

CHAPTER 8

EFFECT OF VISUAL EXPERIENCE BEFORE AND AFTER HATCHING ON LATERALIZED VISUAL BEHAVIOUR

8.1 INTRODUCTION

As discussed in Chapter 1, visual lateralization can be revealed not only by unilateral treatment of the left or right hemisphere of the forebrain with glutamate but also by monocular testing. Using monocular testing, a range of differences between the left eye system (LES) and the right eye system (RES) have been found. For example, chicks using LES are better able to recognize individual chicks and choose to approach a familiar cagemate in preference to an unfamiliar chick (Vallortigara and Andrew, 1991, 1994) and to process topographical information (Rashid and Andrew, 1989; Andrew, 1991) than are chicks using RES. However, chicks using RES are better able to categorize food from non-food (pebble-floor test; see p. 42 for details) than ones using LES (Mench and Andrew, 1986; Zappia and Rogers, 1987). This RES superiority for pebble-floor performance is consistent with the finding that treatment of the left forebrain hemisphere, and not the right, impairs this performance (Howard et al., 1980). In Chapter 7, the effect of glutamate on pebble-floor preference was located in the left visual Wulst and hence it is an aspect of lateralized functioning of the thalamofugal projections.

Lateralization of pebble-floor performance is induced by light exposure of the embryo. Chicks hatched from eggs exposed to light for the last few days before hatching have functional lateralization of pebble-floor performance, but not chicks hatched from eggs incubated in the dark (Rogers, 1991, 1997). Furthermore, lateralization for performance on the pebble-floor can be reversed by occluding the right

eye and exposing the left eye to light on day E19 of incubation for 24 hours. In the chicks with reversed lateralization, the LES has superior performance for the pebble-floor task (Rogers, 1990). This effect of light on pebble-floor performance is consistent with the effect of light exposure on asymmetry of the thalamofugal projections from GLd to the visual Wulst of the chick (Rogers and Sink, 1988; Rogers and Bolden, 1991). It is further evidence that the thalamofugal pathway is involved in pebble-floor performance.

However, not all forms of lateralization of visual behaviours may be determined by exposure of the late embryo to light. Recently, Andrew et al. (in preparation) have found that chicks hatched from eggs incubated in the dark have clear LES/RES differences in a task of choice between a familiar red ball (with a horizontal white bar on the face) and an unfamiliar red ball (with a transformation to a vertical white bar on the face). Chicks hatched following light exposure had less LES/RES difference than dark-incubated chicks. Therefore, it was considered important to investigate whether light exposure of the chick embryo affects lateralization of other forms of visual 'choice' behaviour. In this study, the effect of light exposure on the lateralization of choice between a familiar chick and an unfamiliar chick was investigated.

Social/visual experience with conspecifics is an important factor for social recognition. A series of studies using the duckling have shown that social (particularly visual) experience with conspecifics during the early period posthatching affects preference expressed in tests of filial imprinting (Lickliter and Gottlieb, 1985, 1987; Lickliter et al., 1993). After initial exposure to a maternal imprinting model (a stuffed mallard hen) for 30 minutes at about 24 hours after hatching, ducklings were reared in a group (n=12-17) of broodmates or in isolation during the period between training and testing. In the subsequent preference choice test between the mallard and a redhead

model at 48 hours after hatching, the ducklings which had experienced broodmates made a visual choice for the mallard model but those reared in isolation did not choose (Johnston and Gottlieb, 1985). Further experiments found that even if a duckling was reared with one other duckling after imprinting training, it still did not make a choice in the test of imprinting (Lickliter and Gottlieb, 1985, 1987). Social/visual experience with broodmates may also be important for chicks to express a choice between two individual chicks. In this chapter, effects of social/visual experience with other chicks on performance of the choice test were investigated. Also, the interactive effects of light exposure prior to hatching and posthatching social experience on the functional lateralization were investigated.

8.2 GENERAL METHODS

8.2.1 Incubation and rearing conditions

Fertilised eggs (Black Australorp x White Leghorn) were incubated for the first 15 days in an automatically turning, forced-draught incubator. The details of the incubation conditions were described in Chapter 2 (p. 54). On day E16 of incubation, the eggs were transferred to a dark incubator. On day E18/19, for each batch, half of the eggs were given 24 hours light exposure (200-300 lux) and then returned to the dark incubator for hatching. The other half of the eggs were kept in the dark incubator. For Experiments 1 and 3, 4 batches of eggs were used, but for Experiment 2, only one batch of eggs were used.

The chicks were hatched and kept in the dark incubator after hatching. Ten hours later, they were grouped randomly in pairs per home cage (Experiment 1) or in groups of 10 chicks per cage (Experiments 2 and 3). For the latter, they were kept in groups of 10 chicks for 12 hours and then grouped in pairs per home cage. After being paired, the chicks were reared in grey metal cages (20 cm wide x 45 cm long x 30 cm high) and each chick could see only its cagemate. The rearing cages were illuminated and warmed

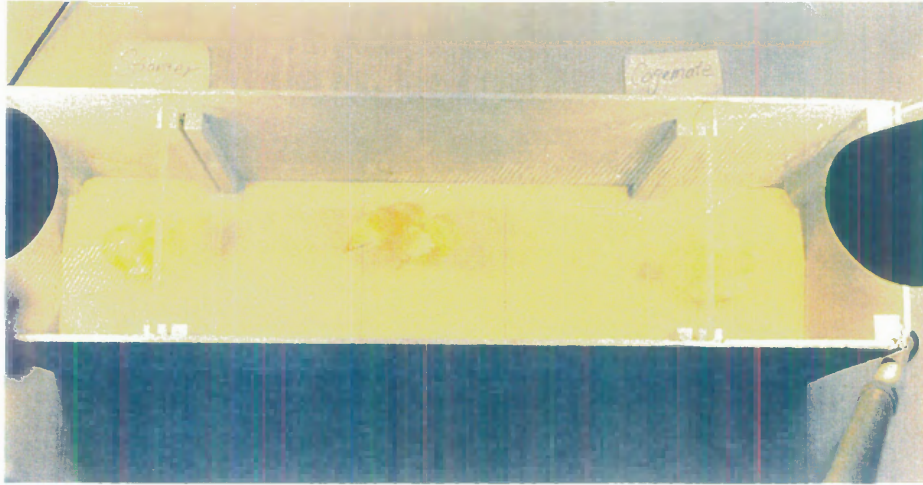
from above by two 25-W light bulbs placed at each end of the cage. Food and water were available ad libitum.

8.2.2 Choice test

On day 3 after hatching, the chicks were given a choice test in a straight runway. The runway was divided into three parts (A, B and C): a central area (B) was the main runway (45 x 20 x 30 cm), into which the test chick was placed, and each end compartment (A and C, 15 x 20 x 30 cm) was separated from it by a transparent plastic partition (Fig. 8.1). A familiar chick (cagemate) and an unfamiliar chick (stranger) were placed in either of these end compartments. The main runway was marked into a middle and two end segments (each 15 cm long; Fig. 8-1B) by pencil lines on the floor paper. The chick to be tested was put in the centre of the main runway. Thus, the chick could choose to approach the familiar and the unfamiliar chick and make a decision to stay with one stimulus, or it could make no choice and either stay in the centre or alternate between the ends of the runway. To balance any influence of positional cues, in half of the tests the cagemate was located in the left end and the stranger in the right end, and for the other half this arrangement was reversed. Each stimulus was illuminated by a 40 W light bulb.

The chicks could be divided according to three testing conditions: chicks tested binocularly (BIN), chicks tested monocularly using the left eye (LES) with the right eye occluded and chicks tested using the right eye (RES) with the left eye occluded. For the chicks tested monocularly, one eye was occluded by a conical piece of tape (2 x 2.5 cm) patched over the left eye or right eye about 20-30 min prior to testing. The eye patches were removed immediately following testing. For each chick, the test lasted 6 min. An overhead video camera (Panasonic, NV-M7) was used to record the behaviour of chicks. Then, the video tape was played back for analysis.

(A)



(B)

