

Lateralisation of Function in the Chicken Fore-Brain

L. J. ROGERS¹ AND J. M. ANSON

Department of Behavioural Biology, Research School of Biological Sciences
Australian National University, Canberra, A.C.T., Australia

(Received 22 January 1979)

ROGERS, L. J. AND J. M. ANSON. *Lateralisation of function in the chicken fore-brain*. PHARMAC. BIOCHEM. BEHAV. 10(5)679-686, 1979.—There is lateralisation of function in the chicken fore-brain. This was revealed by examining the behavioural modifications produced by administration of cycloheximide into the left or right hemisphere on Day 2 of post-hatched life. Visual discrimination learning of a task requiring a search for food was found to be performed either entirely or, at least, to a greater extent by the left hemisphere. Visual habituation learning was not found to be lateralised. The left hemisphere is more involved in auditory habituation than is the right; administration of cycloheximide to the left hemisphere slowed auditory habituation, as did bilateral administration, but treatment of the right hemisphere was ineffective. There are indications that the right hemisphere plays a more important role in response to novelty. A side-preference for response to stimuli seen by the left eye was demonstrated. These results are discussed with reference to head orientation during development in the egg.

Hemispheric lateralisation	Chickens	Visual learning	Auditory habituation	Detection
Response to novelty	Cycloheximide			

HEMISPHERIC specialisation was thought to be a purely human attribute, associated with language [6,12]. But now there is clear evidence that it is also present in the avian brain. In canaries the left hemisphere has dominant control of song production [16]. This functional lateralisation has been demonstrated at the hyperstriatal level of the fore-brain, and it is also evident more peripherally in the hypoglossal nerves [15]. Indeed, Nottebohm has found left hypoglossal dominance in a number of species of song birds [13,14].

Glick *et al.* [8] have shown that there is asymmetry in the nigrostriatal region of the rat cortex both with respect to dopamine levels and side-preference in turning. Although studies of non-human primates have not yet clearly revealed hemispheric specialisation, it seems that it may have developed quite early in evolution. Lateralisation of function may occur more commonly than previously thought, and in a given species it may be present for a number of different behavioural functions. We therefore decided to investigate the possibility that functional lateralisation also occurred in the chicken fore-brain.

Cycloheximide, an inhibitor of ribosomal protein synthesis, was used as a tool in this study. Previous research has shown that bilateral injection of 20 μ g of cycloheximide into each side of the chicken fore-brain in the first week after hatching produces long-lasting changes in a range of behaviours [20], provided that the chicken receives specific types of perceptual input for at least 3 hours after the drug's administration [21]. Learning rate of a task requiring visual

discrimination of food grain from a background of small pebbles is markedly slowed, as is visual habituation and auditory habituation learning [20]. Visual detection of small, novel stimuli entering the peripheral field of vision is slightly enhanced, and attention switching from one stimulus type to another becomes less frequent [19].

Recent studies indicate that cycloheximide causes these behavioural effects by altering amino acid pools, rather than directly by inhibiting protein synthesis. The putative amino acid transmitters, aspartate, glutamate, GABA and taurine, can mimic the action of cycloheximide; and measured changes in amino acid pools after cycloheximide treatment have indicated that cycloheximide produces permanent changes in behaviour, not directly by blocking protein synthesis, but indirectly by altering amino acid pools [9]. Cycloheximide's effect must be a subtle one, at least at the structural level, since no anatomical lesions have yet been detected with either light or electron microscopy [20].

We therefore considered administering cycloheximide into one or other of the fore-brain hemispheres during early development and looking to see which of these behaviours were subsequently affected.

In visual learning tasks chickens can be tested monocularly, and, since the avian brain has complete decussation of the optic nerve fibres, visual input through one eye is restricted to the contralateral tectum [2]. The feed-forward pathway from each tectum goes to its ipsilateral nucleus rotundus [11] and the main efferent pathway from each rotundus nucleus travels to the same side of the fore-brain

¹Present address: Department of Pharmacology, Monash University, Clayton, Victoria, Australia.

[10,18]. Although there are minor pathways from nucleus rotundus to its contralateral fore-brain, and visual information could also cross from one side of the brain to the other in the commissures [26,28], experimental evidence suggests that most visual information entering one eye is processed by the contralateral side of the fore-brain. Bell and Gibbs [1] have shown that chicks trained monocularly to avoid pecking an anthranilate-coated bead form unilateral engrams in the contralateral hemisphere. The ipsilateral hemisphere has access to this stored information, but the memory trace is contralateral. Zeier [29] explained his results with pigeons trained by giving conflicting information to each eye in the same way; that is, by contralateral hemispheric processing of monocular information. The avian brain therefore offers certain advantages in a study of lateralisation of brain function.

METHOD

Housing Conditions

Black australorp-white leghorn cross chickens were hatched in the laboratory and housed in groups of four for the first two days of life. After this time they were isolated visually by placing in separate cages. Chick starter crumbs were always scattered over the cage floor. Constant warmth and light was provided by overhead bulbs (for further details see [20]).

