CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

The studies to be reported in this thesis were concerned with the detailed organization of the two visual pathways and the lateralization of the visual system in the chick. The emphasis was on investigating the structure of these visual pathways, but some aspects of visually guided behaviour were also investigated.

Birds are excellent subjects for studying the relationship between the neuroanatomy of the visual system and visually guided behaviour. Not only do they have a highly developed visual system but they also have excellent visual performance (Delius and Emmerton, 1979; Hodos, 1993). The visual system of birds consist of two visual afferent pathways: the thalamofugal pathway and the tectofugal pathway, which are considered to be homologous to the mammalian geniculocortical pathway and extrageniculocortical pathway respectively (Shimizu and Karten, 1991, 1993). This will be discussed in detail in this chapter in order to introduce the neuroanatomical studies to be reported in subsequent chapters.

To date, most knowledge of the organization of avian visual pathways comes from studies in the pigeon (reviewed by Karten, 1979; Güntürkün, 1991; Güntürkün et al., 1993; Bischof and Watanabe, 1997). It has been generally assumed that the visual systems of other avian species are organized similarly to those of the pigeon. However, it is known that the structure of the retina varies from one avian species to another (Nalbach et al., 1993). For example, the structure of the retina of the pigeon differs from that of the chick (for details see p. 7-9.; Ehrlich, 1981; Emmerton, 1983). There are also some differences in the organization of retinal projections in the pigeon and in the chick, and also in other avian species (Pettigrew, 1979; Ehrlich and Mark, 1984b; Remy and Güntürkün, 1991; also see p. 7-9). These retinal differences between the pigeon and the chick have alerted us to the possibility that there may be differences between the species in the central organization of their visual pathways.

The chick has been used extensively in studies of learning, memory formation, visual lateralization and neuronal development of the visual pathways. In contrast to the present state of knowledge about visual learning, memory and lateralization, knowledge of the organization of the visual pathways in the chick is limited. Therefore, it is important to study the organization of the chick's visual pathways in detail rather than just assuming that it is the same as the pigeon's.

Lateralization of the visual pathways will be discussed in some detail because it is an important aspect of the research to be reported in this thesis. It is known that chicks and pigeons have both functional and structural asymmetries of the visual system (Rogers, 1995, 1997; Güntürkün, 1997a,b). Studies of the chick have shown that lateralization ranges from a neurochemical level to a behavioural level. In addition to visual lateralization, birds have other forms of lateralization, including lateralized control of singing in songbirds (Nottebohm, 1977) and lateralized processes in the acquisition and retention of memory (Patterson et al., 1986; von Fersen and Güntürkün, 1990; McCabe, 1991; Clayton, 1993; Clayton and Krebs, 1994; Sandi et al., 1993; Johnston and Rogers, in press). However, only visual lateralization was investigated in this study.

1.2 ORGANIZATION OF THE AVIAN VISUAL PATHWAYS

One important feature of the avian visual system is complete decussation of the optic nerves in the optic chiasm (Cowan et al., 1961; Drenhaus and Rager, 1992). Therefore, the left optic nerve projects completely to the primary visual nuclei in the right side of the brain, and the right optic nerve projects to the primary visual nuclei in the left side of the brain (Ehrlich and Mark, 1984a and 1984b; Remy and Güntürkün, 1991). The afferents from the nucleus geniculatus lateralis pars dorsalis (GLd; originally termed the nucleus opticus principalis thalami, OPT; Karten et al., 1973) and from the optic tectum form the two main central visual pathways to visual areas in the forebrain. These pathways are called the thalamofugal pathway and the tectofugal pathway respectively (Fig. 1.1).

1.2.1 The thalamofugal visual pathway

Hirschberger (1967) noted a massive direct retinal projection to the contralateral dorsal thalamus of the owl. Karten and Nauta (1968) confirmed this finding in the burrowing owl and the pigeon and, by means of degeneration methods, first traced the projection of this dorsal thalamic complex to the Wulst in the telencephalon. Since then a series of investigations has established the general pattern of the organization of the thalamofugal pathway (Fig. 1.1).

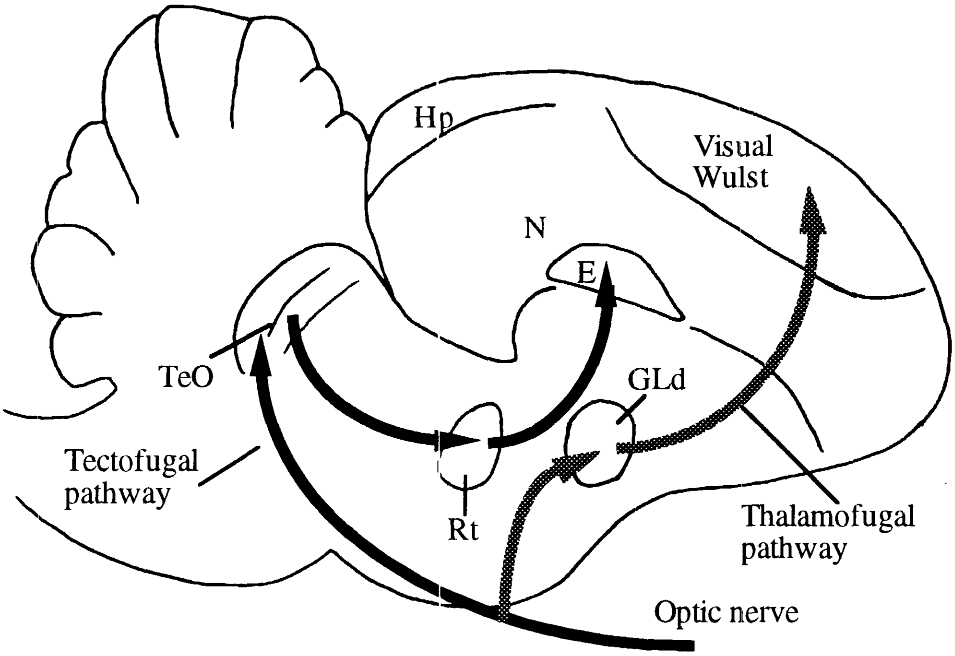

Figure 1.1 Schematic view of the thalamofugal and tectofugal pathways. Abbreviations: E, ectostriatum; GLd, n. geniculatus lateralis pars dorsalis; Hp, hippocampus; N, neostriatum; Rt, n. rotundus; TeO, tectum opticum. Note that the visual Wulst is also called the visual hyperstriatum in the chick.

1.2.1.1 Nucleus geniculatus lateralis pars dorsalis (GLd)

The dorsal thalamic complex, which receives inputs from the retina and then projects to the visual Wulst, was originally designated the nucleus opticus principalis thalami (OPT) by Karten et al. (1973). However, some researchers have referred to the same dorsal thalamic region as the nucleus dorsolateralis anterior thalami (DLA; Repérant et al., 1974; Ehrlich and Mark, 1984a, 1984b; Pateromichelakis, 1981; Miceli et al., 1990). Since recent studies have shown the equivalence of the avian thalamofugal pathway and the mammalian geniculocortical pathway (Shimizu and Karten, 1991, 1993), Güntürkün and Karten (1991) re-designated this region as the nucleus geniculatus lateralis pars dorsalis (GLd). This terminology (GLd) has been adopted by other authors (Engelage and Bischof, 1993; Güntürkün et al., 1993; Veenman et al., 1997) and will also be used in this thesis.

1.2.1.1.1. Internal organization of GLd

Although all of the studies of GLd (or OPT) have shown that this region of the thalamus is not a homogeneous nucleus but can be divided into several subnuclei, some discrepancies exist between different studies on how to delineate these subnuclei (Karten and Hodos, 1967; Hunt and Webster, 1972. Repérant, 1973; Meier et al., 1974; Miceli et al., 1979; Miceli et al., 1990; Ehrlich and Mark, 1984a). In the pigeon, for example, Miceli et al. (1990) subdivided GLd into 6 subcomponents using fluorescent tracing. Güntürkün and Karten (1991) subdivided GLd into 5 subnuclei on the basis of immunocytochemical staining. However, recently, by integrating results obtained from neuro-tract tracing, histochemical and electrophysiological studies, GLd has been divided into 6 subcomponents including four main subnuclei and two noncore subnuclei (Güntürkün et al., 1993b).