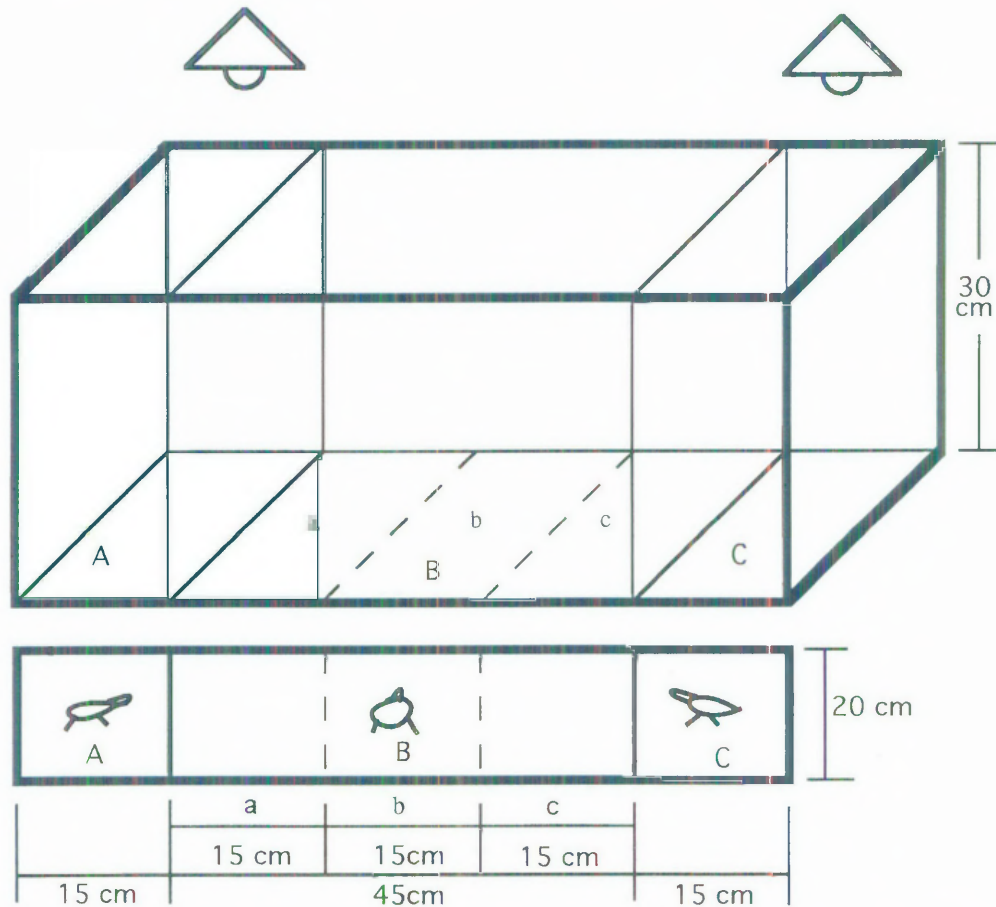


Figure 8.1 A photograph (A) and diagram (B) of the runway used in the choice test. A and C, the two end compartments; B, the main runway; a and c, the two end segments of the main runway; b, the central segment of the main runway. Note that the main runway (a, b and c) is one compartment and segments a, b and c are demarcated only by pencil lines on the floor.

8.2.3 Measurements

The following behaviours were scored:

1) **Latency**: the time from the start of the experiment to the first exit from the central segment of the main runway.

2) **Time in centre**: total time spent in the central segment (b in Fig. 8.1)

3) **Total number of visits**: number of entries into the two end segments (a and b in Fig. 8.1) of the main runway

4) **Preference score and choice score**

The preference score was calculated using the following formula,

$$\text{Preference score} = \frac{\text{Time spent in the end segment near the familiar chick (cagemate)}}{\text{The total time spent in the two end segments (a+c)}}$$

This equation yielded a preference score between 0 and 1.0 for each chick. If the chick preferred to approach the familiar stimulus, the preference score approached 1.0. If the chick preferred to approach the unfamiliar stimulus, the preference score approached 0. The chance level (no preference) was 0.5.

The preference score was also folded so that 0 was considered the same as 1.0 (complete choice of one of the stimuli), 0.1 the same as 0.99 and so on up to 0.49 the same as 0.51 (no choice). These folded data were referred to as **choice scores**. They ranged from 0.5 (no choice) to 1.0 (choice). In this way, chicks that chose to approach either the familiar or the unfamiliar stimulus irrespective of their preference for one or the other could be distinguished from chicks that made no choice.

From the paired chicks, one was tested, and the other one was used as a stimulus. Each chick was used only once as a 'test' chick or a stimulus. Chicks which remained in the central section of the main runway throughout all the test period were excluded from the data analysis.

8.2.4 Statistics

In order to normalize the data, all the measurements were logarithmic ($\log_{10} X$) transformed. The transformed data were analysed by three-way ANOVAs (incubation condition x eye system x sex; in Experiments 1 and 3) or a two-way ANOVA (posthatching experience x sex; in Experiment 2) followed by multiple (*post hoc*) comparisons between the various groups using unpaired t-tests.

8.3 EXPERIMENT 1: Effects of light exposure prior to hatching on lateralization of choice behaviour

8.3.1 Methods

128 chicks (58 of them exposed to light before hatching as mentioned in general methods (p. 217) and 70 of them incubated in the dark) were used in this experiment. All of these chicks were paired at about 10h (8-12h) posthatching directly from the dark incubator. Thus, the chicks could see the cagemate only and had no visual experiences of other chicks before the choice test. Since, for each pair, only one chick was tested and the other chick was used as a stimulus, a total of 64 chicks were tested. The numbers of chicks in the various groups is presented in Table 8-1.

Table 8-1 The numbers of the chicks used in the various groups in Experiment 1

Incubation condition	Light exposure			Dark		
	BIN	LES	RES	BIN	LES	RES
Number of chicks	9	10	10	11	14	10

8.3.2 Results

Figure 8.2 presents mean scores of all the measurements in the choice test in Experiment 1.

8.3.2.1 Latency

The 3-way ANOVA (incubation condition x eye system x sex) revealed significant main effects of incubation condition ($F_{1,51} = 7.54$, $p=0.008$) and eye system ($F_{2,51} = 3.42$, $p=0.04$), but no significant effect of sex ($F_{1,51} = 0.17$, $p=0.68$). There were no significant interactions between any two of the factors or between all three factors. As shown in Fig. 8.2 A and F, the chicks with light exposure during incubation had shorter latencies than the chicks incubated in the dark ($df=61$, $t=-2.64$, $p=0.011$, 2-tailed unpaired t-test). There was a significant difference between the scores of latency for the eye systems tested. The chicks tested with RES had a shorter latency than those tested with either the LES ($df=41$, $t=2.31$, $p=0.026$, 2-tailed unpaired t-test) or BIN ($df=38$, $t=2.08$, $p=0.044$). There was no significant difference between the BIN and LES chicks ($df=41$, $t=-0.48$, $p=0.63$, 2-tailed unpaired t-test).

8.3.2.2 Time in centre

The 3-way ANOVA of the data for total time spent in the central segment of the runway (incubation condition x eye system x sex) revealed significant main effects of incubation condition ($F_{1,51} = 17.89$, $p<0.0001$), but no significant effects of eye system ($F_{2,51} = 1.22$, $p=0.305$) or sex ($F_{1,51} = 1.16$, $p=0.286$). There were also no significant interactions between any two of the factors or between all three factors. As shown in Fig. 8.2 B and F, the chicks incubated in the dark spent more time in the centre than the chicks with light exposure during incubation ($df=61$, $t=-4.07$, $p=0.0001$, 2-tailed unpaired t-test).

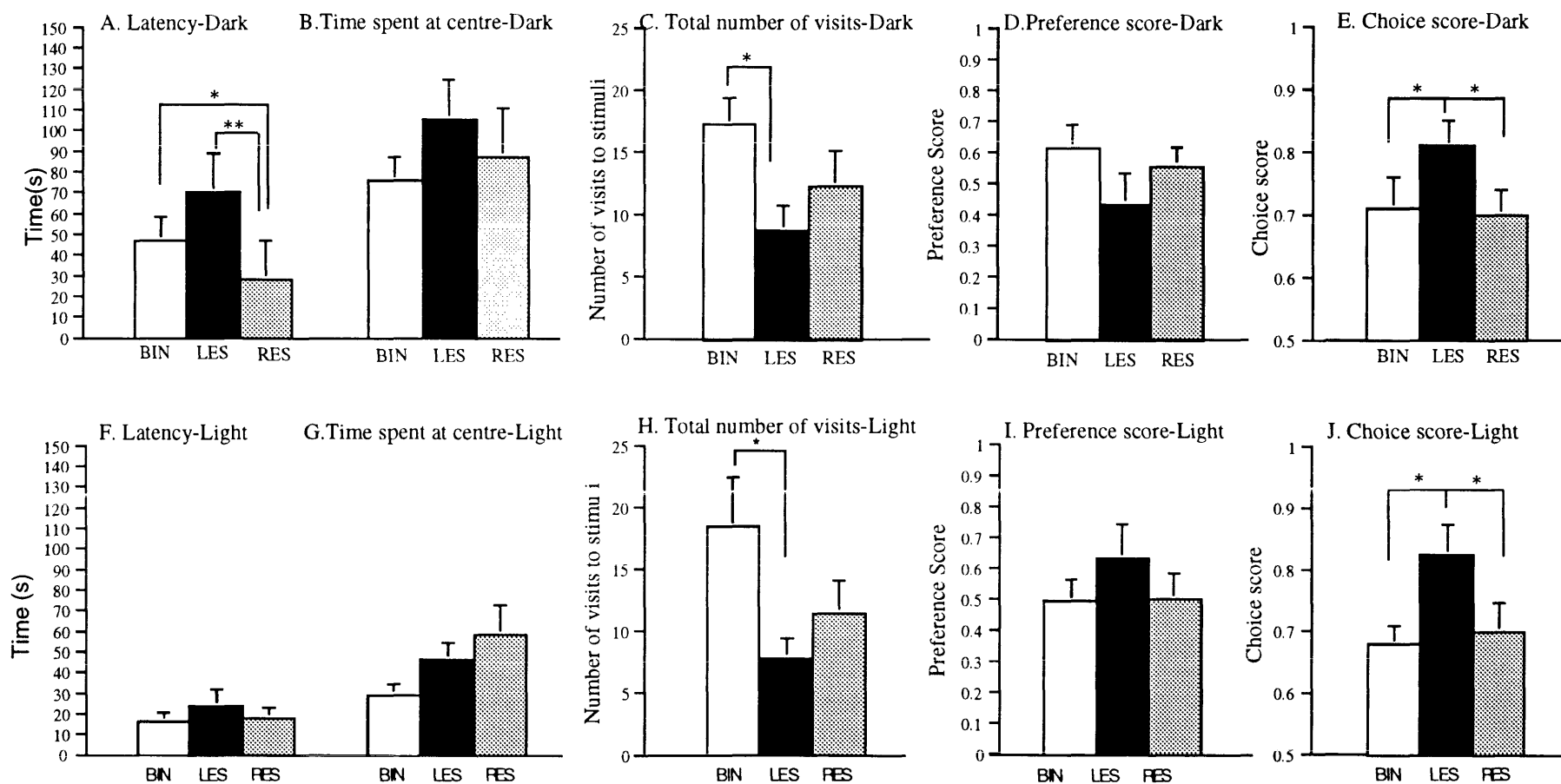


Figure 8.2 The scores (mean \pm SE) measured in the choice test of Experiment 1.