Drug Administration

Drug treatment occurred on Day 2 of life, several hours before the chickens were visually isolated. In the major experiment 48 animals were divided into 3 groups. One group received an intracranial injection of 20 μg of cycloheximide dissolved in 25 μl of boiled 0.9% saline at 35–38°C into the left side of the fore-brain and 25 μl of boiled 0.9% saline into the right side of the fore-brain. In the other group the injections were transposed (i.e., cycloheximide into the right side), and the remaining control group received 25 μl of boiled saline into both sides of the fore-brain. The injections were given free-hand with the animals conscious. A plastic stop on the needle prevented it from penetrating more than 3 mm below the surface of the head. The entry point of the needle was approximately 2 mm from the mid-line and equidistant from the rostral and caudal poles of the hemispheres. The order of injecting saline and cycloheximide into either side of the fore-brain was randomised. The chickens came from two separate hatchings, and equal representatives of each group were tested each time. These 48 chickens were tested on a number of behavioural tasks.

An additional 60 chicks were tested for monocular visual habituation only, and these were divided into 3 groups and injected similarly.

Behavioural Testing

Every chicken in the first three groups was tested on one behavioural test per day from Day 7 to Day 10 of life. On Day 7 they were all tested binocularly on a visual habituation task.

On Day 8 they were tested for visual detection.

On Day 9, each group was divided into two sub-groups each containing eight animals to make a total of six sub-groups. These were tested monocularly on a visual discrimination task of search for food. The eyelids of the left eyes of chickens in three sub-groups (one group treated with cycloheximide in

the left hemisphere of the fore-brain, one treated in the right hemisphere, and the other a control treated with saline only) were sealed together with COAPT (Ethicon, Germany) tissue adhesive 1½ hours before testing. The other three sub-groups, with similar drug treatments had the eyelids on their right eyes sealed. This method of occluding the eye caused remarkably little disturbance in the chickens.

On Day 10 they were all tested for auditory habituation.

An additional 3 treatment groups with 20 chicks each were similarly halved to give 6 sub-groups and tested monocularly for visual habituation on Day 10.

It is only necessary to give a brief description of the behavioural tasks here, because they have all been reported previously in detail; visual habituation, visual discrimination and auditory habituation [21,23], visual detection [22]. Behavioural testing was always done between noon and 3 p.m.

Visual Habituation

A novel visual stimulus, a torch battery, is placed into the home cage four times at approximately 5 min intervals. The time of silent visual fixation of the stimulus is scored each time. A control chicken shows significant waning of this orientation response by the fourth presentation.

Visual Detection

This task measures detection of a small red bead introduced from behind into the peripheral visual field of a feeding chicken. While the chicken is feeding from a small dish fixed in one position in the cage the bead is advanced slowly and silently forward, until it is noticed by the chicken, at which time feeding stops and the chick looks up, usually with a trill, and turns towards the bead. At this time the position of the bead is read from a scale, giving an estimation of the anteroposterior distance from the chick's eye. Beads were presented three times each to the right eye, to the left eye and simultaneously to both eyes. The order of presentation was left-right-together, repeated three times. When beads were presented simultaneously on both sides, the side to which the chicken turned was also scored. Seven hours food deprivation preceded the test.

Visual Discrimination

This task requires search for chick starter crumbs scattered randomly on a background of small pebbles stuck down to a perspex floor. The pebbles overlap with the starter crumbs in their range of colours, shapes, and sizes. The pebbles are, however, more shiny than the grain, and, presumably for this reason, control animals commence pecking with a slight preference for pebbles. But since pebbles cannot be manipulated or swallowed, control animals soon learn to peck almost exclusively at grain. Learning is apparent within 60 pecks. Pecking choices are scored by eye using a manual keyboard attached to an event-recorder. Only new choices are scored and not repeated pecks to the same grain or pebble. Since chickens were tested monocularly on this task and this tends to slow pecking slightly, the usual 3 hour period of food deprivation given prior to testing was extended to 4½ hours. The time taken for the 60 pecks, starting from the first peck, was also measured.

Auditory Habituation

Chickens are deprived of food for 3 hours, and then allowed one minute pecking at food before habituation to an

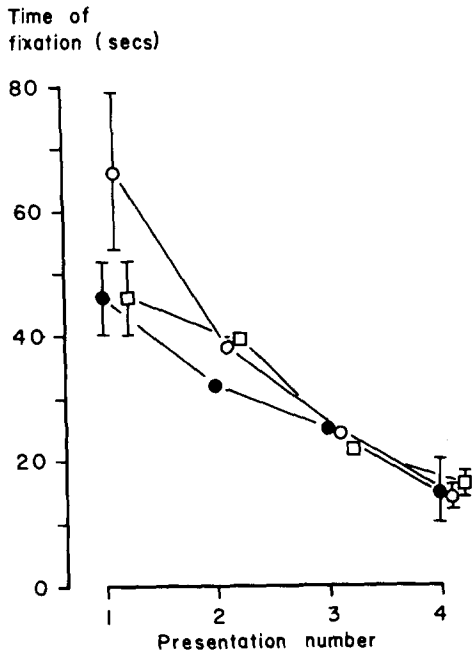


FIG. 1. Visual habituation tested binocularly. The seconds spent fixating the novel visual stimulus on each of four successive presentations is plotted. Mean values are given \pm standard errors for the first and last presentations. ● controls treated with saline in both hemispheres, □ treated with saline in the left hemisphere and cycloheximide in the right, ○ treated with cycloheximide in the left hemisphere and saline in the right. The larger standard error in the first presentation of the group treated with cycloheximide in the left hemisphere results from skewed data with 50% of the chicks scoring higher values than the other two groups; a standard error is not strictly valid for this data, but it is used as a means of visual expression.

auditory stimulus is scored by noting whether the chick stops feeding to attend to a sound made by striking a piece of metal with a metal spoon. The sound is presented every 10 to 20 seconds, and only while the chicken is pecking, until no orientation is seen for three successive presentations. Rate of auditory habituation learning is indicated by the number of presentations necessary.