The four main subnuclei include the nucleus dorsolateralis anterior thalami pars magnocellularis (DLAmc), nucleus dorsolateralis anterior thalami pars lateralis (DLL), nucleus suprarotundus (SpRt) and nucleus lateralis dorsalis nuclei optici principalis thalami (LdOPT; Fig. 1.2). All of these nuclei are retinorecipient and project onto the visual Wulst. In the pigeon, DLL and DLAmc are the two largest subnuclei in GLd. The DLL can be further subdivided into DLL pars dorsalis (DLLd) and DLL pars ventralis (DLLv; Hunt and Webster, 1972; Repérant, 1973; Meier et al., 1974; Miceli et al., 1979; Miceli et al., 1990). The LdOPT is the smallest subnucleus and is located in the caudal-lateral part of GLd (Güntürkün et al., 1993b). The two noncore subnuclei of GLd are the nucleus lateralis anterior (LA) and the nucleus superficialis parvocellularis (SPC; Güntürkün et al., 1993). Although LA receives afferent inputs from the eye, it does not project to the visual Wulst (Bagnoli and Burkhalter, 1983; Miceli et al., 1979; Miceli et al., 1990; Güntürkün et al., 1993). By contrast, the SPC projects topographically to the visual Wulst, although it receives only a small proportion of the retinal afferents (Meier et al., 1974; Miceli et al., 1979; Miceli et al., 1990; Güntürkün et al., 1993b).

Only a few studies have been concerned with the internal organization of GLd in the chick. However, a detailed study of the termination of retinal projections by Ehrlich and Mark (1984a) has revealed that the nucleus dorsolateralis anterior thalami pars lateralis rostralis (DLAlr), DLAmc, DLL and LA are subnuclei of GLd of the chick. These researchers used autoradiographic anterograde transport and degeneration to trace the retinal projections to regions of the thalamus. All of the four subnuclei receive retinal projections (Ehrlich and Mark, 1984a). By means of retrograde tracing studies of the GLd-Wulst projections (see next section for detail), DLAlr and DLL were also identified in the GLd of the chick (Repérant and Miceli, 1974; Ehrlich and Stuchbery, 1986; Rogers and Sink, 1988). In these studies, the DLAlr was designated as the most-rostral part of GLd (Repérant and Miceli, 1974; Ehrlich and Stuchbery, 1986; Rogers and Sink, 1988). In the pigeon, also DLAlr has been identified by many authors (Repérant , 1973; Meier et al., 1974; Miceli et al., 1979; Miceli et al., 1990) but, on the basis of histocytochemical evidence, Güntürkün and Karten (1991) merged this region into the DLL and referred to

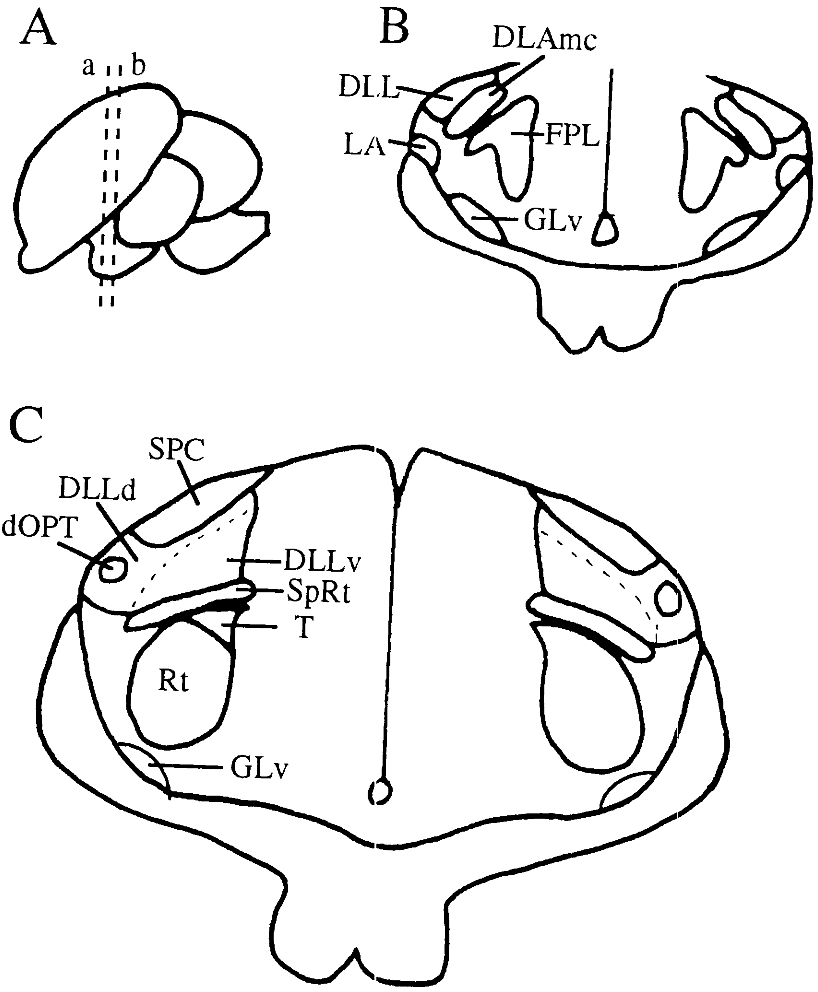

Figure 1.2 Subnuclei of the nucleus geniculatus lateralis pars dorsalis (GLd) in the pigeon.
A is a schematic drawing of the pigeon brain showing the planes of sectioning (dashed line) of the frontal sections B (sectioning at the dashed line a) and C (sectioning at the dashed line b). B and C show the various subnuclei of GLd in the thalamus of the pigeon. Abbreviations: GLv, n. geniculatus lateralis, pars ventralis; DLAmc, n. dorsalateralis anterior thalami pars magnocellularis; DLLd, n. dorsalateralis anterior thalami pars lateralis, pars dorsalis; DLLv, n. dorsalateralis anterior thalami pars lateralis, pars ventralis; LA, nucleus anterior thalami; LdOPT, n. lateralis dorsalis nuclei optici principalis thalami; Rt, n. rotundus; SPC, n. superficialis parvocellularis; SpRt, n. suprarotundus; T, n. triangularis. Based on Miceli et al. (1990) and Güntürkün et al. (1993b).

it as the rostral part of DLL in the pigeon. The DLL of the chick has been subdivided into DLLd and DLLv (Repérant et al., 1974; Ehrlich and Stuchbery, 1986; Rogers and Sink, 1988), although Ehrlich and Mark (1984a) have divided it into three zones. So far, no study has identified the subnuclei SpRt, LdOPT and SPC in the chick, although they are known to occur in the pigeon. Further neuroanatomical and histocytochemical studies are needed to see whether these subnuclei exist in the chick.

1.2.1.1.2 Retina-GLd relationship

Although, in owls, the GLd is retinotopically organized such that the temporal-nasal axis of the retina corresponds to the rostral-caudal axis of the thalamus (Pettigrew, 1979), it is different in the pigeon and chick. In the pigeon, the retina contains two distinct regions, the dorso-temporal red field and the yellow field in the rest of the retina (Güntürkün et al., 1989; Fig. 1.3). The appearance of red and yellow fields arises from the uneven distribution of coloured oil droplets. Although both the red and yellow retinal regions contain five types of oil droplets (red, orange, yellow, greenish yellow and transparent ones; Emmerton, 1983; Güntürkün et al., 1989), the red field is characterised by a high density of red and orange droplets and the yellow field by predominately yellow droplets. Both the red and yellow areas contain an area with high cellular density: the central fovea in the yellow field and the area dorsalis in the red field. The red field of the pigeon, representing the frontal (binocular) visual field, is involved in binocular vision, whereas the yellow field, representing the lateral (monocular) visual field, is involved in monocular vision (Güntürkün et al., 1989).

Remy and Güntürkün (1991) injected Fast Blue and rhodamine into GLd and found no clear topographical relation between the location of labelled neurones in the retina and the locus of GLd injections. However, they demonstrated that GLd of the pigeon receives a large number of retinal inputs from the yellow field of the retina but only extremely few projections from the red field of the retina (Remy and Güntürkün, 1991).