A-E, the results obtained from the dark incubated chicks. F-J, results obtained from the chicks exposed to light prior to hatching. A and F, latency to leave the centre (b) and make the first approach to one of the stimuli. B and G, the time spent in the central segment of the main runway. C and H, the total number of visits to the stimuli (i.e. entries into the end segments of the runway). D and I, Preference score. E and J, choice score. BIN, tested binocularly; LES, tested using the left eye system; RES, tested using the right eye system. (*, $p < 0.05$, 2-tailed t-test).

8.3.2.2 Total number of visits

The 3-way ANOVA (incubation condition x eye system x sex) revealed a significant main effect of eye system ($F_{2,51} = 5.51$, $p=0.007$), but no significant effects of incubation condition ($F_{1,51} = 0.24$, $p=0.62$) or sex ($F_{1,51} = 0.55$, $p=0.46$). There was also no significant interaction between any two of the factors or between all three factors. Because incubation condition did not affect this measurement, the data from both light and dark incubation conditions were put together for further comparisons. The BIN chicks entered segments a and c more than did the LES chicks ($df=41$, $t=3.21$, $p=0.003$, 2-tailed unpaired t-test; Fig. 8.2 C and G). The BIN chicks also tended to approach the stimuli more times than did the RES chicks, but this was not quite significant ($df=38$, $t=1.69$, $p=0.098$). The RES chicks also had a tendency to move more frequently between the stimuli than did the LES chicks, ($df=41$, $t=-1.74$, $p=0.09$, 2-tailed unpaired t-test).

8.3.2.3 Preference score and choice score

Preference score: The 3-way ANOVA (incubation condition x eye system x sex) of preference scores revealed no main effects of incubation condition ($F_{1,51} = 0.012$, $p=0.91$), eye system ($F_{2,51} = 0.11$, $p=0.90$) or sex ($F_{1,51} = 1.72$, $p=0.19$). There was also no significant interaction between any two of the factors or all three factors. The mean preference scores are presented in Fig. 8.2 D and E. The mean scores of the groups were close to 0.5 (chance level). This occurred largely in the LES group because some chicks preferred the familiar stimulus (preference scores close to 1) and others preferred the unfamiliar stimulus (preference scores close to 0). In the BIN and RES groups, the chicks alternated between the two stimuli (see above) and they also had preference scores close to 0.5. In fact, analysis of the choice score, the folded data from the preference score, reveals these group differences (see next section).

Choice score: The choice scores of chicks tested with the different eye systems are presented in Fig. 8.2 E and J. The data are for choice of one stimulus over the other, irrespective of whether that choice is for the familiar or the unfamiliar chick. The 3-way ANOVA revealed significant main effects of eye system ($F_{2,51} = 5.47$, $p=0.007$), but no significant effects of incubation condition ($F_{1,51} = 0.007$, $p=0.98$) or sex ($F_{1,51} = 0.363$, $p=0.55$). There were also no significant interactions between any of the factors. Thus, the data from the chicks with light and dark incubation were lumped together for further multiple comparison between eye systems. The LES chicks had significantly higher choice scores than both the RES and BIN chicks (LES vs. RES, $df=41$, $t=2.60$, $p=0.013$; LES vs. BIN, $df=41$, $t=-2.38$, $p=0.029$, 2-tailed unpaired t-tests). There was no significant difference between the RES and BIN chicks ($df=38$, $t=-0.29$, $p=0.77$, 2-tailed unpaired t-test). Therefore, the LES chicks are more likely to choose one or other of the stimuli than the RES and BIN chicks. This is consistent with the measurement of the total number of visits to the stimuli. The LES chicks, with higher choice scores, had fewer entries into the ends of the runway. They made a choice to approach and tended to stay with their first choice. However, the BIN and RES chicks, with lower choice scores, had a tendency to continue to alternate between the familiar and unfamiliar stimuli. This difference between the LES and RES groups was present in both the light-exposed and dark-incubated chicks. It was, therefore, not affected by light exposure before hatching.

8.3.3 Discussion

Functional lateralization was revealed in the choice scores of chicks hatched from eggs that had received exposure to light and also in chicks that had been incubated in the dark. The chicks tested using LES had higher choice scores (meaning the choice to approach one or other of the stimuli) than chicks tested using BIN or RES. In other words, the chicks using LES made a stronger clear choice between the two stimuli than

those using BIN and RES. This result confirms previous reports that chicks using LES are more likely to make a choice. However, Vallortigara and Andrew (1991), using different strains of chicks ('Hybro', White Leghorn and Warren Sex-link), found that male LES chicks had a preference score above 50% and female LES chicks had a preference score below 50%. This was not the case in the chicks tested in Experiment 1 (see p. 236 for more detailed discussion). A potential reason for the loss of preference in Experiment 1 was investigated in Experiment 2.

The lateralization of choice score found in Experiment 2 is not induced by lateralized light stimulation of the right eye during the late stages of embryonic development, although light exposure did influence the latency and time spent in the centre. The chicks incubated with light exposure had a shorter mean latency to leave the centre in the first instance and stayed for a shorter overall time in the centre than the chicks incubated in the dark. It is important to note that light exposure before hatching did not generate any LES/RES asymmetry in the latency difference between dark and light chicks.

Andrew et al. (in preparation) have also found that differences between LES and RES performance in choice between a familiar and an unfamiliar ball are not generated by light exposure prior to hatching. Thus, although light exposure prior to hatching induces some forms of lateralization, such as for pebble-floor performance (Rogers, 1990, 1997), it has no effect on the lateralization of choice behaviour (at least for choice between conspecific individuals or between familiar and unfamiliar stimuli).

It was unexpected that the BIN chicks would show no preference between the familiar and unfamiliar chicks. Using the same strain of chicks (Black Australorp x White Leghorn), Andrew et al. (in preparation) also found that BIN chicks expressed a

lack of choice between the familiar and unfamiliar ball in a similar runway choice test on day 3. In both experiments, choice behaviour of the BIN chicks was similar to the RES chicks, suggesting that the RES may be dominant for controlling this behaviour on day 3. However, Vallortigara and Andrew (1991) found that BIN chicks, like LES chicks, are capable of discriminating familiar from unfamiliar chicks (or balls) when tested on day 3. In the studies of Vallortigara and Andrew (1991) and Vallortigara (1992a), the chicks were obtained from the hatchery and reared in groups of 4-5 chicks for 20 minutes and therefore they had visual/social experience with a group of chicks before being separated into pairs. However, our chicks in Experiment 1 had been paired directly after being taken from the dark incubator in which they could only hear and have body contact with each other. Therefore, after hatching they had received no visual/limited social experience with other chicks besides the cagemate. Thus, considering that there are only subtle differences in appearance between individual young chicks of the strain used, it is possible that visual/social experience with other chicks during the early period posthatching is essential if the chick is to recognise individual chicks in the choice test. Experiment 2 was designed to examine this possible reason for the absence of preference in Experiment 1.

8.4 EXPERIMENT 2 :Early visual/social experience and choice behaviour

In this experiment, the effect of early visual/social experience posthatching on performance of the choice test was investigated. Chicks were given additional experience with a group of chicks hatched from the same batch.

8.4.1 Methods

Forty chicks were used in this experiment. The eggs were exposed to light from day E17 to 20 of incubation and then transported into a dark incubator for hatching. At

about 10 h posthatching, the chicks were transferred from the dark incubator and were separated into two groups. Group (1) with visual/social experience (VE group; n=20): a group of 10 chicks was reared together in light for 12h. During this period, they had visual, auditory, tactile and social contact each other. Then they were allocated into pairs and placed into home cages. Thus, VE chicks had sensory/social experience with other chicks besides the cagemate. Group (2) had no visual experience posthatching (NVE; n=20): a group of 10 chicks was reared in a dark room for 12 h. During this period, they could not see each other, but could hear each other and also have body contact. Then they were allocated into pairs and placed in homecages. On day 3, the chicks were tested only in the binocular condition in the choice test. Because each group had 10 chicks used as familiar stimuli, only 10 chicks were tested in each group.

8.4.2 Results

As all of the chicks in this experiment had received light exposure before hatching and only their posthatching experience was different, the scores of all measurements were analysed by 2-way ANOVA analyses (posthatching-experience x sex). There were significant main effects of posthatching-experience on the choice scores ($F_{1,15}=16.42$ $p=0.001$) and the total number of entries into the end segments of the runway ($F_{1,15}=8.38$, $p=0.01$), but no significant main effect of posthatching experience on any other measures. No significant main effects of sex were found for any of the score and there were also no significant interactions between sex and posthatching-experience. Therefore, only the factor of posthatching-experience was analysed further. The scores of all measurements are presented in Fig. 8.3.