RESULTS

Visual Habituation

Binocular testing. In this test there were three groups each containing 16 animals, one group treated with cycloheximide in the left side of the fore-brain, another group treated with cycloheximide in the right side and the third a control group. All showed significant waning of the orientation response over the four presentations of the novel visual stimulus (Fig. 1). Since there was no significant difference between the groups in time of fixation on the fourth presentation, all three groups habituated at the same rate. Indeed, no significant differences between the groups were found for any one of the presentations. However, the group treated in the left side appeared to behave differently on the first presentation; the time of fixation was more variable and it tended to be longer. **Monocular testing.** A similar tendency for the time of fixation to be longer and more variable was seen for the first

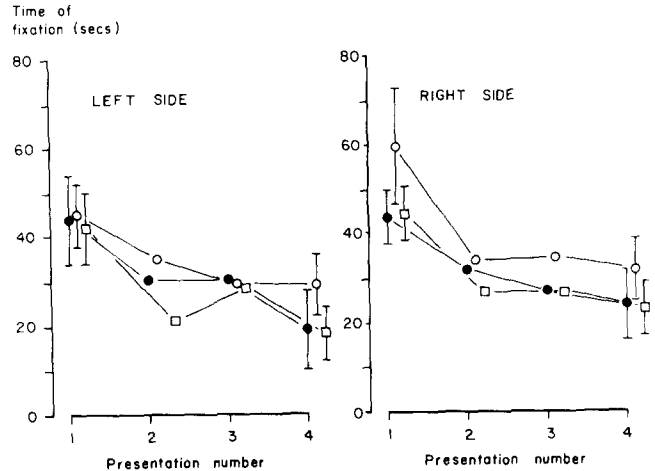


FIG. 2. Visual habituation tested monocularly. The symbols and values are the same as those in Fig. 1. 'Left Side' refers to left eye occlusion. 'Right Side' refers to right eye occlusion.

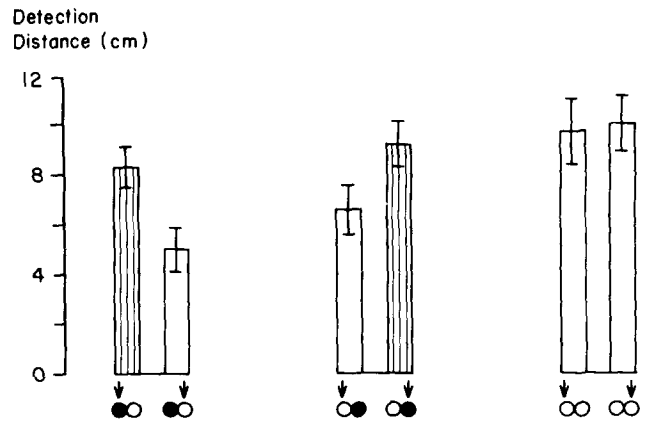


FIG. 3. Visual detection with one stimulus presented at a time. The mean distance (\pm standard error) of the object from the front of the cage, and the chick, is presented for each eye. The circles indicate the treatment given to each side of the fore-brain; a black circle indicates the side treated with cycloheximide, and an open circle indicates the side treated with saline. An arrow to the left side represents use of the right eye or introduction of the novel object into the right peripheral field of vision. An arrow to the right side represents introduction of the object into the left peripheral field of vision. There are three presentations on each side to each animal, and a mean value of these is calculated for each animal. The means presented are overall group means. The differences between the left and right sides for both the cycloheximide treated groups are significant (see text).

presentation of the novel visual stimulus to the group treated in the left side of the brain and tested with the right eye occluded. Otherwise no differences were observed between any of the groups, regardless of side treated or the eye used in testing (Fig. 2). Monocular testing for visual habituation by this method was more difficult than binocular (as evidenced by the greater variability and duration of fixation times for the fourth presentation), because it was not always possible to ensure that the stimulus was in the visual field of the open eye throughout each presentation.

TABLE 1
VISUAL DETECTION WHEN STIMULI PRESENTED
SIMULTANEOUSLY TO BOTH EYES

Side Treated With Cycloheximide	Percentage Detections With Left Eye	Ratio of Number of Animals with all 3 Detections with Right Eye To Those With All 3 Detections With Left Eye	Preferred Eye
Left	40	6:1	Right
Right	60	0:3	Left
Control	60	1:2	Left

Visual Detection when the small novel stimuli are presented simultaneously to both eyes. The side to which the animal turns is recorded for 3 such presentations. The number of detections made with the left eye (i.e. responses of turning to the left side) are expressed as a percentage of the total for each group. The other column gives data for those animals with exclusive use of the left or right eye, expressed as a ratio. This data is taken as an indication of eye preference in this task.

