brain and the completely decussating eye-to-brain visual pathways, the position of a stimulus in the visual space surrounding a bird would be expected to influence not only the likelihood of **response** to that stimulus but also the nature of the response. Stimuli received in the left visual field may be more likely to elicit attack or copulation responses. Of course, the bird may well overcome any such initial bias on responding by always turning its head to use both fields of vision, at least to use **the** small area of binocular overlap, before it responds. If so, this should be **evident** in the head movements made before

responding. No measurements of these have yet been made, It remains quite possible that in situations requiring rapid **responses**, possibly attack **pecks**, there is a left-side bias for increased likelihood of a response being elicited.

When chickens must discriminate fine differences between grains or seeds and the background they usually use their binocular, frontal field of vision. Although the RES dominates the **biocular** field for pecking to feed, a side-bias in discriminating grain and pecking would only be evident when peripheral vision is used, such as when grains pecked at bounce either left or right. Performance of this kind should be best in the right visual field.

Certainly, when a chicken is feeding and discriminating grain or seed in the frontal field, it would be much more likely to be distracted by stimuli, possibly predators or other birds, moving into the left peripheral field of vision, rather than the right. The response to novelty in the left visual field is greatest; thus feeding is more likely to be disrupted by a response of fear, attack or even copulation.

Recognition of these side-biases may be important for care of commercially raised chickens, If, for **example**, the food trough is placed so that new animals approaching it are likely to approach a **feeding** animal from the latter's left **side**, more disruption of feeding, and possibly increased aggression, may occur.

The order of a group standing at the feeding dish may have a considerable amount to do with these side-biases. Movement of feeders which disrupts such orders **may** increase aggression and disrupt the peck-order. All of these predictions are directly testable.

In the case of copulation, the directing of circling of the cock during courtship waltzing may determine whether mounting will occur or not (a greater chance of mounting if circling is in the anticlockwise direction). Alternatively, the cock may choose to waltz in one direction or the other depending on its motivational **state**, whether it intends to copulate or not. Either way, the visual field asymmetry would be incorporated into the courtship display (Rogers 1985).

Polypeepers are used to reduce aggression in large flocks of intensively reared chickens. They would seem to achieve this by occlusion of the binocular field of vision. **However**, it may be necessary to occlude only the left eye in order to reduce aggression, This is provided, of course, that occlusion of the left binocular field **only** will suffice, a factor which needs to be tested since the experiments to date have used monocular occlusion of the complete visual field on one or the other side. The occlusion of the left **eye** should also occur early enough. In the experiments demonstrating LES-RES asymmetry for attack and copulation **the** monocular occlusion was made by placing the eye patches over the **eyes** before testing commenced and these patches remained in place throughout the next 10 days or so of testing. With this paradigm, chicks using the LES showed elevated scores but those using their RES remained low (at control levels) throughout the entire testing period. In another experiment the chicks were tested binocularly for attack and copulation until the second week of life. The eye-patches were then applied, at which time the LES **performance** dropped to base-line levels while the RES remained high, as predicted (Zappia & Rogers, 1985). However, this asymmetry was only temporary; subsequently\*, the RES scores increased to those of the LES. For this reason, it would seem necessary to put the

monocular-polypeeper on the chicken before attack and copulation performance levels increase under the influence of testosterone's action. In the experiments reported here juvenile attack and copulatory behaviours were stimulated in early life by testosterone treatment. In the normal course of development these hormonal and behavioural changes do not occur until puberty. This would be the age at which to apply the monocular **occluder**.

Application of a monocular polypeeper to the left eye would not only be expected to be sufficient to reduce aggression, but it would **leave an** unobstructed RES available for discrimination of grain for feeding. The polypeepers which occlude the binocular field of both eyes must either **cause** deficits in visual discrimination of food grains, since unobstructed visual discrimination learning primarily uses the binocular field, or it must require behavioural adjustments to overcome the loss of visual field. The monocular, **occluder** of the left eye may obviate any need for such adjustments.

#### IV. ASYMMETRY AND DOMESTICATION

Preliminary evidence suggests that asymmetry of brain function is present in the feral strain collected from North West Island, and now breeding at the University of New England. Asymmetry of brain function in the chicken has therefore not simply been selected for by domestication.

##### (a) Methods

Eggs of the feral chickens were incubated in dark, force draft incubators until day 19 of incubation, at which time they were placed into a lighted incubator until hatching. After hatching they were held in groups of 4 for the first 3 days of life. Half of the animals were injected with glutamate (5 L 100 mM) into the left hemisphere and 5 L of 0.9% pyrogen-free saline into the right hemisphere. The other half received glutamate in the right hemisphere and saline in the left.

**On day 3**, each chicken was placed in an individual cage (9 cm square by 12 cm high) which isolated it visually, but not auditorally, from the other chickens. Testing for attack and copulation commenced on day 7 of life and continued daily until day 15. These behaviours were scored using standard hand-thrust tests (Zappia and Rogers 1983).