Although the preference score of the VE group did not differ significantly from the NVE group ($df=17$, $t=-0.06$, $p=0.95$; Fig. 8.3D), there was a significant difference in the choice scores ($df=17$, $t=4.52$, $p=0.0003$, 2-tailed t-test; Fig. 8.3E). As in Experiment 1, the analysis of mean preference scores did not reveal group differences and the

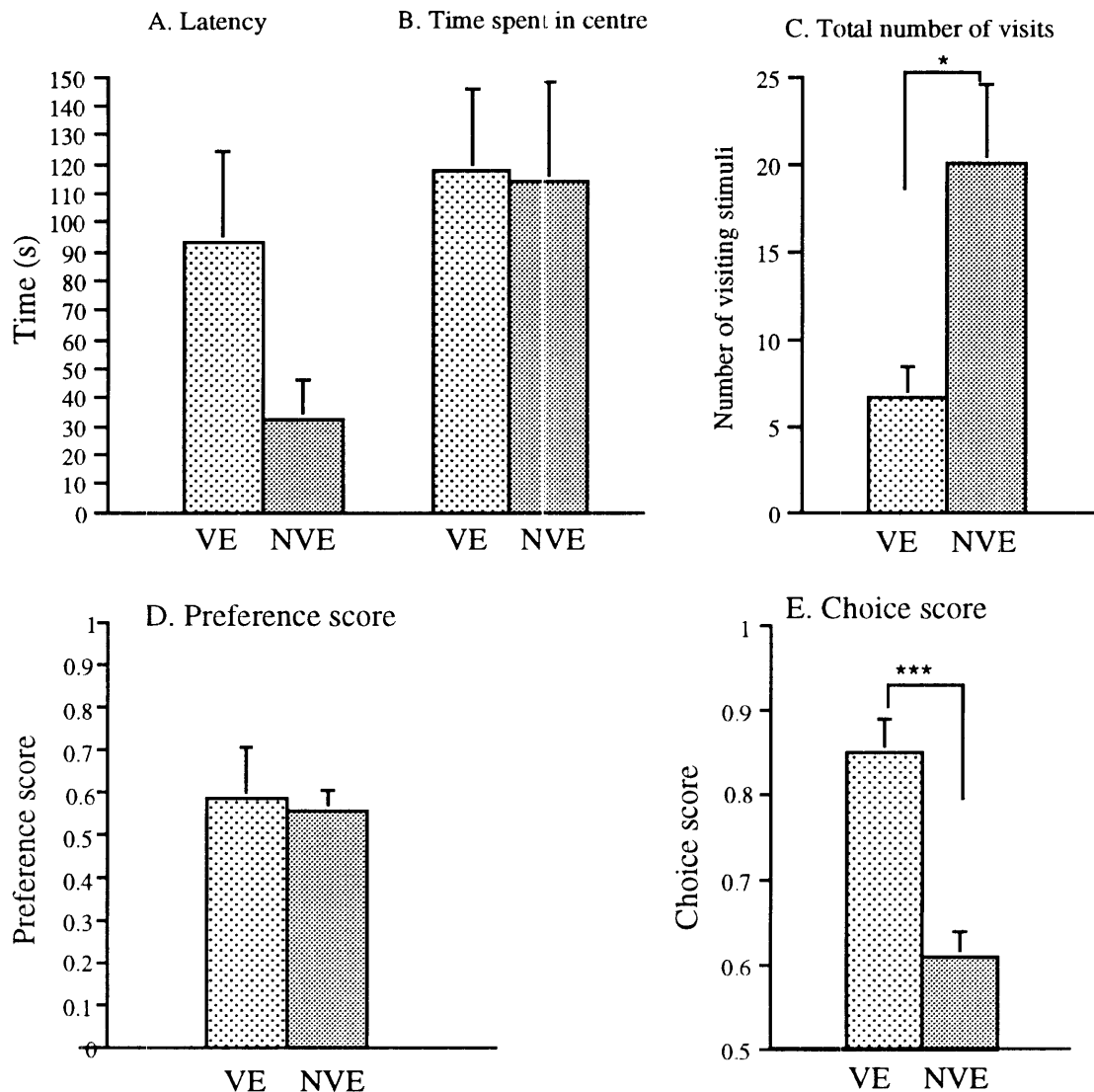


Figure 8.3 The scores (mean \pm SE) measured in the choice test of Experiment 2.

A, latency to make the first approach to one of the stimuli. B, the time spent in the central segment of the main runway. C, the total number of visits to the stimuli, meaning the number of times the tested chicks entered the end segments of the runway. D, preference score. E, choice score. VE, group of chicks with posthatching visual/social experience; NVE, group of chicks that had no posthatching visual experience.

preference did not diverge significantly from 50% (no preference). The VE chicks had a high choice score (had made a clear choice to stay with one or other of the two stimuli). However, the choice score of the NVE chicks was close to chance level. In contrast, the NVE chicks had a higher number of entries into the segments of the runways than the VE chicks ($df=17$, $t=-2.49$, $p=0.023$, 2-tailed t-test). The NVE chicks entered the end segments of the runway a mean ($\pm SE$) of 19.9 ± 4.5 times, but the VE chicks did so only 6.6 ± 1.8 times (Fig. 8.3C).

Although there was a tendency for the NVE group to have a shorter latency than the VE group (Fig. 8.3A), this difference was not significant ($df=17$, $t=1.69$, $p=0.11$, 2-tailed unpaired t-test). There was no difference in the time spent in the centre between the VE and NVE groups (Fig. 8.3B). For both groups, the chicks spent less time in the centre of the runway than in the end segments of the runway next to the familiar or unfamiliar chick.

8.4.3 Discussion

Chicks with posthatching visual experience of other chicks have higher choice scores than those without this experience. They discriminate between familiar and unfamiliar chicks and then choose to stay close to the one or the other stimulus; i.e., they make a clear choice. Chicks which have no visual experience of other chicks besides the cagemate have preference scores at chance levels. Chicks with posthatching experience have lower numbers of entries to the end segments close to the stimuli than those without this experience. Thus, the chicks with early visual/social experience may have visited the stimuli a few times, noticed the difference between the familiar and unfamiliar chick and made a choice to stay with a preferred stimulus. The chicks without visual experiences with a group of broodmates could either not discriminate between the familiar and unfamiliar chick, and therefore alternated between them, or

could discriminate and were not motivated to make a choice. These results suggest that early visual/social experience is a crucial factor determining either the ability to discriminate the subtle differences between conspecific individuals or the capacity to make a choice. In bobwhite quail chicks, visual/social experience with broodmates has also been found to be important in determining choice between a stuffed bobwhite hen and a model of another quail species (McBride and Lickliter, 1993). After hatching the quail chicks were reared in groups with 8-10 broodmates or in isolation from other quail chicks or in a condition in which they could see one chick (partial isolation). When they were tested for choice between a stuffed bobwhite hen and a model of another quail species on day 3, only those reared in groups having visual/social experience with broodmates showed a preference to approach the bobwhite hen. The quails reared in the other two conditions, even those having visual experience with one broodmate, had no preference. This result is consistent with our results that the posthatching experience is an important factor determining preference.

In the chick, the features of the head, particularly the features of the facial region, play an important role in individual recognition (Guhl and Ortman, 1953; Candland, 1969). Visual/social experiences with a group of chicks may be crucial for chicks to discriminate the subtle differences in facial features between individuals. For chicks having no early visual experience with other chicks, it may be more difficult to discriminate subtle facial differences in the strain of chick used in this experiment. It is consistent with this explanation that chicks without visual experience alternate between familiar and unfamiliar chicks but do not express a preference.

8.5 EXPERIMENT 3: Effects of early visual/social experience on lateralization of social decision making

The results of Experiment 2 suggest that early visual/social experience posthatching is one of the crucial factors determining either the ability to discriminate the subtle differences between conspecific individuals or the capacity to make a choice. On the other hand, Experiment 1 has revealed that young chicks, which had no early visual experience, showed lateralized performance in a choice test. In this experiment, effects of early visual/social experience on this lateralization were investigated. The possible interaction between visual experience posthatching and light exposure before hatching was investigated.

8.5.1 Methods

A total of 178 chicks was used in this experiment, 91 of them hatched from eggs with light exposure for 24 hours on day E19 of incubation and 87 of them with no light experience before hatching. After hatching, the chicks were reared in groups of 8-10 chicks for 12 h. Then they were assigned randomly to pairs in which they remained until testing on day 3. Table 8-2 shows the number of chicks tested in the various groups (note that only one chick of each pair was tested).

Table 8-2 The number of chicks in various groups tested in Experiment 3

Incubation condition	Light exposure			Dark		
	BIN	LES	RES	BIN	LES	RES
Eye system						
Number of chicks	15	15	15	14	14	16

8.5.2 Results

Figure 8.4 presents mean scores of all the measurements in the choice test in Experiment 3.