Visual Detection

After cycloheximide treatment of either the left or right side of the fore-brain, an inequality in detection distance was found between each eye (Fig. 3). The eye contralateral to the side of the brain treated with saline required closer proximity of the novel object before it was detected; whereas the eye contralateral to the side treated with cycloheximide retained a detection distance which was the same as that for controls treated with saline in both sides. Within each treated group the difference in detection distance between eyes was significant at the level of $0.01 < p < 0.02$ for the group injected in the left side and $0.02 < p < 0.05$ for the group injected in the right side (2-tailed Wilcoxon Matched Pairs tests). There were no differences between eyes in the groups treated with saline in both the left and right sides.

In control animals and in those treated with cycloheximide in the right side there was a slight preference to use the left eye to detect novel stimuli, as indicated by the side to which the animals turned when stimuli were presented simultaneously to both eyes. In those treated in the left side this preference was reversed. This is shown by the percentage of detections with the left eye, and the ratio of the number of chickens which make all three of their detections with the right eye to the number which make all three to the left eye (see Table 1).

Visual Discrimination

A group of chickens is said to have learnt to discriminate grains of food from pebbles, if the mean number of pecks at pebbles (i.e., errors) in the last 20 pecks is in the region of 2 or 3. Since there are on average 3 grains and 8 pebbles per square inch of floor, random pecking would score about 14.5 errors in 20 pecks. Control performance on this task has been reported in detail previously.

The data for the mean number of errors in the last 20 pecks is presented in Fig. 4. When the left eye was occluded, learning occurred if the left side of the fore-brain was treated with saline regardless of whether the right side was treated with saline or cycloheximide. When the left eye was

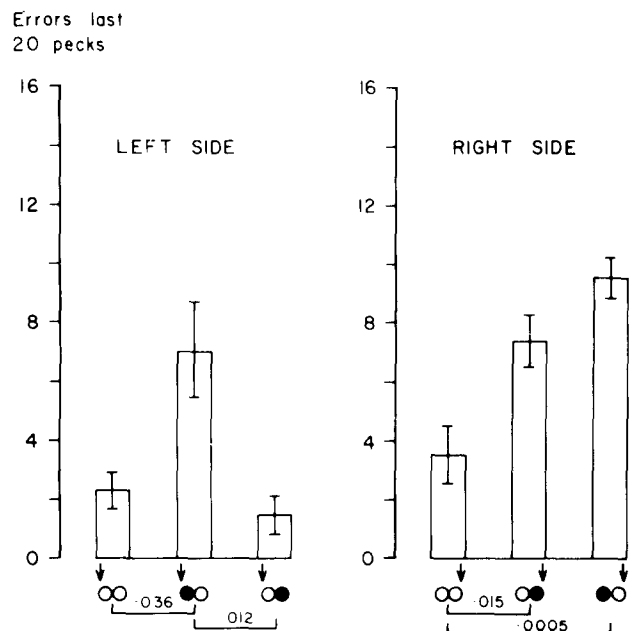


FIG. 4. Visual discrimination learning. Rate of learning is indicated by the number of errors in the last 20 pecks of testing. Slower learning gives higher values. Means and standard errors are plotted for each group. The circles underneath represent the treatment given each group, as in Fig. 3. 'Left side' means that the left eye was occluded, and 'Right side' means that the right eye was occluded. Mann-Whitney U tests have been applied between each group and every other group. Significant *p* values are given at the bottom of the figure.

occluded the the left side of the fore-brain had also been treated with cycloheximide, significantly less learning occurred. The probability values for Mann-Whitney U-tests of significance between these groups are given at the bottom of the figure.

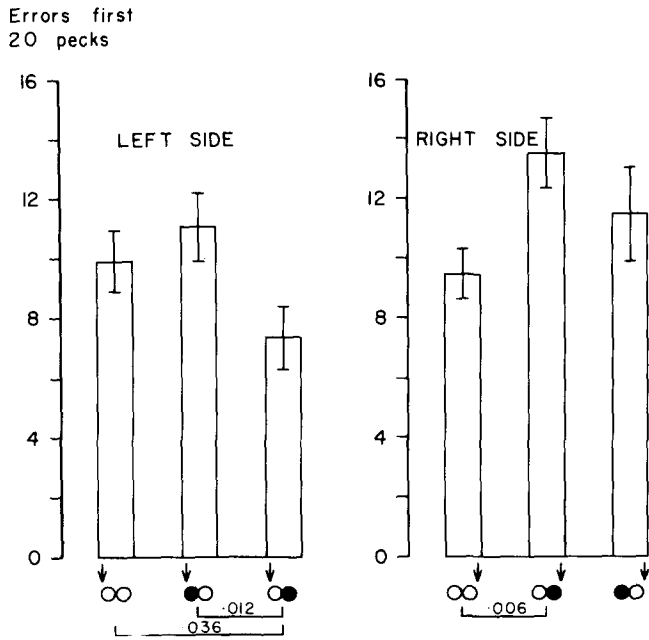


FIG. 5. Visual discrimination. The data is in the same form as that presented in Fig. 4, the only difference being that the values are for the first 20 pecks of testing.