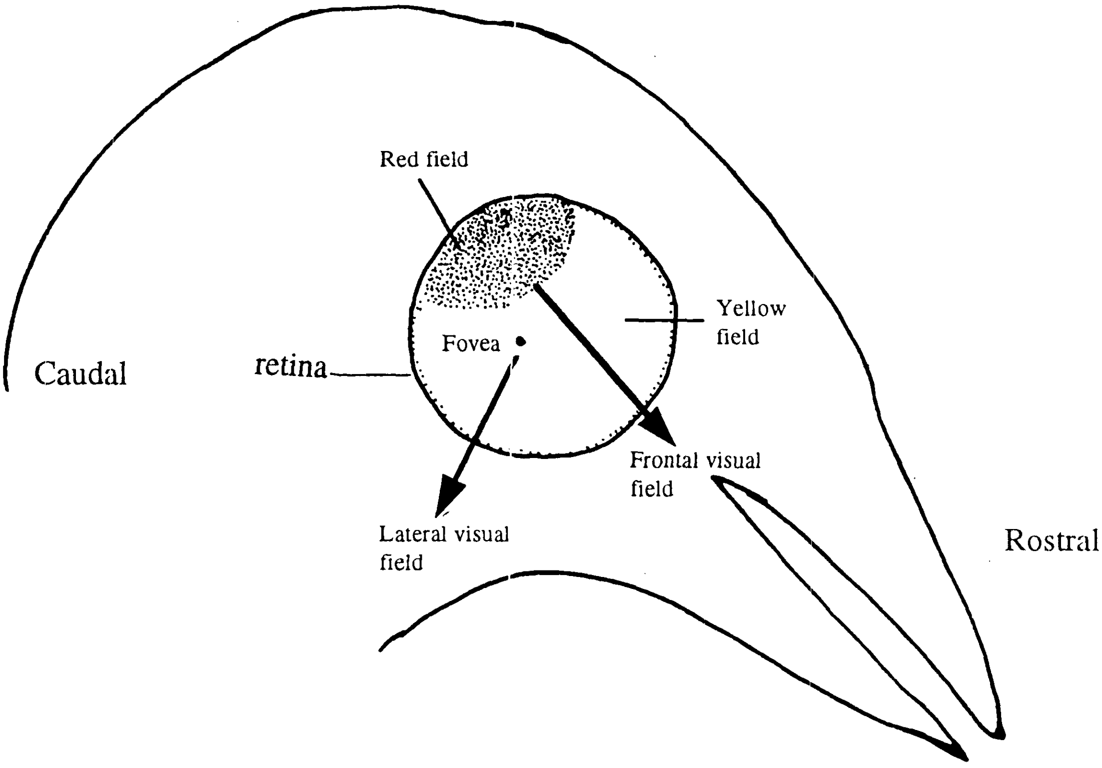

Figure 1.3 A daigrammatic view of the pigeon's retina divided into the dorsotemporal red field and the remaining yellow field. The area with dots is the red field of the retina and the rest of the retina is the yellow field. The fovea is located in the centre of the yellow field. A second area with high ganglian cell density (the area dorsalis) is located in the red field. The schematic drawing of the skull shows direction of the head. Note that the red field represents the frontal visual field and the yellow field represents the lateral visual field, as indicated by the arrows.

The result is consistent with physiological results showing, in the pigeon, that only a few (about 15%) out of a total 167 GLd neurones recorded had their receptive fields in the red field (Britten, 1987, Ph.D thesis cited by Güntürkün, 1991) and that none out of 170 Wulst neurones recorded had their receptive fields in the red field (Miceli et al., 1979). Therefore, Remy and Güntürkün (1991) suggested that GLd is mainly involved in the visual analysis of objects in the monocular, lateral field of vision (Güntürkün and Karten, 1991). In fact, it has been suggested that the thalamofugal pathway has "frontal blindness" in the pigeon (Manns and Güntürkün, 1997).

However, in the chick, the retina lacks the two subdivisions of red versus yellow field. Also, the chick has only one central region of the retina which approximates a fovea (Ehrlich, 1981). Circumscribed lesions in the retina do not reveal a precise retinotopic representation within GLd in the chick (Ehrlich and Mark, 1984b). Since all discrete lesions placed in different regions of the chick's retina cause degeneration in both GLd and the optic tectum (Ehrlich and Mark, 1984b), it seems that all areas of the retina are represented in both GLd and the optic tectum (for detail of the tectofugal pathway see p.24). This is consistent with electrophysiological studies showing that the entire visual field of the eye is represented in the visual Wulst of the chick (Wilson, 1980a; Denton, 1981). Therefore, it is possible that GLd (i.e. the thalamofugal pathway) is involved in processing visual information from both the lateral (monocular) and frontal (binocular) visual fields in the chick, whereas this does not appear to be the case in the pigeon.

1.2.1.1.3 Electrophysiology of the GLd

The receptive field properties of neurones in GLd have been studied in owls (Pettigrew, 1979), pigeons (Britto et al., 1975; Jassik-Gerschenfeld et al., 1976; Maxwell and Granda, 1979) and chicks (Pateromichelakis, 1981). All of these studies have shown that the receptive field size of GLd units is small; for example, they are an average size of 15^0 (range 3-29^0) in chicks and 16^0 in pigeons. In the chick, Pateromichelakis (1981) has classified GLd neurones into five types: (1) uniform-field general movement detectors (22% of the total units tested), which respond indiscriminately to small moving objects; (2) centre-periphery general movement detectors (22%); (3) dark object detectors (uniform-field, 29%) responding to large dark edges or other large targets; (4) directional movement detectors (8%) with directional sensitivity; (5) illumination detectors (with wide-field, 19%) responding to the 'on' or 'off' of diffuse light but not to moving stimuli.

1.2.1.2. The Visual Wulst

The Wulst is a parasagittal elevation in the rostral roof of the avian forebrain and varies in shape across species. For example, the Wulst of the owl (*Speotyto cunicularia*) is larger and more elevated than those of the pigeon and chick (Karten et al., 1973; Kuenzel and Masson, 1988). The Wulst extends from the midline to the vallecula, a shallow groove at the lateral border. Cytoarchitectonically, the Wulst is a multilayered structure with at least four layers. It contains the hyperstriatum accessorium (HA), the nucleus intercalatus of hyperstriatum accessorium (IHA), the hyperstriatum intercalatum superior (HIS) and the hyperstriatum dorsale (HD), arranged in order from dorsal to ventral regions (Karten et al., 1973; Wilson, 1980a; Fig. 1.4). According to physiological and anatomical findings, the Wulst contains two functional areas: one is a larger visual area and the other is a small somatosensory area which is located rostral to the visual area (Delius and Bennetto, 1972; Karten et al., 1973; Wilson, 1980a; Denton, 1981; Wild, 1987). In the owl (*Speotyto cunicularia*), a shallow transverse sulcus divides the large Wulst into two subdivisions: a small 'anterior Wulst' can be distinguished

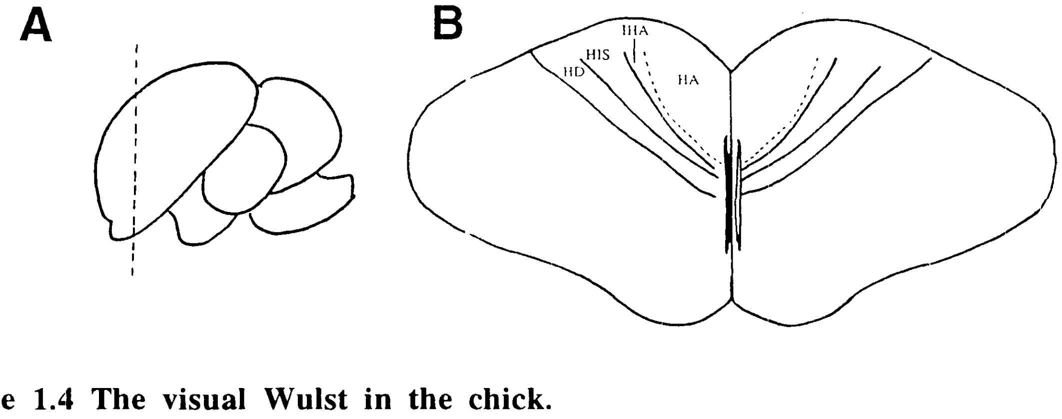

Figure 1.4 The visual Wulst in the chick.
A is schematic drawing of the pigeon brain showing the plane of sectioning (dashed line) of the frontal section B. B shows the various layers of the Wulst. Abbreviations: HA, hyperstriatum accessorium; IHA, n. intercalatus hyperstriatum accessorium; HIS. hyperstriatum intercalatus superior; HD, hyperstriatum dorsale.