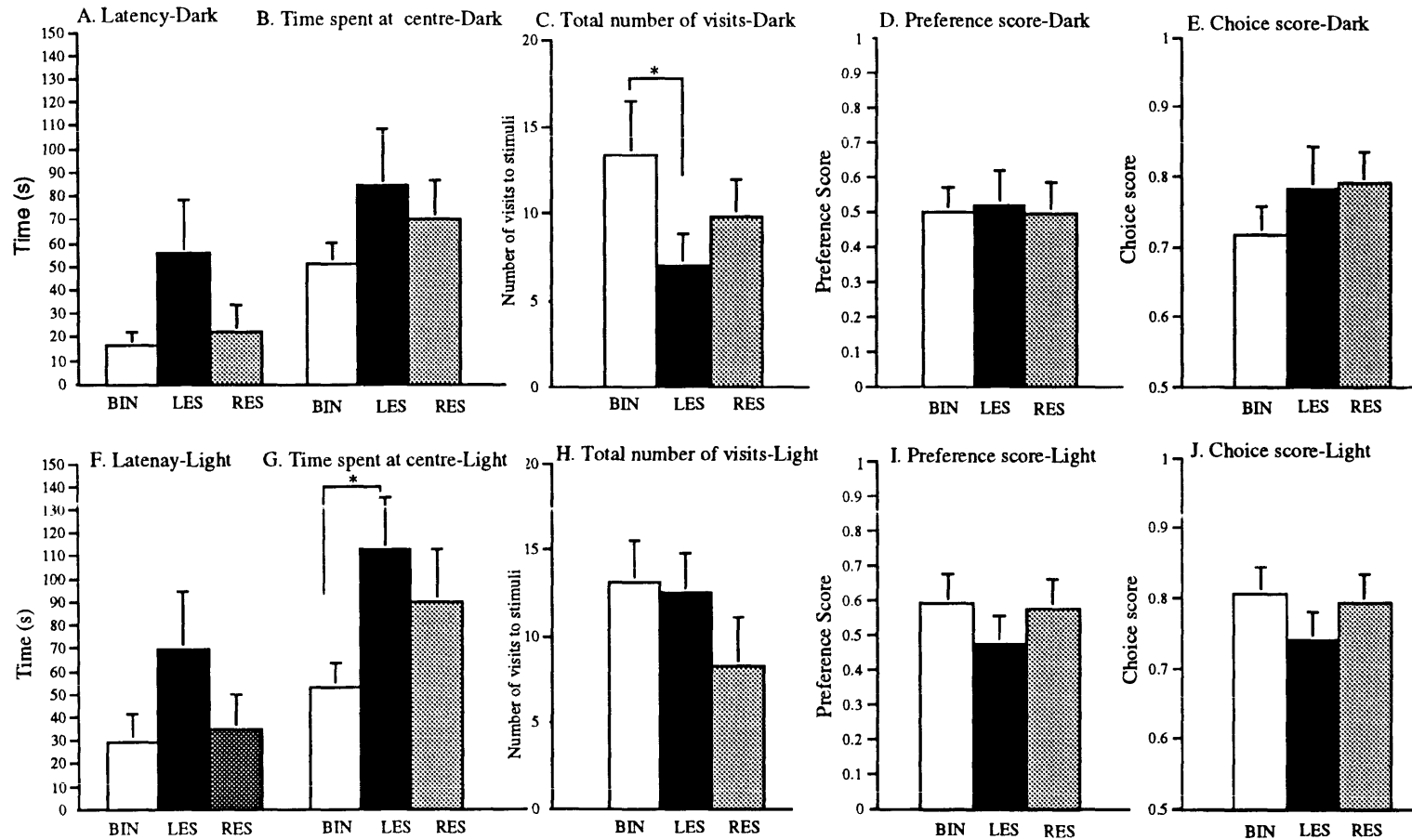


Figure 8.4 The scores (mean \pm SE) measured in the choice test of Experiment 3.

A-E, results obtained from the dark incubated chicks. F-J, results obtained from the chicks exposed to light prior to hatching. A and F, latency to make the first approach to one of the stimuli. B and G, the time spent in the central segment of the main runway. C and H, the total number of visits to the stimuli (i.e. entries into the end segments of the runway). D and I, Preference score. E and J, choice score. BIN, tested binocularly; LES, tested using the left eye system; RES, tested using the right eye system. (*, $p < 0.05$; 2-tailed unpaired t-test).

8.5.2.1 Latency

The 3-way ANOVA of latency (incubation condition x eye system x sex) revealed no significant main effects of incubation ($F_{1,75}=0.44$, $p=0.51$), eye system ($F_{2,75}=2.30$, $p=0.11$) or sex ($F_{1,75}=2.97$, $p=0.09$). There were also no interactions between any two of these factors or all three factors.

8.5.2.2 Time in centre

The 3-way ANOVA of (incubation condition x eye system x sex) revealed only a significant effect of sex ($F_{1,75}=5.38$, $p=0.023$). The female chicks spent a longer time in the centre than the males (97.5 ± 12.8 s for female versus 58.2 ± 7.8 s for male; $df=85$, $t=-2.35$, $p=0.02$, 2-tailed unpaired t-test). There was no interaction between sex and the incubation condition or the eye system.

There was no significant main effect of incubation condition ($F_{1,75}=0.25$, $p=0.62$). Although, as shown in Fig. 8.5 B and F, the LES chicks tended to stay longer in the centre of the runway, no significant effect of eye system was revealed by the ANOVA analysis ($F_{2,75}=1.72$, $p=0.19$). There was also no significant interaction between the incubation and eye system ($F_{2,75}=0.52$, $p=0.59$).

8.5.2.3 Total number of visits to the stimuli

Figure 8.4C and H shows the total number of visits to the stimuli by chicks tested using the LES, RES and BIN. The 3-way ANOVA revealed no significant effects of incubation condition ($F_{1,75}=0.34$, $p=0.56$) or eye system ($F_{2,75}=2.19$, $p=0.12$). However, the interaction between the incubation condition and eye system was significant ($F_{2,75}=3.12$, $p=0.050$). This is because the dark-incubated BIN chicks had a higher number of entries into the ends of the main runway ($df=25$, $t=2.25$, $p=0.033$, 2-tailed unpaired t-test; Fig. 8.5C). There was a significant effect of sex ($F_{1,75}=4.95$,

$p=0.029$). The male chicks entered the end segments four times more than the female chicks (12.6 ± 1.5 times for male versus 8.6 ± 1.4 for female; $df=85$, $t=2.03$, $p=0.045$). However, there was no interaction between sex and incubation condition ($F_{1,75}=0.02$, $p=0.89$), or between sex and eye system tested ($F_{2,75}=0.44$, $p=0.65$) or all three factors ($F_{2,75}=1.34$, $p=0.27$).

8.5.2.1 Preference score and choice score

Preference score: The preference scores were presented in Fig. 8.4 D and I. The 3-way ANOVA (incubation condition x eye system x sex) shows no significant main effects of incubation ($F_{1,75}=0.43$, $p=0.52$), eye system ($F_{2,75}=0.25$, $p=0.78$) or sex ($F_{1,75}=0.54$, $p=0.47$). There were also no interactions between any two of the factors or between all three factors. As discussed above, the analysis based on mean preference score did not reveal group differences, the data of the choice score was analysed.

Choice score: Figure 8.4 E and J presents the choice score of all six groups. The 3-way ANOVA (incubation condition x eye system x sex) revealed no significant main effects of incubation condition ($F_{1,75}=0.39$, $p=0.53$), eye system ($F_{2,75}=0.33$, $p=0.72$) or sex ($F_{1,75}=2.63$, $p=0.11$). There were also no interactions between any two or all three factors.

8.5.3 Discussion

It is unexpected that no lateralization occurred in this experiment. The BIN, LES and RES groups all made choices. Compared to Experiment 1, chicks in this experiment had posthatching experience with a group of chicks besides the cagemate; therefore, one explanation of the results is that the posthatching experience removed the lateralization of choice behaviour. It seems that the RES chicks in this experiment (with posthatching experience; Fig. 8.4) had higher choice scores than the RES chick in Experiment 1 (no

posthatching experience; Fig. 8.2). It is possible that the capability of the RES to discriminate the subtle differences between individual chicks or to make a decision to approach a stimulus depends on visual/social experience with other chicks, but that of LES does not .

In this experiment, light exposure prior to hatching did not affect the choice score, preference score, latency and time spent in centre. There is an interaction between incubation and eye system only for number of entries to the end segments of the runway, but there is no significant dark-incubation/light exposure difference and also no significant LES/RES difference for this score. Therefore, light exposure prior to hatching does not influence chicks to choose to approach familiar or unfamiliar chicks.

8.6 GENERAL DISCUSSION

In general, this study confirms lateralization of young chicks for distinguishing a familiar from an unfamiliar conspecific in that chicks using the LES had a higher choice score than those using the RES (Vallortigara and Andrew, 1991; Vallortigara, 1992). This result was found only for chicks raised in pairs but not for those given visual/social experience with a group of chicks. No significant sex difference was found. However, Vallortigara and Andrew (1991), using a different strain of chicks, found that the male LES chicks preferred to approach the familiar chick and the female LES chicks preferred to approach the unfamiliar one. In this study, we found that some LES chicks chose the familiar chick and others chose the unfamiliar chick, and this was not linked to the sex of the chicks. Using the same strain of chicks, Andrew et al. (in preparation) found a similar result in a choice test of a familiar ball versus an unfamiliar ball. Therefore, it seems that there may be a strain difference in performance of this test.

In Experiment 3, it is clear that both LES and RES chicks can discriminate familiar from unfamiliar individuals and then make a clear choice to stay with one of them. Because these chicks had a posthatching experience with a group of broodmates, it seems that the posthatching experience removes the LES/RES difference. It is possible that the choice test used in this study is relatively easier for the chicks having posthatching experience of a group chicks than for those having no experience with other chicks except the cagemate. For the strain of chicks used in this study, there are only very subtle visual differences between individuals; therefore it should be difficult for the chicks to discriminate the subtle differences and recognize them during a short testing period. The situation may be different for the chicks having posthatching experience. Because these chicks have had time to learn to discriminate subtle differences, they may find it easy to make a choice during the testing period. Alternatively, it is also possible that RES chicks having no visual/social experience with other chicks may be able to discriminate the differences between individuals but cannot make a choice.