When the right eye was occluded learning occurred if both sides of the brain had been treated with saline. But, when the right eye was occluded after cycloheximide treatment of either the right side or the left side of the fore-brain, learning was significantly slower or absent. There was a tendency for the group treated with cycloheximide in the left side and tested with the right eye occluded to make more errors than the group treated with cycloheximide in the right side and tested with the right eye occluded, but this was not significant. In addition, although only new choices of grain or pebbles were scored in this test, chickens in the group treated with the drug in the left side and tested with the right eye occluded were often observed to peck repeatedly in rapid bursts at the same pebble.

Figure 5 presents data for the number of pecks at pebbles in the first 20 pecks of the visual discrimination test. Given the ratio of grains to pebbles on the floor, a chicken pecking at random would score in the region of 14.5 errors in 20 pecks. When the right side had been treated with cycloheximide and left eye was occluded, the number of errors in the first 20 pecks was depressed below that expected for random choice. The number of errors in the first 20 pecks for this group was significantly lower than the same scores for both the other groups tested with the right eye occluded.

The group treated with cycloheximide in the right side and tested with the right eye occluded made significantly more errors in the first 20 pecks than did its control group, treated with saline on both sides and tested with the right eye occluded. For this reason another parameter must be assessed in order to determine whether any learning has occurred, even if the criterion of 2 or 3 errors was not reached in the last 20 pecks. That parameter is the fall in errors between the first and last 20 pecks, tested by a 2-tailed Wilcoxon Matched Pairs test. The fall was significant at the $p < 0.02$ level for all groups except two, the group treated

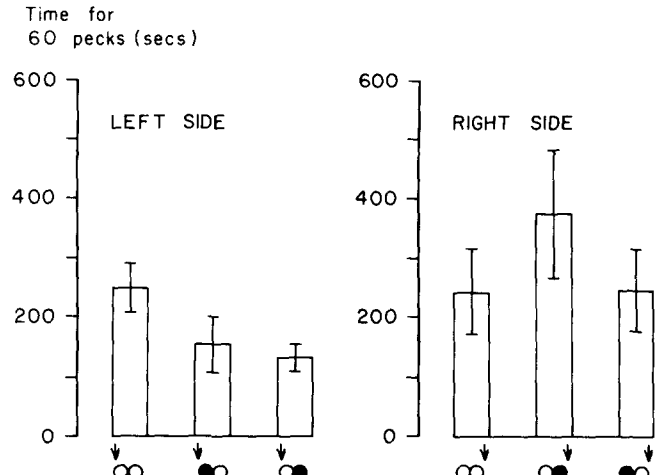


FIG. 6. Visual discrimination learning. The time taken from the first peck to the last peck of the test is plotted as means \pm standard errors for each group. The symbols are as in Fig. 4.

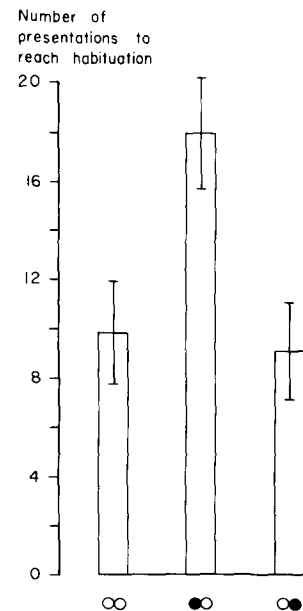


FIG. 7. Auditory habituation. The mean number of presentations of the auditory stimulus necessary for the chick to habituate (\pm standard error) is plotted for each group. The symbols underneath represent the treatment given each group, as in Fig. 4.

with cycloheximide in the left side and with the left eye occluded and the group treated with cycloheximide in the left side and tested with the right eye occluded.

Therefore, although the group treated with cycloheximide in the right side and tested with the right eye occluded still pecked a large number of pebbles in the last 20 pecks, it did show a drop in errors over the period of testing.

Figure 6 gives the times for each group to complete their 60 pecks. In general, the chicks with their right eyes occluded pecked more slowly than those with their left eyes occluded ($p = 0.036$, 2-tailed Mann-Whitney U test for all the chicks with their left eyes occluded versus all those with their right eyes occluded).

Auditory Habituation

Treatment of the right side of the fore-brain with cycloheximide was without effect on auditory habituation; the number of presentations to reach habituation was not significantly different from that for the control group. Treatment of the left side of the fore-brain slowed the rate of auditory habituation two-fold ($0.002 < p < 0.02$ for the difference between the groups treated on the left and right sides; 2-tailed Mann-Whitney U tests, Fig. 7).

DISCUSSION

By administering cycloheximide to either the right or the left hemispheres of the chicken fore-brain on Day 2 of post-hatched life, it has been possible to demonstrate that there is lateralisation of a number of fore-brain functions.

The left and the right sides of the fore-brain are not equal in their ability to learn a visual discrimination task. Rate of learning the visual discrimination task, which requires search for food grains scattered on a background of small pebbles, can be measured by the number of errors in the last 20 pecks of the task. Performance of chicks tested with the left eye occluded was found to be independent of the treatment given to the right side of the fore-brain. As long as the left hemisphere had not been injected with cycloheximide, learning occurred when testing was done with the left eye occluded, regardless of whether the right hemisphere had been treated with cycloheximide or the saline vehicle. In contrast, with the right eye occluded learning performance was not independent of treatment of the left side of the fore-brain with cycloheximide. When the left hemisphere had been treated with cycloheximide and the chicken was tested with the right eye occluded, no discrimination was made between grains and pebbles in the last 20 pecks of the task, even when the right hemisphere was free of cycloheximide.