clearly from the caudal larger Wulst region (Karten et al., 1973). The two subdivisions of the owl's Wulst are also distinguished from each other by cytoarchitectural and functional criteria (Karten et al., 1973; Karten et al., 1978). The anterior Wulst is the somatosensory area, whereas the posterior subdivision is referred to as 'the visual Wulst' in the owl (Karten et al., 1973; Karten et al., 1978). However, in the pigeon and chick there is no clear anatomical difference between the anterior and posterior parts of the Wulst (Karten et al., 1973; Wilson, 1980a; Deng and Wang, 1992). Although it is generally agreed that the somatosensory area is located at the rostral part of the Wulst and the visual area at the caudal part of the Wulst in the pigeon and chick (Delius and Bennetto, 1972; Karten et al., 1973; Miceli et al., 1979; Wilson, 1980a; Denton, 1981; Wild, 1987; Funke, 1989), Deng and Wang (1992, 1993) have revealed that the somatosensory area and visual area overlap partly in the Wulst of pigeons. To date, the organization of the somatosensory area in the Wulst of chicks is not known.

Originally, the term 'visual Wulst' was used to refer to the telencephalic projection area of GLd, the major recipients of GLd input being IHA and HD (Karten et al., 1973), but recently the definition of the 'visual Wulst' has been extended to all of HA, IHA, HIS and HD (Chaves et al., 1993; Güntürkün et al., 1993b; Shimizu et al., 1995) since electrophysiological studies have shown that visually-driven neurones are located in HA, IHA and HIS (in pigeon, Deng and Wang, 1992; Miceli et al., 1979; in chick, Denton, 1981; Wilson, 1980). In addition, IHA and HD receive afferents from GLd, then IHA and HIS/HD project predominantly to HA (Shimizu et al., 1995). On the other hand, the term 'visual hyperstriatum' has been used frequently to refer to the telencephalic region of the thalamofugal visual pathway in chicks with a meaning similar to the 'visual Wulst' (Boxer and Stanford, 1985; Ehrlich and Stuchbery, 1986; Rogers and Sink, 1988; Wilson, 1980a, 1980b). In this thesis, the term 'visual Wulst' will be used to refer to the visual area of HA, IHA, HIS and HD.

Electrophysiological studies have shown that the visual Wulst is retinotopically organized in the owl (Pettigrew and Konishi, 1976a, 1976b), pigeon (Perisic et al., 1971) and chick (Wilson, 1980a, 1980b; Denton, 1981). For example, in the chick, the superior-inferior axis of the visual field corresponds to the anterior-posterior Wulst (Wilson, 1980a; Denton, 1981), whereas the nasal-temporal axis is represented in a complex manner along the dorsoventral axis of the visual Wulst (Denton, 1981). In the owl, most of the visual Wulst neurones are involved in binocular visual processing and have small receptive fields (1^0; Pettigerw and Kinishi, 1976a). However, in the pigeon and chick, only a few Wulst neurones are binocular, although the Wulst receives visual inputs from both the ipsilateral and contralateral eyes (Miceli et al., 1979; Wilson, 1980b; Deng and Wang, 1993). In the pigeon the smallest receptive field is about 2^0 and the largest receptive field has been reported to be 10^0 (Revzin, 1969) or 50^0 (Miceli et al., 1979). In the chick, the receptive field sizes are in the range of 20-45^0 (Wilson, 1980b). The receptive fields are circular, oval or rectangular in shape (in the owl: Pettigrew and Konishi, 1976a, 1976b; in the pigeon: Miceli et al., 1979; in the chick: Wilson, 1980b). In the chick, there is a preponderance of visual Wulst cells (78%) which respond to moving stimuli with a clear preference for edges and bars at a particular orientation, and some of them (<10%) have selectivity for stimulus length. A few are, in addition, sensitive to the direction of movement of the stimulus (Wilson, 1980b).

1.2.1.3 The GLd-visual Wulst projections

Using degeneration methods, Karten and Nauta (1968) first traced the connections between GLd and the visual Wulst of the pigeon and owl. By lesioning of GLd, they found that the GLd projected bilaterally to the visual Wulst in the pigeon and owl (Karten and Nauta, 1968; Karten et al., 1973). Their finding was confirmed by other authors using histological techniques, including degeneration as well as anterograde and retrograde labelling, and electrophysiological methods in the pigeon (Hunt and Webster, 1972; Mihailovic et al., 1974; Miceli et al., 1990), owl (Bagnoli et al., 1990), chick (Repérant et al., 1974; Ehrlich and Stuchbery, 1986; Wilson, 1980a) and other avian species (Nixdorf and Bischof, 1982; Watanabe et al., 1983; Yamada and Sugita, 1993). The GLd-Wulst projections of the pigeon have been studied most extensively.

1.2.1.3.1 In the pigeon

The efferents from the various subnuclei of GLd, except LA, project bilaterally to each side of the visual Wulst with a predominantly ipsilateral bias (Güntürkün et al., 1993b; Fig. 1.5). There are also efferents of GLd that project via the dorsal supraoptic decussation (SODd) to the contralateral visual Wulst (Hunt and Webster, 1972; Karten et al., 1973). The SODd includes inhibitory fibres (Mihailovic et al., 1974) and excitatory cholinergic fibres (Güntürkün and Karten, 1991; Güntürkün et al., 1993b), which project from GLd to the contralateral visual Wulst. By means of double-labelling procedures, injecting the fluorescent tracers Fast Blue, Evans Yellow or Nuclear Yellow into the left or right Wulst separately, Miceli and Repérant (1982) found that there are three neuronal populations in GLd. These are ipsilaterally projecting neurones, contralaterally projecting neurones and bilaterally projecting neurones. The latter have axon collaterals which project to both the ipsilateral and contralateral Wulst. The organization can be summarised as follows (Fig. 1.5):

DLAmc: Although both cholinergic and GABAergic neurones have been found in DLAmc, only cholinergic neurones project to both the ipsilateral and contralateral Wulst (Miceli and Repérant, 1982; Güntürkün et al., 1993b). Some bilateral-projecting neurones have also been found in DLAmc (Miceli and Repérant, 1982).

DLL: Both cholinergic and cholecystokininergic neurones project to the visual Wulst (Güntürkün et al., 1993b). One major area, known as DLLv, has ipsilateral projections, whereas the dorsal portion of DLLd projects to the contralateral Wulst. One area located between these two regions projects to both the ipsilateral and contralateral visual Wulst (Mihailovic et al., 1974; Miceli et al., 1979; Miceli and Repérant, 1982). In