In fact, as shown in Experiment 2, posthatching experience with a group of broodmates elevated the choice score. It is possible that because the choice test is relatively easy for chicks having posthatching experience, even the RES can recognize different individuals, causing failure to reveal lateralization. Vallortigara and Andrew (1991) tested chicks monocularly with a choice between the familiar ball (horizontal bar on the ball's face) and unfamiliar stimulus (a ball with a transformation). When the unfamiliar ball was transformed to a small extent (a bar at 45°), lateralization was shown clearly in that only the LES chicks made a clear choice. However, when the transformation was large (a ball with no bar on the face or a ball with a continuous horizontal or vertical band), lateralization was not found because both the LES chicks and RES chicks made a clear choice. However, Vallortigara and Andrew (1991, 1994)

have suggested that the function of the RES is to categorize the stimuli into different types and the function of the LES is to discriminate subtle differences. Changing the ball with a large transformation, different strategies are used by the RES and LES. The RES may recognize it as a different stimulus from the familiar ball but the LES may discriminate differences between the two balls. Therefore, both the RES and LES chicks can make choices. This explanation is not applicable to the experiments reported here because the stimuli had not been modified and also the stimuli (two chicks) could not be separated into two different categories.

It becomes clear that lateralization of the choice between familiar and unfamiliar is not generated by light exposure prior to hatching (Andrew et al., in preparation; this study). In this aspect it is different from the lateralization of pebble-floor performance, which depends on light experience prior to hatching. Different neural mechanisms must be involved in the lateralized visual processing of social choice performance and pebble-floor performance.

To date, no studies have been carried out to investigate which visual pathway is involved in the recognition of conspecific individuals in the chick and in the decision processes needed in order to choose between familiar and unfamiliar conspecifics. One possibility is that the tectofugal visual pathway has a larger role than the thalamofugal pathway in this particular performance. In the pigeon, Watanabe (1992) has examined the effects of ectostriatal lesions on discrimination between pigeons and quails or between two pigeons (recognition of individual differences) using operant conditioning procedures. The pigeons were trained to discriminate between photographs of pigeons and quails or between photographs of two pigeons with differently coloured feathers (individual discrimination). After reaching criterion (90% correct), the subjects received brain lesions in the Wulst or ectostriatum. The ectostriatal lesions caused deficits in

discrimination between two pigeons but not in discrimination between a pigeon and a quail. Thus, at least in the pigeon, the tectofugal pathway is involved in visual processing for recognition of individual conspecifics.

In the pigeon, the tectofugal pathway is organized asymmetrically in terms of the size of the tectal neurones and the number of tectofugal projections (Güntürkün, 1997a, 1997b and 1997c; also see Chapter 1, p. 34). But, in Chapter 6, no marked degree of asymmetry of the tectofugal projections was found in chicks, even after they had been exposed to light before hatching. Therefore, even though the tectofugal pathway may be involved in transmission of the visual information for recognition and responding to individuals, it is likely that higher centres in the forebrain play an important role in this functional lateralization.

Although, at this stage, we have no information about which forebrain area is involved in this lateralization, the intermediate medial hyperstriatum ventrale (IMHV) is one possible candidate for this role. Although there is no direct connection between the ectostriatum and IMHV of the chick (Bradley et al., 1985), the ectostriatum may project indirectly to IMHV through the archistriatum intermedium or lateral part of the intermediate neostriatum (Ritchie, 1979; Bradley et al., 1985). Johnson and Horn (1987) found that lesions in IMHV impair a chick's preference to approach an imprinting stimulus. Lesioning studies and glutamate treatment have also revealed that the left and right IMHV play different roles in storage and recall of imprinting memory (Cipolla-Neto et al., 1982; Johnston and Rogers, in press). Furthermore, at the neurochemical level, MK-801 binding asymmetry exists in the IMHV of dark-incubated chicks and this asymmetry is reversed by imprinting learning (Johnston et al., 1995). Lateralization of imprinting also does not depend on light exposure. The chicks used for imprinting studies are incubated and hatched in the dark and they have lateralization in the

formation and recall of imprinting memory (Cipolla-Neto et al, 1982; also see Chapter 1, p. 40). Thus, for lateralization of choice to approach familiar/unfamiliar chicks and lateralization of imprinting (which are related behaviours) light exposure of the embryo has no influence.

In conclusion, functional lateralization of choice between familiar and unfamiliar chicks is clear. The chicks using LES are able to recognizing the difference between individual conspecifics and then to make a choice to approach one or the other. Those using the RES do not choose to approach one in preference to the other but alternate between the two chicks. This lateralization does not depend on light exposure during the last stages of incubation. Light stimulation of the right eye prior to hatching may put the RES/the left visual Wulst (as indicated in Chapter 7) in charge for the pebble-floor performance, but it is not the case for some other tasks such as the choice test used in this chapter. Localized treatment of glutamate could be used to precisely investigate which visual pathway or which forebrain area(s) are involved in individual recognition and performance of choice between familiar and unfamiliar chicks, the tectofugal visual pathway being proposed here as the important pathway.

CHAPTER 9

GENERAL DISCUSSION

In this chapter, general aspects of the results reported in this thesis will be considered. Detailed discussion of the results reported in each chapter has been included in the previous chapters.

Although, previously, the retinal structure and retinal projections of the chick were known to differ noticeably from those of the pigeon (Ehrlich, 1981; Emmerton, 1983; Ehrlich and Mark, 1984b; Remy and Güntürkün, 1991; Güntürkün, 1991), many authors had assumed that the central visual pathways of the chick had the same organization as those of the pigeon, or very similar to it. As a result, knowledge of the organization of the pigeon's visual system was frequently used to explain findings about the behaviour of chicks, including lateralized performance, learning and memory. However, the experiments reported in Chapters 4, 5 and 6 of this thesis show that there are clear differences between the chick and the pigeon in the organization of the central visual pathways. In this chapter, the significance of this organization of the visual pathways in the chick will be discussed with reference to studies of visual behaviour in the chick, particularly with respect to functional lateralization.

9.1 FUNCTIONAL ORGANIZATION OF THE THALAMOFUGAL PATHWAY IN THE CHICK

Because the optic nerves project entirely to the contralateral GLd (Ehrlich and Mark, 1984a) and to the contralateral TeO (Crossland and Uchwat, 1979; Ehrlich and Mark, 1984a), the bilateral projections from GLd on each side of the thalamus to the visual Wulst in each hemisphere and from TeO on each side of the brain to the Rt nuclei

are essential for binocular processing and intraocular interaction of information. This is because only by bilateral projections can the information from the left and right eyes be superimposed on the same neural structure (the visual Wulst, or the Rt and the ectostriatum). The results reported in Chapters 4 and 5 provide clear evidence that in the chick the organization of the bilateral projections in the thalamofugal pathway is different from that of the tectofugal pathway. This difference lies in the fact that different cell populations project to either the ipsilateral or the contralateral forebrain in the thalamofugal pathway, whereas a large percentage of tectofugal neurones have collaterals by which they project to both the ipsilateral and contralateral Rt.

Miceli and Repérant (1982) have found that GLd of the pigeon contains many bilaterally projecting neurones which send efferents to both the ipsilateral and contralateral visual Wulst. It was thought that these bilaterally projecting neurones might play a role in binocular vision (Miceli and Repérant, 1982). However, Remy and Güntürkün (1991) found that the thalamofugal pathway of the pigeon is involved only in processing visual information from the lateral visual field, which indicates that these bilaterally projecting neurones are not used for binocular vision. Instead, it would appear that the function of these neurones may be to coordinate visual inputs from equivalent regions of the left and right lateral visual field. Differing from the pigeon, the thalamofugal pathway of the chick receives visual inputs from both the lateral and frontal visual fields (Wilson, 1980a; Denton, 1981; Ehrlich and Mark, 1984b), and there are no bilaterally projecting neurones in the GLd of the chick (Chapter 4; Fig. 4.12, p.128 and Fig. 9.1). It has been suggested (Chapter 4) that different kinds of visual information could be transmitted in the ipsilateral and contralateral projections to the visual Wulst (i.e. transmitted through separate channels). Therefore, in the chick, projections from the GLd to both the ipsilateral and contralateral visual Wulst may not coordinate inputs from the left and right lateral visual fields. Also, it is possible that,