A comparison between the number of pecks at pebbles in the first 20 pecks and in the last 20 pecks of the task can be taken as another criterion for learning, or shift of preference. When the right side of the fore-brain had been treated with cycloheximide and left eye was occluded in the test, the number of errors in the first 20 pecks was significantly lower than that for the other two groups tested with their left eyes occluded. This probably indicates that for this group some learning was already apparent in the first 20 pecks. Indeed this group did learn well as seen by the mean of less than 2 errors in the last 20 pecks and a significant fall in errors between the first and last 20 pecks. The group appears to be learning at a slightly enhanced rate compared to its control test with left eye occlusion and treated with saline on both sides of the fore-brain, which could be taken to suggest that normal operation of the right hemisphere can slightly slow visual discrimination learning.

The other anomalous result in the first 20 pecks is that of the group treated with cycloheximide in the right hemisphere and tested with the right eye occluded. This group made significantly more pecks at pebbles than did its control group treated with saline in both hemispheres and also tested with the right eye occluded. Consequently, even though this group was still making a high number of errors in the last 20 pecks, and on this criterion alone would seem not to have learnt, there was a significant fall in errors between the first and last 20 pecks. This means that there was a significant shift in preference away from pebbles towards grain, and some learning could be said to have occurred.

In summary, three groups learnt the visual discrimination task well (to a criterion of 2 or 3 errors in the last 20 pecks). They were both the control groups treated with saline in both sides of the fore-brain, and the group treated with cycloheximide in the right side and tested with the left eye occluded. Two groups showed no learning at all. They were those treated with cycloheximide in the left side and tested with either the right eye or the left eye occluded. The remaining group, treated with cycloheximide in the right and tested with the right eye occluded showed a shift from pebbles to grain, which could indicate learning but at a much slower rate. Therefore, assuming that most input from one eye goes to the contralateral hemisphere, the left side of the chicken fore-brain appears to play a more important role in visual discrimination learning than does the right. In our results there is also a slight, but not significant, tendency for this lateralisation of visual discrimination learning to be present in the control, saline-treated animals, and this has been confirmed by R. J. Andrew (personal communication), who has repeated these tests on untreated chicks.

Possibly connected to its capacity for visual discrimination learning, the left hemisphere appears to "drive" pecking at a slightly faster rate than does the right. Faster pecking was scored in those groups tested with left-eye occlusion irrespective of whether learning did or did not occur. Since pecking rate is not associated with learning rate, cycloheximide treatment does not cause slowed learning on this task simply by altering the motivation to feed.

In contrast to the visual discrimination learning, visual habituation learning was not found to be functionally lateralised in the chicken fore-brain. If either the left or the right side of the fore-brain was treated with cycloheximide, visual habituation occurred at the same rate as in controls, treated on both sides with saline, no matter whether the left or the right eye was occluded during the test. This result is in contrast to the slowing of visual habituation learning which occurs after both sides of the brain have been treated with cycloheximide [20]. The failure of unilateral administration to produce slowed visual habituation cannot be explained by this being an effectively lower dose than the bilateral one, since bilateral administration of $10 \mu\text{g}$ in $5 \mu\text{l}$ of saline produces a significant slowing of visual habituation [19]. As long as one hemisphere is free of cycloheximide, visual habituation can occur and for this function each eye has access to both the right and left sides of the fore-brain.

This is not so for auditory habituation. Cycloheximide treatment of the left hemisphere slows auditory habituation to the same extent that bilateral treatment also slows it [20]. However, treatment of the right hemisphere is completely without effect on auditory habituation. Therefore, it is apparent that auditory habituation learning occurs, either entirely or to a greater extent, in the left side of the fore-brain.

The function of the right side of the fore-brain is, as yet, less clear. However, our results do indicate that it may be somewhat more involved with response to novelty than is the left hemisphere. In the visual habituation task those chicks treated with cycloheximide in the left side of the fore-brain and tested either binocularly or with the right eye occluded tended to respond to the novel stimulus for a longer time on its first presentation than did any of the other groups. Also, in the visual detection task control animals were found to be more likely to respond to the novel visual stimulus when it was in the left peripheral field of vision; that is when objects were presented simultaneously in both fields of

vision, the chicks turned more frequently towards the object presented on the left side. This greater response to novel objects in the left peripheral field of vision may not result from the left eye being better at detection, because, when only one object was presented at a time in either the left or the right visual field, the distance at which control animals detected it was the same for both eyes. It therefore appears that the observed difference in side preference is generated at the level of decision making.

The detection test failed to reveal any lateralisation of detection ability in those animals which had received unilateral treatment with cycloheximide. Cycloheximide treatment caused an imbalance in the distance of detection in favour of the eye contralateral to the treated hemisphere, regardless of which hemisphere this was. We have previously reported defects in behaviour which occur after cycloheximide treatment [20], and it is therefore worth mentioning in passing that this is the first example of better performance in those areas of the brain treated with cycloheximide during their development.

In summary, while both sides of the brain can perform the learning required for visual habituation, visual discrimination learning and auditory habituation learning are either located in or performed better by the left hemisphere, and the left hemisphere is slightly more motivated to peck in the visual discrimination task. The right hemisphere appears to be more responsive to novel visual stimuli.