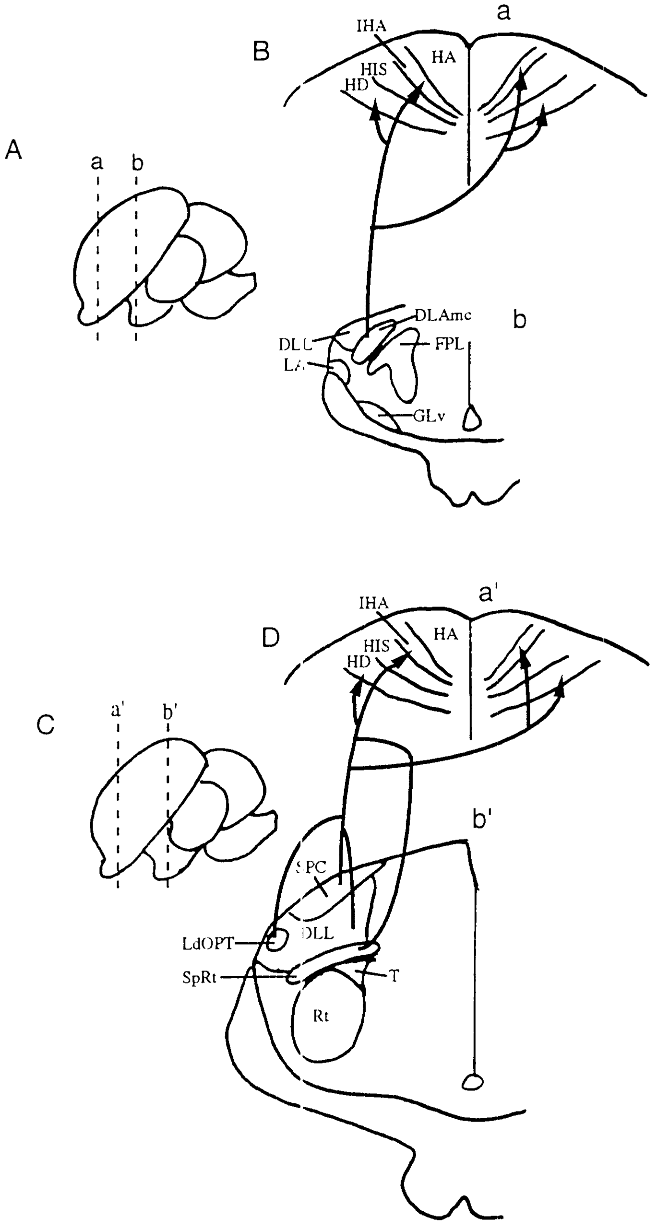

Figure 1.5 Visual projections from GLd to the visual Wulst of the pigeon. A and C are schematic drawings of the brain showing the sectioning plate (dashed line) of the frontal sections of brain shown in B (a and b) and D (a' and b'). B and D show the visual projections from various subnuclei of GLd in the thalamus to the visual Wulst in the forebrain. Abbreviations: GLd, n. geniculatus lateralis, pars dorsalis; GLv, n. geniculatus lateralis, pars ventralis; HA, hyperstriatum accessorium; IHA, n. intercalatus hyperstriatum accessorium; HIS, hyperstriatum intercalatum superior; HD, hyperstriatum dorsale; DLAmc, n. dorsalateralis anterior thalami pars magnocellularis; DLL, n. dorsolateralis anterior thalami pars lateralis; LA, nucleus anterior thalami; LdOPT, n. lateralis dorsalis nuclei optici principalis thalami; Rt, n. rotundus; SPC, n. superficialis parvocellularis; SpRt, n. suprarotundus; T, n. triangularis. Based on Güntürkün et al. (1993b).

the DLLd, 9-38% of neurones have axon collaterals projecting to both the ipsilateral and contralateral visual Wulst.

SpRt: The SpRt contains both cholecystokininergic and GABAergic neurones. Only cholecystokininergic neurones project to the ipsilateral visual Wulst (Miceli et al., 1990; Güntürkün and Karten, 1991).

LdOPT: In the LdOPT, a small population of substance P-like immunoreactive perikaryas are found. However, although it is believed that LdOPT projects to the visual Wulst (Güntürkün et al., 1993b), the organization of this projection is still unknown.

SPC: The SPC contains cholinergic, cholecystokininergic and substance P-ergic neurones (Güntürkün and Karten, 1991; Güntürkün et al., 1993b). The SPC projects to both the ipsilateral and contralateral visual Wulst. Miceli and Repérant (1982) have reported that between 18 and 46% of the total SPC neurones are bilaterally projecting neurones.

In the visual Wulst, the IHA and HD receive thalamofugal fibres from GLd and then HD project mainly to HA (Shimizu et al., 1995). The GLd-Wulst projections are organized topographically. Miceli et al. (1990) have reported that DLLv projects to the rostral area of the Wulst and DLLd projects to the intermediate region of the visual Wulst. Furthermore, the SPC projects to both intermediate and caudal Wulst, but DLAlr, DLAmc and SpRt project to all of the Wulst.

It should be noted, however, that not all researchers agree on this topographical pattern. Some authors argue that, although projections from DLL, DLAmc and SpRt are independent of each other, all of these regions are organized in the same pattern: lateral thalamus to lateral Wulst, rostral thalamus to the rostral Wulst (Güntürkün et al., 1993b).

1.2.1.3.2 In the chick

The general pattern of the GLd-Wulst projections in the chick is similar to that of the pigeon. So far the results from four studies in the chick have shown that GLd projects bilaterally to the visual Wulst, with an ipsilateral bias (Repérant et al., 1974; Ehrlich and Stuchbery, 1986; Rogers and Sink, 1988; Adret and Rogers, 1989). The efferents of DLAlr project mainly to the contralateral Wulst and only a few to the ipsilateral Wulst. The DLLd efferents are mainly contralaterally projecting neurones, whereas neurones in DLLv give rise to ipsilateral projections. In DLL, the distribution areas of the ipsilateral and contralateral projecting neurones overlap partially. However, when a Fluorogold and True Blue double-labelling procedure was used, no double labelled neurones were found in GLd (Adret and Rogers, 1989). So far, we do not know how efferents from the DLAmc, LdOPT, SPC are organized with respect to projection to the Wulst in the chick.

1.2.1.4 Neurobehavioural studies of the thalamofugal pathway

Although there have been quite extensive neurobehavioural studies of the thalamofugal pathways using adult pigeons (reviewed by Benowitz, 1980; Güntürkün, 1991), there have been only a few similar studies using other avian species (Stettener and Schultz, 1967; Benowitz and Lee-Teng, 1973). In the pigeon, lesions of the GLd or the visual Wulst cause little or no impairment of simple brightness, colour or pattern discriminations (Pritz et al., 1970; Hodos et al., 1973; Reley et al., 1988). Using assessment of a more difficult psychophysical task, lesions of the GLd (Hodos and Bonbright, 1974; Mulvanny, 1979) or the Wulst (Pasternak and Hodos, 1977) have been shown to cause minor but stable impairment of visual discrimination of intensity difference thresholds or line orientation difference thresholds. Therefore, it was once thought that the thalamofugal pathway had only a limited role in processing visual information (Hodos, 1993). Watanabe (1992,1993,1996), using an operant procedure, found that lesions of the visual Wulst did not cause deficits in visual discrimination between food and non-food stimuli in the pigeon. Also, lesions of the visual Wulst of the pigeon did not have any effects the birds' ability to discriminate between two pigeons or between a pigeon and a bird of another species.

However, Remy and Güntürkün (1991) have reported that the GLd receives very few retinal inputs from the red field which represents the frontal visual field and, furthermore, the thalamofugal pathway has been suggested to have 'frontal blindness' in the pigeon (Manns and Güntürkün, 1997; for details see p.8). It is possible, therefore, that the lack of effects from lesions of the thalamofugal pathway may have resulted from placing the stimuli in the incorrect part of the retina (using the frontal visual field instead of the lateral field). In fact, Güntürkün (1996) has reported that lesions of GLd reduce visual acuity in the lateral but not frontal visual field of the pigeon. Thus, the thalamofugal pathway may be important for visual performance in the lateral visual field of the pigeon (Güntürkün, 1996). However, the thalamofugal pathway may not be totally uninvolved with the processing of the retinal red field (i.e. the frontal visual field) because, when lesions of the thalamofugal pathway are combined with lesions of the tectofugal pathway, the effects are much greater than those of the tectofugal pathway lesions alone on visual intensity and pattern discrimination (eg. on the discrimination of a vertical bar from a horizontal bar, or a triangle with its apex upward from a triangle with its apex down, etc.; Hodos et al., 1973; Hodos and Bonbright, 1974; Reley et al., 1988) and on visual acuity performance (Hodos et al., 1984; Macko and Hodos, 1984).

Stettner and Schultz (1967) found marked deficits in pattern reversal learning (a set of three horizontal stripes versus a set of three vertical stripes) after ablation of the visual Wulst in Bobwhite quail, although there was no noticeable effect on the initial acquisition of a simple pattern discrimination. The same result has been found in chicks (Benowitz and Lee-Teng, 1973) and pigeons (Macphail, 1971, 1976; Shimizu and Hodos, 1989). Shimizu and Hodos (1989) have reported that the lesions of the nucleus intercalatus of the hyperstriatum accessorium (IHA) and of the hyperstriatum dorsale

(HD) are responsible for a reversal deficit, whereas lesions in the other laminae of the visual Wulst do not affect this type of performance (HA and HIS). On the other hand, Chaves et al. (1993) have reported that rotundal lesions, not GLd-lesions, produce extensive deficits in colour-reversal learning, but it should be noted that the nucleus rotundus, not the GLd, is involved the colour-vision processing (Pritz et al., 1970; Varela et al., 1993). In addition, marked deficits have been found in delayed matching-to-sample performance after lesioning the visual Wulst in pigeons (Pasternak, 1977). Both reversal learning and delayed matching performance involve higher information processing, as well as simple visual discrimination. Thus, it is possible that tasks requiring higher information processing may be more effective in revealing the function of the avian visual Wulst.