For attack testing the hand is thrust with arched fingers at the level of the **chicken's** beak. Responses range from avert gaze to active sparring and attack leaping, and the score is made according to a ranking order from 0 to 10. For copulation testing the flattened hand is thrust at the level of the **chicken's** chest and then held stationary. Responses range from no mounting of the hand (zero score) to mounting the hand with crouching, treading and pelvic thrusting (maximum score of 10). Each of these tests were repeated three times daily and a mean score taken.

##### (b) Results

After being isolated, 70% of feral chicks treated with glutamate in the left hemisphere failed to eat enough to maintain a normal rate of body growth rate, and possibly also to drink enough. Many of these animals died before testing commenced on day 7. By comparison only 30% of the chicks treated with glutamate in the right hemisphere showed the same effects. It should be noted that no such lack of ability to maintain body weight is evident in the australorp x leghorn strain.

In this preliminary experiment **only 6** feral chicks (male and female) remained in each group to be tested for attack and copulation. Unlike the previous findings for australorp x leghorn chickens, there was no difference in attack performance between the groups of feral chicks treated in the left or right hemispheres. Both groups scored very high levels of attack, a result which we have also found in untreated feral chickens. However, the group treated with glutamate in the left hemisphere showed elevated copulation scores while that treated in the right did not (e.g.  $P = 0.002$  for a 1-tailed U-test comparison of the scores on day 15).

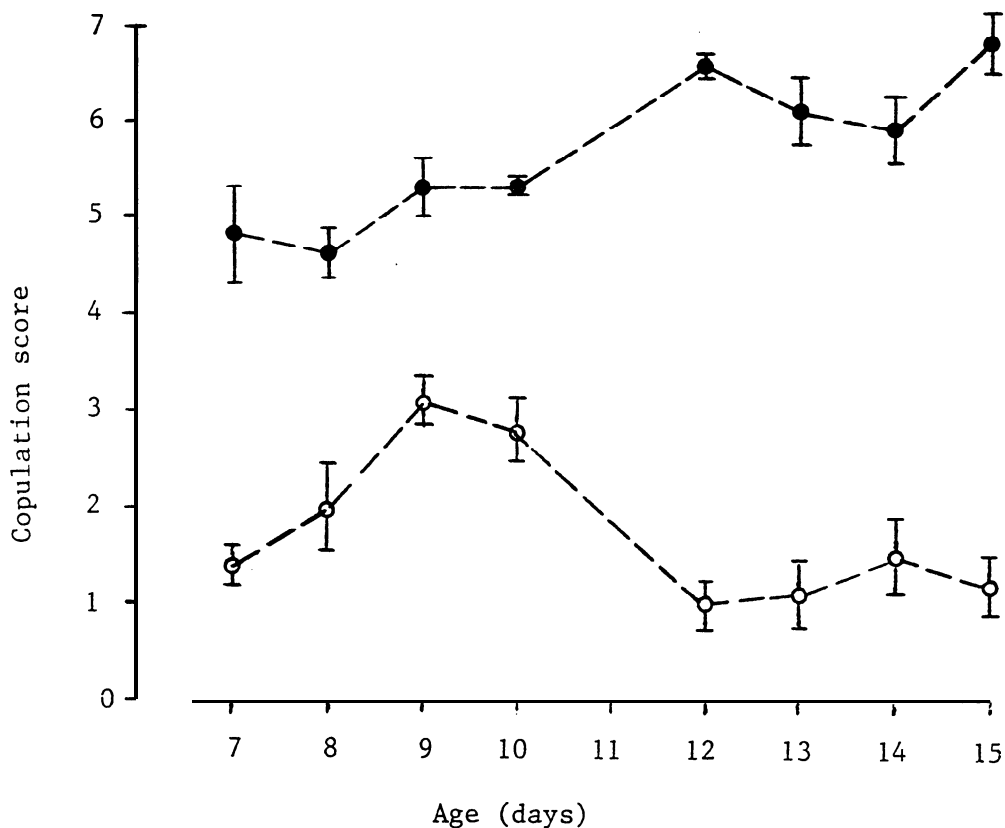


Figure 1: Copulation performance plotted as a mean daily score together with standard error, from days 7 to 15 of post-hatch life (n = 6 per group).  $\bullet$  represents the groups treated with glutamate in the left hemisphere on day 2, and  $\circ$  the group treated with glutamate in the right hemisphere.

### (c) Discussion

The same asymmetry for control of copulation found previously in the australorp x leghorn strain is present in the feral strain. (Note that the intracranial injection technique reveals asymmetry in both males and females of the commercial strain, and we also found no sex difference in the feral strain when using this technique). As attack scores were so high in all the feral chickens no 'asymmetry for this behaviour could be revealed using a pharmacological method which unmasks attack behaviour. Perhaps asymmetry for control of attack can be demonstrated by monocular testing, but, as mentioned earlier, this too has problems for attack scoring.

The high number of feral chicks which failed to feed adequately after glutamate treatment of the left hemisphere is interesting given previous suggestion from experiments with commercial strains that it is the left

hemisphere which directs pecking to feed. The effect in ferals is more dramatic. It is also the left hemisphere which processes learning to visually discriminate food grains, and these data for feral chicks may suggest that disruption of its development by glutamate can become life threatening.