Although visual habituation may be lateralised in regions other than those effected by the present injections, a possible explanation why it may not be functionally lateralised in the fore-brain, while visual discrimination and auditory habituation are, can be based on differences between the tasks in the way in which the receptors receive information and pass it on to the fore-brain. Considering chickens tested binocularly and binaurally, in both the visual discrimination and the auditory habituation tasks information would be received jointly by both sides of the fore-brain. In the visual discrimination task pecking is in the binocular field of vision, and in the auditory habituation task both ears receive the auditory stimulus. It may therefore have been unnecessary to duplicate in each hemisphere the neural circuits used in learning these tasks. However, visual habituation is performed almost exclusively with use of the peripheral field of vision (the chicken examines the novel visual stimulus with only one eye), and consequently each side of the fore-brain may need to contain the capacity for visual habituation learning. It was found that animals tested monocularly habituated at the same rate as controls regardless of whether the hemisphere ipsilateral or contralateral to the eye being tested had been treated with cycloheximide. This implies that each eye has access to the circuits for visual habituation in both sides of the fore-brain, which contrasts to the results for visual discrimination learning in the binocular field, and suggests that these two visual tasks may use different neural pathways. As Nye [17] has suggested for pigeons and Friedman [5] for doves, information from the frontal and peripheral areas of the visual field may be processed by different pathways. Access to both hemispheres by pathways which receive input from the peripheral field of vision could be important to survival in the natural environment, since these pathways are likely to be the ones used to detect predators and they would allow decisions and responses to be made without turning the head.

The left-sided localisation of auditory habituation learning

presents itself as an evolutionary precedent for left-hemispheric dominance control as found in canaries [16]. However, there is a 50% chance of this coincidence even if the circuits involved are completely unrelated. Functional lateralisation in the brain may be more widespread than previously thought, and it is certainly not an attribute peculiar to humans and their ability for language.

Lateralisation of hemispheric function in the chicken may not require complex genetic programming for development, since it could result secondarily from the position of the chicken in the egg. At all times during embryonic development the left eye and ear of the chick are shielded by the yolk sac or the chicken's body [4]. From Days 3 to 14 of incubation the chick is lying on its left side on the yolk sac with its eye facing outwards to the shell. For the next two days, while the embryo is migrating inside the egg, the yolk sac comes to cover the entire head, and then from Day 17 to hatching the head is re-exposed but it is now turned so that the left eye and ear are pressed against the body and the right eye and ear are exposed to inputs through the shell and air sac. The last 3 days before hatching may be critical in determining lateralisation of function in the fore-brain. On Days 18 and 19 retinal activity can be detected, and light evoked potentials can be recorded on the surface of the fore-brain [25]. Also, Saunders *et al.* [24] have demonstrated a sudden marked lowering of the threshold for auditory detection between Days 18 and 20, which they attribute to the clearing of fluids from the middle ear. During these last few days of incubation it is conceivable that the right eye and ear are receiving more input and these are relayed to the left hemisphere. The left hemisphere of the brain may therefore be making memories in advance of the right. Memories can be made at this age, since it is possible to imprint chicks to both auditory and visual stimuli before hatching [3,7]. Also, Bell and Gibbs [1] have shown that day old chicks form unilateral engrams of a one-shot, avoidance learning task; monocular training and testing demonstrated that the memory was laid down in the hemisphere contralateral to the eye used in training. It is therefore possible that at hatching the left hemisphere already contains engrams which are absent from the right, and that this forms the basis for subsequent differentiation between the hemispheres, such that the left hemisphere is concerned with complex processing of information connected with attention switching and required for learning, while the right side is more concerned with short-term response to novelty. It is possible that the right hemisphere scans the environment selecting inputs which can be further processed by the left hemisphere.

The ability of cycloheximide to reveal this hemispheric lateralisation may not be paralleled by biochemical estimates of the amount of protein synthesis block in each side of the fore-brain after unilateral administration of this dose of the drug, since Woolston *et al.* [27] report that as early as 5 min after unilateral administration of the drug there is an 80% block of protein synthesis on both sides of the fore-brain. However, M. E. Gibbs (see addendum) has found significantly different degrees of protein synthesis inhibition in each hemisphere 30 min after unilateral administration of cycloheximide. Irrespective of which of these findings is correct, there must be a molecular substrate which correlates with the behavioural differences resulting from left or right side administration, and this could be localised changes in amino acid pools occurring within minutes of the cycloheximide treatment [9].

ACKNOWLEDGEMENT

We are most grateful to Prof. A. L. A. Boura for assistance in preparation of this manuscript.