1.2.2 The tectofugal pathway

It has been known for some time that the majority of optic tract fibres terminate in the optic tectum (TeO; Cowan et al., 1961). Karten and his coworkers conducted a series of experiments demonstrating that the optic tectum projects to the nucleus rotundus thalami (Rt), which projects in turn on the ectostriatum (E) of the forebrain (Karten and Revzin, 1966/1967; Karten and Hodos, 1970; Benowitz and Karten, 1976; Fig. 1.6) and thus establishing the general pattern of the tectofugal pathway. This pathway provides a primary channel for sending visual information to the forebrain.

1.2.2.1 The optic tectum

The optic tectum is a highly laminated structure which has been subdivided into various layers according to cytoarchitectural criteria (Repérant, 1973; Webster, 1974). The most commonly used nomenclatures are Cajal's numerical system (Cajal, 1891,1911; cited by Repérant, 1973; Webster, 1974), which numbers the tectal laminae from 1 to 15 starting with the most external lamina, and the alphabetic system of Cowan et al. (1961). These two nomenclature systems have no major differences and both of them are

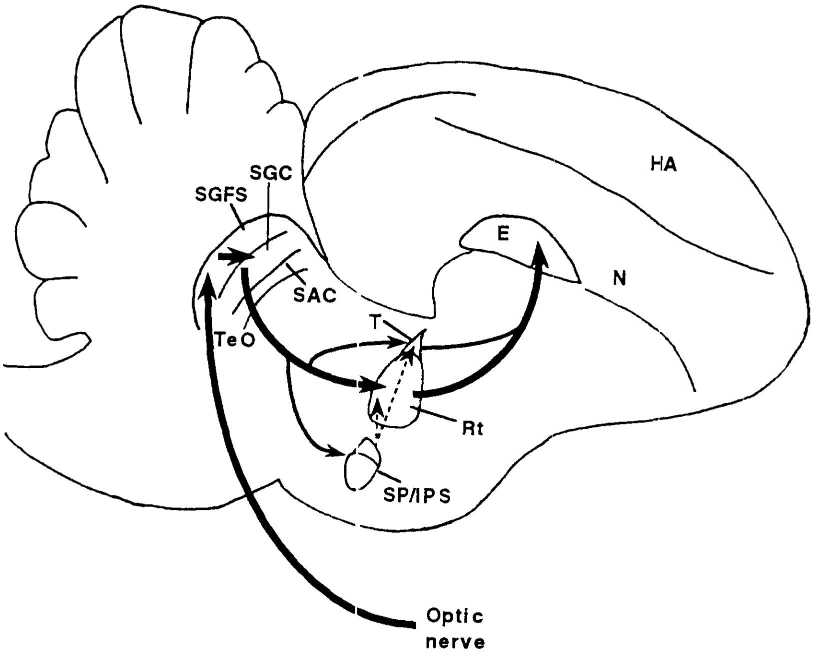

Figure 1.6 Schematic view of the tectofugal pathway showing the afferent and efferent projections of n. rotundus (Rt) and n. triangularis (T). Abbreviations: E, ectostriatum; HA, hyperstriatum accessorium; IPS, n. interstitio-pretecto-subpretectalis; N, neostriatum; SAC, stratum album centrale; SGC, stratum griseum centrale; SGFS, stratum griseum et fibrosum superficiale; SP, n. subpretectalis; TeO, tectum opticum. ----►, inhibitory projections; ——►, excitatory projections.

indicated in Fig. 1.7. The Cowan system (1961) was adapted from Jungherr's six-layer scheme for the domestic hen (1944). The Cowan scheme is now commonly used (for example, Karten and Hodos, 1967; Kuenzel and Masson, 1988) and is also used in this thesis (see Chapters 5 and 6).

In the system of Cowan et al., layer SO (stratum opticum) is the most superficial of the tectal layers and is formed primarily by the incoming axons of the retinal ganglian cells.

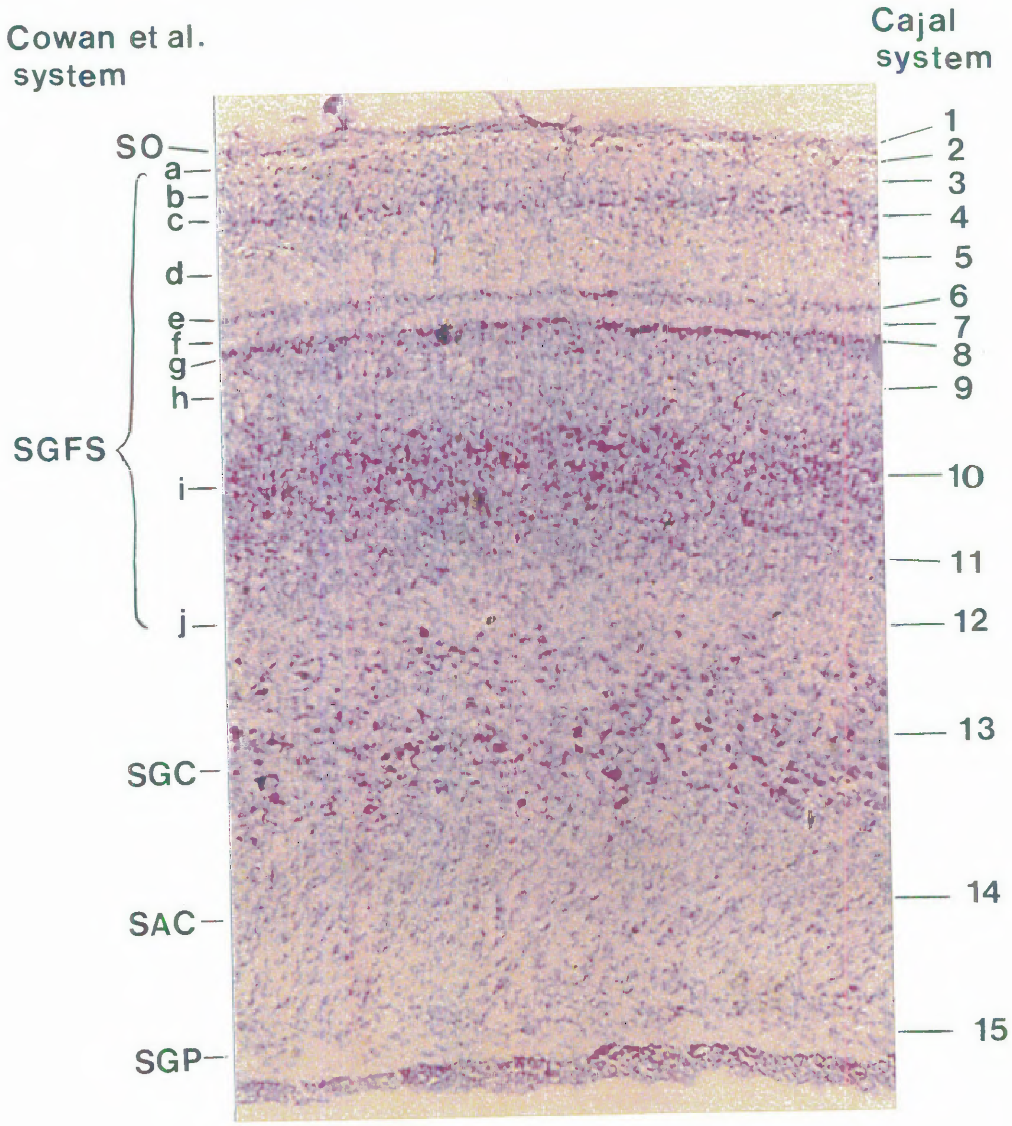

Figure 1.7 Nissl stained section of the chick tectum illustrating its laminar appearance and the tectal nomenclature of Cowan et al. (1960) and Cajal (1911).