Thalamofugal Pathway

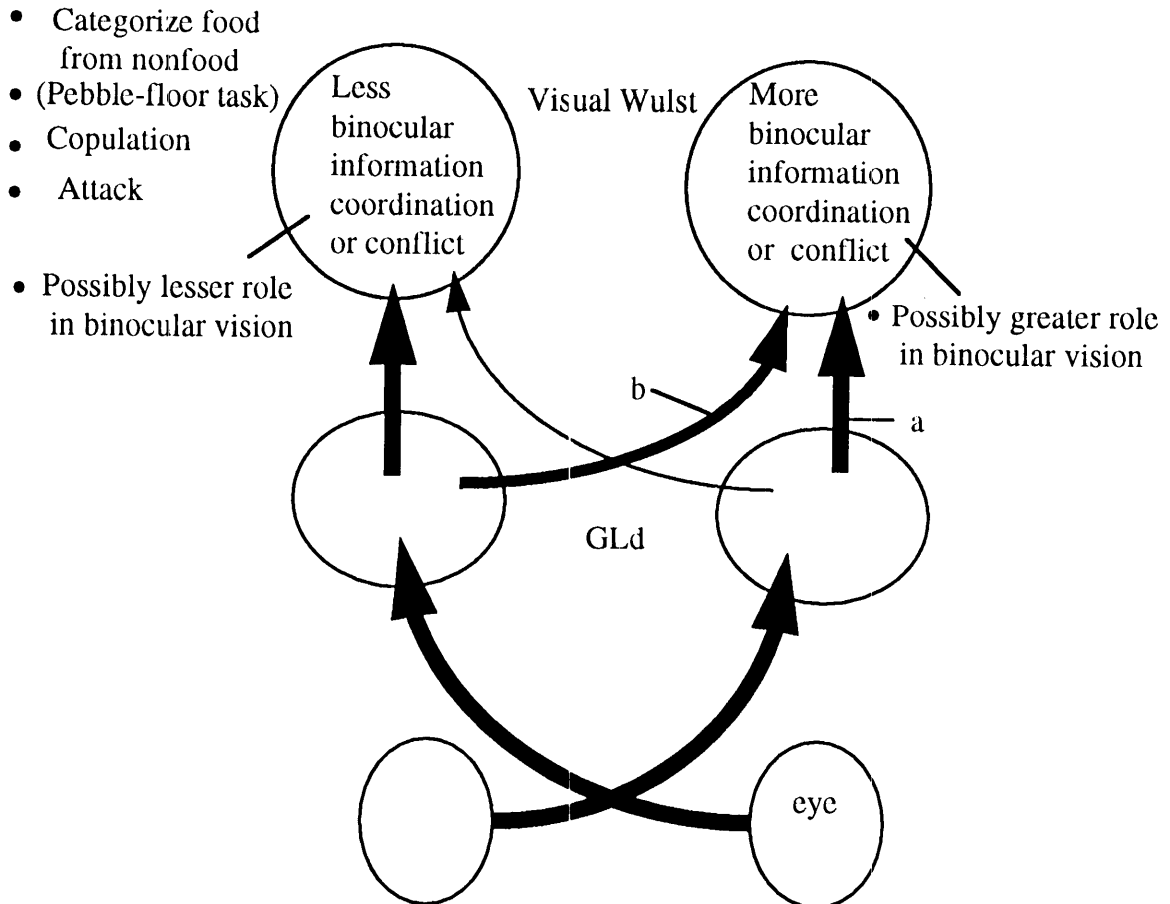


Figure 9.1 Organization of the thalamofugal visual pathway and its functions based on the studies in this thesis and by Rogers (1996). Note that there are no bilaterally projecting neurones in the GLd. The ipsilateral and contralateral projections of the GLd send different information from the two eyes to each visual Wulst. There is asymmetry in the contralateral GLd-Wulst projections (there are more contralateral projections from the left GLd to the right visual Wulst than from the right GLd to the left visual Wulst). This asymmetry allows greater coordination or conflict between information from the left and right eyes in the right visual Wulst than the left visual Wulst (see text for more detail). The left visual Wulst is involved in performance of the pebble-floor task and inhibition of copulation and attack responses. a, projections from the ipsilaterally projecting neurones of GLd; b, projections from the contralaterally projecting neurones of GLd.

although the visual Wulst of the chick receives visual inputs from the frontal (binocular) visual field, it is not involved in binocular vision. Wilson (1980b) has reported that there are few binocular neurones in the visual Wulst of the chick. Instead, the left and right visual Wulst may be involved in processing quite separate visual information. Since, in many avian species, each eye can focus independently at a different distance and move independently to scan the environment (Wallman and Pettigrew, 1985; Wallman and Letelier, 1993), even in the frontal visual field the two eyes may send different information to the forebrain (Wallman and Pettigrew, 1985; Vallortigara and Andrew, 1994a). Some of this different information transmitted from the eyes may be processed differentially in the left and right visual Wulst of the chick. It should be noted, however, that in owls the thalamofugal pathway is involved in binocular vision (Pettigrew, 1979): in the well-developed Wulst numerous binocular cells have been identified (Pettigrew, 1979, Wagner and Frost, 1994). It appears, therefore, that the Wulst may have a range of different functions in different species. If the Wulst is used for binocular vision in the chick, the right visual Wulst would be likely to have a greater role in this process than the left visual Wulst as a result of the asymmetry in the contralateral GLd-Wulst projections (see Fig. 9.1). In fact, Wilson (1980a, 1980b and personal communication) recorded only in the left visual Wulst of chick and found few binocular neurones. It is possible to predict that more binocular units would be found in the right than left Wulst of the chick.

9.2 FUNCTIONAL ORGANIZATION OF THE TECTO-FUGAL PATHWAY

Contrasting with the thalamofugal pathway, there are many bilaterally projecting neurones in the optic tectum of the chick (Chapter 5; Fig. 5.12, p. 167). Therefore, after receiving input from the contralateral eye, tectal neurones send the same information to both the ipsilateral and contralateral Rt and then on to the ectostriata in each hemisphere. There are also lots of ipsilaterally projecting neurones and some

Tectofugal Pathway

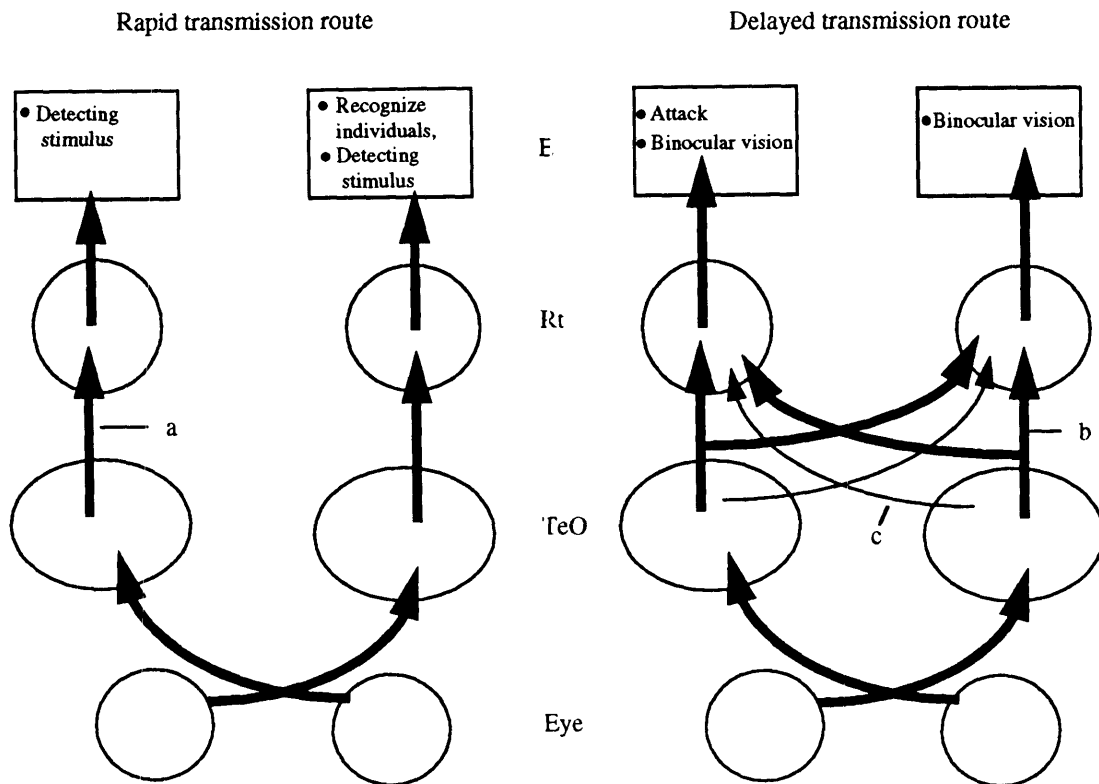


Figure 9.2 Organization of the tectofugal pathway of the chick used for proposed two-stage visual transmission and its possible functions based on the studies in this thesis. A, the first stage rapid visual transmission. After the optic tectum (TeO) receives inputs from the contralateral eye, visual information is transmitted rapidly through the large, myelinated axons of the ipsilaterally projecting neurones to the n. rotundus (Rt) and then to the ipsilateral ectostriatum (E). Thus, by this route of visual transmission, information from the eye is transmitted to the contralateral Rt and the contralateral E only. This pathway is proposed to be involved in distinguishing familiar from unfamiliar individuals and detecting the stimulus. B, the second delayed transmission pathway. After TeO receives inputs from the contralateral eye, visual information is transmitted with a delay through small, unmyelinated axons of the bilaterally projecting neurones to both the ipsilateral and contralateral Rt. Visual information may also be transmitted through small, myelinated axons of a few contralaterally projecting neurones to the contralateral Rt only. The Rt projects to the E. This delayed transmission may be involved in binocular vision. The left E was found to be involved in the inhibition of attack responses (for more detail see text). a, projections from the ipsilaterally projecting neurones in the TeO; b, projections from the bilaterally projecting neurones in the TeO; c, projections from the contralaterally projecting neurones in the TeO.

contralaterally projecting neurones without collaterals. It is most interesting that the TeO neurones projecting to the ipsilateral Rt have large, myelinated axons but the TeO neurones projecting bilaterally to both of the Rt nuclei and neurones projecting to the contralateral Rt have small, unmyelinated axons (Saleh and Ehrlich, 1984; Ngo et al., 1994). This organization suggests two stages of visual transmission in the tectofugal pathway of the chick: the first involves rapid transmission and the second involves a delayed transmission (Chapter 5; Fig. 9.2). In the rapid transmission component, the visual information is transmitted through the pathway TeO-ipsilateral Rt-ectostriatum. In the delayed transmission component, visual information is transmitted through the pathway TeO-contralateral Rt-ectostriatum and also TeO-ipsilaterally Rt-ectostriatum. Considering that the optic nerves project only to the contralateral TeO in the tectofugal pathway, visual information will be transmitted rapidly solely to the Rt contralateral to a given eye and to the contralateral ectostriatum. It will be transmitted slowly to both the ipsilateral and contralateral Rt and ectostriata in the delayed transmission system. Therefore, the proposed first stage rapid transmission would involve lateralized information processing, whereas the second stage may involve both binocular visual processing and coordination of activities of the left and right Rt (and ectostriata). The latter is reinforced by the fact that the TeO projects to both the ipsilateral and contralateral Rt in a similar topographical manner in the chick (Chapter 5). It is possible that the rapid neural transmission may be used for detecting the stimulus and priming the neuronal activities of the particular forebrain area(s). Then the delayed neural transmission following may be used for further binocular information processing, including the information used to perceive depth. However, so far, no experiments have been carried out to investigate the physiological characteristics of the proposed two-stage neural transmission and properties of possible binocular neurones in Rt or the ectostriatum in the chick and other birds. Nor is it known whether the pigeon has similar organization and neurotransmission as that proposed for the chick.