REFERENCES

1. Bell, G. A. and M. E. Gibbs. Unilateral storage of monocular engram in day-old chick. *Brain Res.* **124**: 263–270, 1977.
2. Cowan, W. M., L. Adamson and T. P. S. Powell. An experimental study of the avian visual system. *J. Anat. Lond.* **95**: 545–563, 1961.
3. Dimond, S. J. Effects of photic stimulation before hatching on the development of fear in chicks. *J. comp. physiol. Psychol.* **65**: 320–324, 1968.
4. Freeman, B. M. and M. A. Vince. *Development of the Avian Embryo*. London: Chapman and Hall, 1974.
5. Friedman, M. B. How birds use their eyes. In: *Neural and Endocrine Aspects of Behaviour in Birds*, edited by P. Wright, P. Caryl and D. Vowles. Amsterdam: Elsevier, 1975, pp. 181–204.
6. Geschwind, N. The anatomical basis of hemispheric differentiation. In: *Hemisphere Function in the Human Brain*, edited by S. J. Dimond and J. G. Beaumont. London: Elek Science, 1974, pp. 7–24.
7. Grier, J. B., S. A. Counter and W. M. Shearer. Prenatal auditory imprinting in chickens. *Science* **155**: 1692–1693, 1967.
8. Glick, S. D., T. P. Jerussi and B. Zimmerberg. Behavioural and neuropharmacological correlates of nigrostriatal asymmetry in rats. In: *Lateralisation in the Nervous System*, edited by S. Harnard, R. W. Doty, L. Goldstein, J. Jaynes and G. Krauthamer. New York: Academic Press, 1977, pp. 216–249.
9. Hambley, J. W. and L. J. Rogers. Retarded learning induced by amino acids in the neonatal chick. *Neuroscience* (in press).
10. Karten, H. J., W. Hodos, W. J. H. Nauta and A. M. Revzin. Neural connections of the "Visual Wulst" of the avian telencephalon. Experimental studies in the pigeon (*Columbia livia*) and owl (*Speotyto cunicularia*). *J. comp. Neurol.* **150**: 253–278, 1973.
11. Karten, H. J. and A. M. Revzin. The afferent connections of the nucleus rotundus in the pigeon. *Brain Res.* **2**: 368–377, 1966.
12. Levy, J. Psychobiological implications of bilateral symmetry. In: *Hemisphere Function in the Human Brain*, edited by S. J. Dimond and J. G. Beaumont. London: Elek Science, 1974, pp. 121–177.
13. Nottebohm, F. Neural lateralisation of vocal control in a Passerine bird. 1. Song. *J. exp. Zool.* **177**: 229–262, 1971.
14. Nottebohm, F. Vocal behaviour in birds. In: *Avian Biology*, edited by D. S. Farner and J. R. King. New York: Academic Press, 1975, pp. 287–332.
15. Nottebohm, F. Left hypoglossal dominance in the control of canary and white-crowned sparrow song. *J. comp. Physiol.* **108**: 171–192, 1976.
16. Nottebohm, F. Asymmetries in neural control of vocalisation in the canary. In: *Lateralisation in the Nervous System*, edited by S. Harnard, R. W. Doty, L. Goldstein, J. Jaynes and G. Krauthamer. New York: Academic Press, 1977, pp. 23–44.
17. Nye, P. W. On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Res.* **13**: 559–574, 1973.
18. Revzin, A. M. and H. J. Karten. Rostral projections of the optic tectum and the nucleus rotundus in the pigeon. *Brain Res.* **3**: 264–276, 1966/67.
19. Rogers, L. J. and J. M. Anson. Cycloheximide produces attentional persistence and slowed learning in chickens. *Pharmac. Biochem. Behav.* **9**: 735–740, 1979.
20. Rogers, L. J., H. D. Drennen and R. F. Mark. Inhibition of memory formation in the imprinting period: irreversible action of cycloheximide in young chickens. *Brain Res.* **79**: 213–233, 1974.
21. Rogers, L. J. and H. D. Drennen. Cycloheximide interacts with visual input to produce permanent slowing of visual learning in chickens. *Brain Res.* **158**: 479–482, 1978.
22. Rogers, L. J. and F. A. Miles. Centrifugal control of the avian retina. V. Effects of lesions of the isthmo-optic nucleus on visual behaviour. *Brain Res.* **48**: 147–156, 1972.
23. Rogers, L. J., R. Oettinger, J. Szer and R. F. Mark. Separate chemical inhibitors of long-term and short-term memory: contrasting effects of cycloheximide, ouabain and ethacrynic acid on various learning tasks in chickens. *Proc. R. Soc.* **196**: 171–195, 1977.
24. Saunders, J. C., R. B. Coles and G. R. Gates. The development of auditory evoked responses in the cochlea and cochlear nuclei of the chick. *Brain Res.* **63**: 59–74, 1973.
25. Sedláček, J. Development of the optic afferent system in chick embryos. In: *Advances in Psychobiology*, Vol. 1, edited by G. Newton and A. Reisen, 1972, pp. 129–170.
26. Van Teinhoven, A. and L. P. Juhasz. The chicken telencephalon, diencephalon and mesencephalon in stereotaxic coordinates. *J. comp. Neurol.* **118**: 185–197, 1962.
27. Woolston, M. E., I. G. Morgan and J. W. Hambley. Biochemical effects of cycloheximide in developing chick brain. *Pharmac. Biochem. Behav.* **10**: 245–249, 1979.
28. Yoshikawa, T. *Atlas of the Brains of Domestic Animals*. Tokyo: University of Tokyo Press, 1968.
29. Zeier, H. Interhemispheric interactions. In: *Neural and Endocrine Aspects of Behaviour in Birds*, edited by P. Wright, P. Caryl and D. Vowles. Amsterdam: Elsevier, 1975, pp. 163–180.

Addendum

Gibbs, M. E., A. L. Richdale and K. T. Ng. Biochemical aspects of protein synthesis inhibition by cycloheximide in one or both hemispheres of the chick brain. *Pharmac. Biochem. Behav.*, in press.