Further experiments need to be conducted using the feral strain, but it can already be seen that asymmetry of brain function is present in this strain.

## V. FACTORS AFFECTING ASYMMETRY

While domestication has apparently **not selected** for the presence of brain asymmetry in the chicken, incubation conditions can have significant effects on it. **Rogers and Anson (1979)** suggested that the asymmetry of brain function in chickens may, at **least** in part, be generated by unequal growth of the left and right hemispheres, which occurs as a result of unequal light input into the left and **right** eyes **before** hatching.

In the last days of incubation, **when** the visual pathways from eye to brain are making functional connections, the chick: embryo is oriented in the egg such that the body and **wing occlude** the left eye, leaving the right eye exposed to light **entering** through the egg shell and membranes. The greater amount of light received by the right **eye**, they argued, may stimulated growth of the **left** hemisphere. in advance of the right and so lay the basis for asymmetry. This **hypothesis** gained support from experiments in which eggs were incubated in **darkness** during the last 3 days of **incubation** (**Rogers 1982; Zappia and Rogers 1983**). **The chicks** hatched from these eggs were still asymmetrical in brain function, but half the population had the orientation in one direction and half in the other so that no over-all population asymmetry or bias was present. Further studies showed that as little as 2 to 3 hours of light exposure on day 19 of incubation is sufficient to orient the direction of brain asymmetry so that all individuals are asymmetrical in the same direction and a **population bias is present**.

Testosterone, 5 **-dihydrotestosterone** and oestrogen treatment can also alter the direction of brain asymmetry in chickens (**Zappia and Rogers 1985; Bullock 1985**). These hormones reverse the direction of LES-RES asymmetry for visual discrimination learning, and shift hemispheric dominance for control of copulation.

Brain asymmetry **in** the chicken can therefore be affected by factors under farm management control; **viz., light** exposure during incubation and hormonal exposure during post-hatching development. Various procedures used in raising chickens **commercially** may be inadvertently manipulating asymmetry either to advantage or disadvantage for productivity or for welfare of the chickens. I believe that we need to understand these factors. Whether the chicks are hatched from **eggs** incubated under light or darkness may have important effects on behaviour in flocks, since one might expect the behavioural organisation of a flock of birds with a consistent bias in the direction of individual brain asymmetries to differ from a flock in which there is no bias in the direction of individual brain asymmetries. Whether these differences would be manifest in, say, different levels of aggression, which is feasible, can now be determined.

Of course, the monocular polypeeper suggested here could only be successfully applied, if at **all**, to **chicks** with a flock bias in the direction of asymmetry.

## REFERENCES

- ANDREW, R.J. (1982). In \*Advances in Vertebrate Neuroethology\*, eds J-P. Ewert and D. Ingle. (Plenum: New York)
- ANDREW, R.J. and BRENNAN, A. (1983). Anim. Behav. 31: 1166.
- ANDREW, R.J. and ROGERS, L.J. (1972). Nature, 237: 343.
- ANDREW, R.J., MENCH, J. and RAINEY, C. (1982). In 'Analysis of Visual Behaviour'. p. 197. eds D.J. Ingle, M.A. Goodale and R.J.W. Mansfield, (MIT Press: Mass.).
- BULLOCK, S.P. (1985). Ph.D. Thesis, in preparation, Monash University.
- DENENBERG, V.H. (1981). Behav. Brain. Sci., 4: 1.
- GASTON, K.E. and GASTON, M.G. (1984). Brain Res. 303: 190.
- HAMBLEY, J.W. and ROGERS, L.J. (1979). Neurosci. 4: 677,
- HARNARD, S.R., DOTY, D.W., GOLDSTEIN, L., JAYNES, J. and RRAUTHAMER, G., eds (1977). 'Lateralisation in the Nervous System', (Academic Press: New York).
- HOWARD, K.J., ROGERS, L.J. and BOURA, A.L.A. (1980). Brain Res. 188: 369.
- ROGERS, L.J. (1980). Bird Behav. 2: 1.
- ROGERS, L.J. (1982). Nature (London). 297: 223.
- ROGERS, L.J. (1985). Advances in Study of Behav. 16: 187.
- ROGERS, L.J. and ANSON, J.M. (1978). Pharm. Biochem. Behav. 9: 735.
- ROGERS, L.J. and ANSON, J.M. (1979). Pharm. Biochem. Behav. 10: 679.
- ROGERS, L.J. and HAMBLEY, J.W. (1982). Behav. Brain Res., 4: 1.
- ROGERS, L.J., DRENNEN, H.D. and MARK, R.F. (1974). Brain Res., 79: 213.
- ROGERS, L.J., ZAPPIA, J.V. and BULLOCK, S.P. (1985). Experientia. in press,
- ZAPPIA, J.V. and ROGERS, L.J. (1983). Dev. Brain Res. 11: 93.
- ZAPPIA, J.V. and ROGERS, L.J. (1985). Submitted to Behav. Brain Res.