9.3 STRUCTURAL ASYMMETRY OF THE TWO VISUAL PATHWAYS

Another aspect of the organization of the avian visual pathways is the presence of asymmetry in the number of projections that cross the midline from left to right versus right to left. Using HRP and fluorescent tracers FG and TB, asymmetry of the thalamofugal projections had been shown in three strains of chicks: two strains of domestic chicks and a feral strain of chicks (Boxer and Stanford, 1985; Rogers and Sink, 1988, Adret and Rogers, 1989; Rogers and Krebs, 1996). In Chapter 4, using the retrograde tracer RITC, this asymmetry was not only confirmed but also located in the contralateral projections. There is a higher number of contralateral projections from the left GLd to the right visual Wulst than contralateral projections from the right GLd to the left visual Wulst (Fig. 9.1). However, the left and right visual Wulst regions receive equal numbers of ipsilateral GLd inputs. Therefore, since the GLd receives retinal input from only the contralateral eye, the right visual Wulst receives more visual inputs from its ipsilateral eye than the left visual Wulst does from its ipsilateral eye. As discussed above, because GLd contains almost no bilaterally projecting neurones, each visual Wulst receives different information from the contralateral GLd and ipsilateral GLd (and it comes from different eyes). The projections from GLd to both the ipsilateral and contralateral visual Wulst may be used to coordinate processing of information from the left and right eyes; each Wulst receives different information from the two eyes (through the ipsilateral and contralateral GLd). Alternatively, this information from the two eyes may conflict in the visual Wulst. In view of the fact that there is no difference in the number of ipsilateral GLd-Wulst projections between the left and right visual Wulst, more contralateral GLd projections may cause more conflict in the right visual Wulst. The potential exists for more conflict between information received from the left and right eyes to occur in the right Wulst than in the left Wulst (Fig. 9.1; this will be discussed later again for lateralization of pebble-floor performance).

Asymmetry of the tectofugal projections has been found in the pigeon: there are more contralateral projections from right TeO to the left Rt than from the left TeO to the right Rt (Güntürkün, 1997b). The results of the experiment reported in Chapter 6 show that there is a minor asymmetry in the chick's tectofugal projections and the direction appears to be opposite to that found in the pigeon. However, this tendency was significant only for *c/i* ratio and for the proportion of projections from the ventral tectum. Using anterograde tracing, Hellmann and Güntürkün (1996) have found that the dorsal TeO projects to the GLd and the ventral TeO projects to the Rt in the pigeon. However, results reported in Chapter 5 show that, in the chick, both the dorsal and ventral TeO project to the Rt, although there are differences between the organization of the dorsal and ventral TeO and asymmetry exists in the ventral but not in the dorsal TeO-Rt projections. Compared to the thalamofugal projections, less asymmetry in the contralateral TeO-Rt projections may be suitable for information processing for binocular vision and coordination of the left and right Rt (and ectostriata), as discussed above.

9.4 NEURAL MECHANISMS OF FUNCTIONAL LATERALIZATION

The different degrees of asymmetry in the two visual pathways of the chick (much greater in the thalamofugal pathway than the tectofugal pathway) imply that different roles may be played by the two visual pathways in functional lateralization. In Chapter 7, by localized injection of small amounts of glutamate into the various forebrain areas, it was revealed that the visual Wulst (forebrain area of the thalamofugal pathway) and the ectostriatum (forebrain area of the tectofugal pathway) contribute differentially to lateralization of pebble-floor performance and attack and copulation responses. This experiment provided direct evidence that the thalamofugal pathway, but not the tectofugal pathway, is involved in the lateralization of pebble-grain categorisation. The

involvement of the thalamofugal visual projections in the lateralization of pebble-grain performance has been inferred because it does not occur in dark-incubated chicks, which lack asymmetry of these projections (Rogers, 1996; Chapter 7). One possible explanation for the dominance of the left visual Wulst in pebble-grain categorisation is that the left Wulst has less conflict between information from the two eyes than the right visual Wulst, as discussed above. It would appear that binocular vision may not be important for pebble-grain categorisation, because the left visual Wulst receives most of its input from one eye only. This raises a question about depth perception, which would be an important aspect of pecking in the task. Information on depth could be obtained by parallax, which would be monocular (RES), or by convergence or stereopsis, which both require binocular input. If binocular visual inputs are used for depth assessment in pebble-floor performance, it could depend on processing of binocular visual inputs from the frontal visual field via the tectofugal pathway. However, since glutamate treatment of the ectostriatum had no effect, this processing cannot be essential for performance of the pebble-floor task.

The results reported in Chapter 7 have also shown that the two visual pathways are involved differentially in lateralization of copulation and attack responses. Glutamate treatment of the left visual Wulst affects both copulation and attack responses, but glutamate treatment of the left ectostriatum affects only attack. A possible reason for this result is that attack requires tracking of a moving target and thus binocular vision is necessary for the attack response (as shown in Fig. 7.2, p. 196) but this is not so for copulation (as shown in Fig. 7.3, p. 198). Therefore, the second-stage neural transmission in the tectofugal pathway may be important for controlling attack behaviour because this involves processing binocular information, although the first-stage transmission may be involved also.

Because of the complete decussation of the optic nerves and lack of the corpus callosum in the avian brain, it had been assumed that the input from each eye projects almost entirely to the contralateral forebrain and that monocular testing reveals the function of the contralateral hemisphere only. Therefore, the term 'left eye system' (LES) has usually been interpreted to mean the left eye-right hemisphere system and 'right eye system' (RES) to mean the right eye-left hemisphere system (Andrew, 1983; Mench and Andrew, 1986; Rogers et al., 1985; Zappia and Rogers, 1987; Vallortigara, 1989). However, following the findings that there are substantial projections from GLd to both the ipsilateral and contralateral visual Wulst or from TeO to both the ipsilateral and contralateral Rt in the chick and other birds (Adret and Rogers, 1989; Bischof and Niemann, 1990; Güntürkün et al., 1993; Ngo et al., 1994; Chapters 4 and 5 of this thesis), it is clear that input from each eye goes to both sides of the forebrain. The modified definitions, that LES refers to the neural structures fed by the left eye and RES refers to the neural structures fed by the right eye without reference to one or the other hemisphere (Andrew, 1988) reflect the real condition of monocular testing and the organization of the visual pathways. Whether the results of monocular testing reflect the function of the contralateral hemisphere or both hemispheres may depend on the tasks tested and which visual pathway is involved in the performance of these tasks. For example, the RES is found by monocular testing to have an advantage in the pebble-floor task and this reflects functioning of the left visual Wulst, since glutamate treatment of only the left visual Wulst impairs pebble-floor performance (Chapter 7).

It is unquestionable that functional differences exist between LES and RES (Vallortigara and Andrew, 1994; Rogers, 1996; Güntürkün, 1997a). As reviewed in Chapter 1 (p.43-51), a range of behaviours are lateralized in the chick. In this thesis lateralization of individual recognition was reported. In Experiment 1, reported in Chapter 8, the results were consistent with those of Vallortigara and Andrew (1991,

1994): the LES chicks have higher choice scores than the RES chicks. It is likely that the tectofugal visual pathway is involved in this particular behaviour because the ectostriatum is involved in individual recognition, in the pigeon at least (Watanabe, 1992; discussed in Chapter 8). Also, this form of lateralization is present in dark-incubated as well as light-exposed chicks, which may explain why this particular behaviour does not rely on light exposure causing lateralization in the thalamofugal projections. However, since there is only minor asymmetry of the tectofugal projections in the chick, the functional lateralization seen in the choice test cannot depend on asymmetry of the tectofugal pathway. According to my proposed two-stage transmission of visual information in the tectofugal pathway, if the visual processing involved in individual recognition is transmitted in the first stage, it will be transmitted only from the eye to the contralateral Rt and then the contralateral ectostriatum. If it is transmitted also in the second stage, visual information will be sent to the Rt and the ectostriatum on both sides of the brain but after a delay period. Given that there is lateralization of performance in the individual recognition task, visual lateralization could be primed via the first-stage rapid processing. If so, here binocular vision is not necessary. Although lateralization of individual recognition is not related to asymmetry of the afferent visual pathways, higher centres in the forebrain may play an important role. One of the possible forebrain areas is the IMHV, as discussed in Chapter 8 (p. 239).

Evidence discussed in this thesis has demonstrated a dissociation between the pebble-grain (food versus nonfood) categorisation and the individual (chick versus chick) discrimination and choice. Information processing for the former (food-nonfood categorisation) is associated with the thalamofugal pathway, but information processing of the latter (individual chick discrimination) may utilize the tectofugal pathway, but be located in higher centres. This form of dissociation has also been found in the pigeon.

By lesioning studies, Watanabe (1991, 1992, 1996) has found a dissociation between the individual (pigeon discrimination) and species (pigeon versus quail) or food versus nonfood discriminations in that lesions of the ectostriatum impair only discrimination between individuals and not between species or between food versus nonfood discrimination. Therefore, to fully understand the functional lateralization of LES versus RES (as well as the left hemisphere versus right hemisphere), it may be essential to analyse the relative contribution of the visual pathways to these lateralizations, as well as to consider species differences.