Note: In the system of Cowan et al., layer SGFS is subdivided into 10 sublaminae named from a to j. These sublayers (a-j) are equivalent to layers 2-11 of Cajal's numerical system.

Layer SGFS (stratum griseum et fibrosum superficiale) is a heterogeneous layer with 10 readily identifiable cellular and plexiform sublayers (a-j). The optic nerve terminates in the superficial laminae a-f of SGFS (i.e. layers 2-7 of the numerical system of Cajal) with a complete retinotopic organization (Hamdi and Whitteridge, 1954; McGill et al., 1966; Crossland and Uchwat, 1979; Remy and Güntürkün, 1991). The superior half of the retina maps onto the postero-ventral part of TeO while the anterior quadrants of the retina map onto the posterior and dorsal parts (reviewed by Jassik-Gerschenfed and Hardy, 1984). This retinotopic arrangement is maintained in the deep layers of the tectum (Hamdi and Whitteridge, 1954; Bilge, 1971).

Layer SGC (stratum griseum centrale) consists of a rather homogeneous population of large multipolar neurones. These neurones are the origin of the major tectofugal visual projections, which terminate in the Rt (Karten and Revzin, 1966; Benowitz and Karten, 1976). Due to the extension of their dendrites into the superficial layers (into sublayer c of SGFS), SGC neurones are able to receive direct retinal inputs (Hunt and Künzle, 1976; Güntürkün, 1997b).

Layer SAC (stratum album centrale) is composed mainly of tectal efferent and afferent axons and a scattered population of large multipolar neurones. Layer SGP (stratum griseum periventriculare) is a cellular layer lining the tectal ventricle located in the dorsal region of the optic lobe.

For both the pigeon and chick, the neurones in both the superficial (SGFS) and deep (SGA and SAC) layers are activated optimally, and often exclusively, by visual stimuli (Jassik-Gerschenfeld and Guichard, 1972; Cotter,1976; Jassik-Gerschenfeld and Hardy, 1984). In contrast to these cells, there are bimodal neurones responding to both visual and somatic (or auditory) inputs and some nonvisual neurones responding to somatic or auditory stimulus in the deep layers of the chick (Cotter,1976). In all of the tectal layers of the pigeon, the majority of neurones (70%) are most sensitive to moving stimuli and about 30% of them are, in addition, directionally sensitive (Jassik-Gerschenfeld and Guichard, 1972). However, the tectal cells of the various layers have different receptive fields. As a rule, the size of the receptive field increases from the superficial layers (0.5-4^0 with a regular shape) to the deep layers, i.e. SGC (150-180^0 with irregular shapes). Deep cells also habituate more quickly to moving stimuli than superficial ones and show more inhibitory surround responses (reviewed by Jassik-Gerschenfeld and Hardy, 1984). In addition, some tectal neurones are responsive to a change from one colour to another (Jassik-Gerschenfeld et al., 1977).

1.2.2.2 Nucleus rotundus

The nucleus rotundus (Rt) is the largest nucleus in the avian thalamus and its mid-dorsal extension is called the nucleus triangularis (T). In the chick, the principal type of neurone in Rt is large and multiangular with thick, specially oriented dendrites (Ngo et al, 1992; Tömböl et al., 1992). These principal multiangular neurones receive terminations of the tecto-Rt fibres and they project to the ectostriatum (Ngo et al, 1992a; Watanabe et al., 1985; Tömböl et al., 1992). By retrograde tracing following the injection of HRP into the ectostriatum of the pigeon, Benowitz and Karten (1976) revealed that Rt consists of 5 subdivisions: anteromedial, dorsal anterior, medial, posterior and ventral divisions. Using the same method, Nixdorf and Bischof (1982) confirmed the finding of Benowitz and Karten in the zebra finch and further divided Rt into 7 subdivisions. However, only six subdivisions of Rt have been determined by histochemical mapping of acetylcholinestrase (AChE) activity in the chick (Martinez-de-la-Torre et al., 1990). Unfortunately, there is no consistent criterion used to define these subdivisions and it is also uncertain into how many subdivisions Rt can be divided. Furthermore, these subdivisions are difficult to detect in normal cytoarchitectonic preparations, even though T is seen as clearly distinct from Rt with Nissl staining. (This issue will be discussed in more detail in Chapter 5 of this thesis, p.140, p.161).

Many neurones in Rt (80%) have large receptive fields (140-180^0) and are sensitive to motion with directional selectivity (Revzin, 1970,1979). The Rt neurones also respond selectively to different wavelengths of light (Maxwell and Granda, 1979). Opponent colour units have been found in the Rt of pigeons (Yazulla and Granda, 1973). In fact, electrophysiological evidence has strongly suggested the existence of functional subdivisions within the Rt of the pigeon (Revzin, 1979; Wang and Frost, 1992; Wang et al., 1993). Neurones in the dorsal-posterior part of Rt respond selectively to motion in depth. The dorsal-anterior Rt contains the colour-sensitive neurones. Neurones in the anterior-central Rt respond to changing the level of illumination. The neurones in the ventral subdivision respond to looming images. The 'looming' cells respond to motion in depth and may compute 'time to collision' (Wang and Frost, 1992; Wang et al., 1993).

1.2.2.3 The ectostriatum

The ectostriatum is the telencephalic structure of the tectofugal pathway and it contains a central core and a peripheral belt region (Karten and Hodos, 1970; Watanabe et al., 1985). Recently, by mapping the endogenous cytochrome oxidase activity, Hellmann et al. (1995) have revealed that the ectostriatal core contains at least two subdivisions: (1) the medial, central and ventrolateral part of the ectostriatum with high levels of cytochrome oxidase activity; (2) the centroventral and dorsolateral ectostriatum with weak cytochrome oxidase activity.

Properties of the ectostriatal neurones are similar to those of the rotundal neurones. Their receptive fields are large, often extending over the entire visual field of the contralateral eye (Kimberly et al., 1971; Engelage and Bischof, 1996). These neurones respond to moving stimuli with directional sensitivity (Kimberly et al., 1971; Engelage and Bischof, 1996). In the zebra finch, many 'looming' neurones, responding to stimuli moving towards the eye, have also been found (Engelage and Bischof, 1996). To date, no equivalent study of the ectostriatum of the chick has been carried out. Also, although regional differences of visually evoked potentials have been shown in the ectostriatum of the zebra finch (Engelage and Bischof, 1996), so far we do not know whether the ectostriatum has functional subdivisions similar to those in Rt.

1.2.2.4 The tecto-rotundo-ectostriatal pathway

The tecto-rotundal projections arise from the deep layer SGC of the tectum; SGC receives input from the superficial layer SGFS of the tectum (Benowitz and Karten, 1976; Hunt and Künzel, 1976; Fig. 1.6). It should be noted that the tecto-Rt projections lack retinotopical organization, although retino-tectal projections are retinotopically organised (Hamdi and Whitteridge, 1954; Crossland and Uchwat, 1979; Ehrlich and Mark, 1984b; Benowitz and Karten, 1976).

In both the pigeon and chick, a point-to-point relationship between the retina and optic tectum has been shown and, in general, the superior and inferior retina project to the ventral and dorsal tectum, respectively, and the nasal and temporal retina project to the posterior and anterior tectum, respectively (Hamdi and Whitteridge, 1954; Crossland and Uchwat, 1979; Remy and Güntürkün, 1991). However, this retinotopical relationship is not maintained in the tecto-Rt projections. Using the retrograde horseradish peroxidase method, Benowitz and Karten (1976) distinguished in the pigeon four sublaminae within SGC, each projecting topographically to one of the subdivisions of the ipsilateral Rt and T in the pigeon. The cells in the superficial SGC project to the anterior subdivision of Rt, whereas deeper SGC neurones project to the medial and caudal subdivisions of Rt. The deepest sublayer of SGC projects to T in the pigeon (Benowitz and Karten, 1976). So far, no such study has been conducted using other avian species.

For many years, it was believed that most of the efferents from SGC project to the ipsilateral Rt in birds and there were only a very few, if any, contralateral projections

(Benowitz and Karten, 1976; Hunt and Künzel, 1976; Bischof and Niemann, 1990). Recently, by using more sensitive anterograde (PHA-L) and retrograde (Rhodamine B isothiocyanate, RITC) tracers, a substantial number of contralateral TeO-Rt projections has been revealed in the chick (Ngo et al., 1994), pigeon (Güntürkün et al., 1993) and zebra finch (Bischof and Niemann, 1990). In these species the efferents from the tectum cross over partially, via the supraoptic decussation, pars ventralis (SODv), and reach the contralateral Rt and T (Bischof and Niemann, 1990; Ngo et al., 1994). However, the possible topographical organization of this contralateral projection awaits examination. Recently, Hellmann and Güntürkün (1996) reported that, following injection of the anterograde tracer biotinylated dextranamine into the ventral tectum of the pigeon, the entire Rt was labelled. However, after injection of anterograde tracer into the dorsal tectum of the pigeon, only GLd, and not the Rt, was labelled. Therefore, the projections from the dorsal optic tectum to the GLd may have input to the thalamofugal projections in the pigeon.

The optic tectum projects not only to Rt and T but also to the pretectal nuclei, n. subpretectalis/n. interstitio-pretecto-subpretectalis (SP/IPS; Karten and Revzin, 1966; Hunt and Kunzel, 1976; Bischof and Niemann, 1990). Since SP/IPS, in turn, project to the ipsilateral Rt, the tecto-SP/IPS-Rt projections are an indirect tecto-rotundal route of connection (Benowitz and Karten, 1976; Fig. 1.6). Although the tecto-Rt projections are the main afferents to Rt, the SP/IPS-Rt projections may also play an important role in visual information processing by Rt. In fact, some studies have suggested that the tectum provides excitatory projections to Rt, whereas SP/IPS provide inhibitory projections to Rt (Ngo et al., 1992b; Gao et al., 1995; Mpodozis et al., 1996).

The subdivisions of Rt and T further project topographically to distinct parts of the ectostriatum core (Benowitz and Karten, 1976; Nixdorf and Bischof, 1982). In the pigeon, the anterior dorsal Rt projects to the anterior ectostriatum, the ventral subdivision of Rt to the lateral ectostriatum, the caudal Rt to the caudal ectostriatum (Benowitz and Karten, 1976). So far, no study has been carried out to investigate the possible topographical Rt-ectostriatal projections of the chick. The core of the ectostriatum in turn projects upon the peripheral belt (Karten, 1979).

1.2.2.5 Neurobehavioural studies of the tectofugal pathway

So far, the behavioural function of the tectofugal pathway has been investigated only in the pigeon. It has been repeatedly found that lesions of one or more tectofugal structures cause severe deficits in visual discrimination performance. For example, extensive tectal lesions cause a strong and intractable deficit of brightness and pattern visual discrimination (Javis, 1974; Hodos and Karten, 1974), which is more severe than that produced by lesions in the Rt and the ectostriatum (Hodos and Karten, 1966, 1970). Rotundal and ectostriatal lesions in pigeons generate similar deficits in the discrimination of simple colour, visual intensity and geometric pattern (Hodos and Karten, 1966, 1970; Reley et al., 1988; Bessette and Hodos, 1989) as well as deficits in visual acuity (Hodos et al., 1984; Macko and Hodos, 1984). These lesions also elevate the intensity-difference threshold (Hodos and Bonbright, 1974; Hodos et al., 1988; Reley et al., 1988) and line-orientation-difference threshold in pigeons (Mulvanny, 1979). Therefore, the tectofugal pathway plays a dominant role in visual discrimination. Since combined lesions of the tectofugal and thalamofugal pathways produce significantly more severe deficits in discrimination performance, particularly in spatial resolution tasks, than do lesions of the tectofugal pathway alone (Hodos et al., 1973; Hodos and Bonbright, 1974; Hodos et al., 1984; Macko and Hodos, 1984), interaction between the two pathways may be important for visual discrimination performance, particularly for more complex problems.

Recently, the effects of ectostriatal lesions on some complex cognitive function were examined in the pigeon. Watanabe (1991) found that pigeons with ectostriatal lesions could not discriminate triangles from three randomly arranged lines, but they still maintained the ability to discriminate food (grain) from non-food (such as stone, twigs, nuts etc.; this will be discussed in Chapter 7 in more detail, p.209). The pigeons were also trained to discriminate between pigeons and other avian species (conspecific discrimination), or between two pigeons (individual discrimination), or between two species of birds excluding pigeons (species discrimination; Watanabe, 1992,1994,1996). After the pigeons had reached the criterion (90% discrimination on two successive series of trials), the ectostriata of these pigeons were lesioned bilaterally. Ectostriatal lesions caused deficits in individual discrimination and species discrimination (excluding pigeons) but no deficits in discrimination of pigeons from other avian species. Therefore, although the ectostriatum is involved in higher cognitive functions, and is used in individual recognition, it has no function in distinguishing food from non-food, or conspecific birds from other avian species. To date, it is not known which forebrain areas are involved in these categorizations. Also, no similar study has been carried out in avian species other than the pigeon.

1.2.2.6 The tecto-DLP-NI/NC projections

In addition to the tecto-Rt-ectostriatum projections, a second tectofugal pathway has been found in pigeons (Gamlin and Cohen, 1986; Fig. 1.8). The connection between the optic tectum and the nucleus dorsolateralis posterior (DLP) was first revealed in pigeons by Karten and Revzin (1966). Gamlin and Cohen (1986) confirmed the existence of the tecto-DLP projections and, further, found that only the caudal region of DLP (DLPc) is a tectorecipient region. In turn, DLP projects to a subarea of the neostriatum intermedium (NI) and the neostriatum caudale (NC; Gamlin and Cohen, 1986; Wild, 1987). Güntürkün (1984) has recorded visually evoked potentials in the NC and suggested that the NC is a primary visual area.

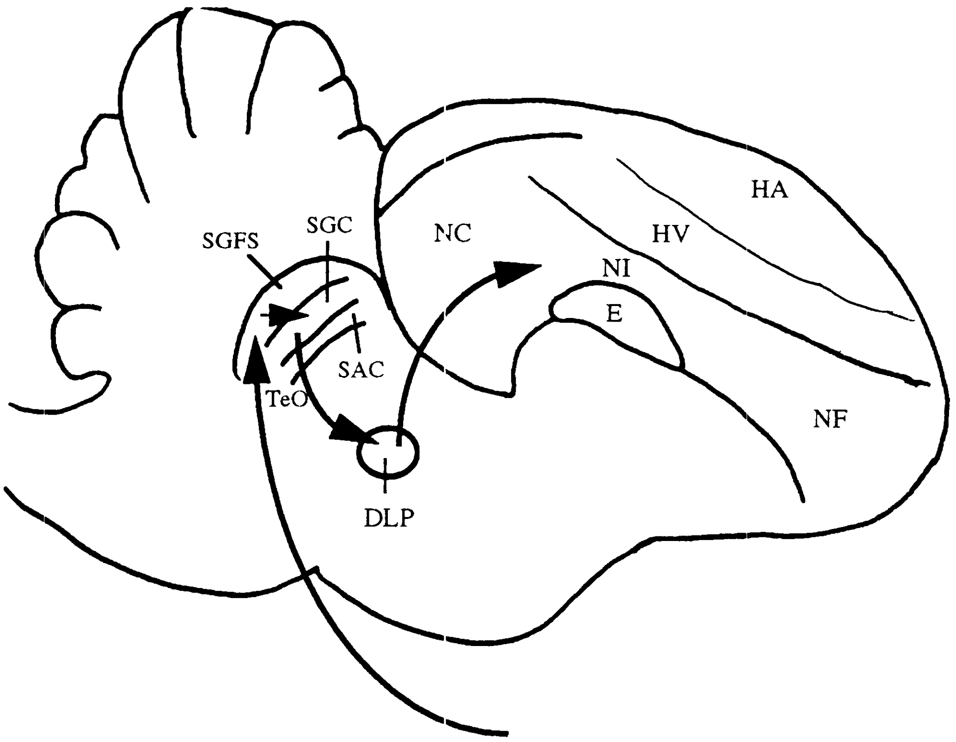

Figure 1.8 A schematic illustration of the tecto-DLP-NI/NC projections. Abbreviations: DLP, nucleus dorsolateralis posterior thalami; E, ectostriatum; HA, hyperstriatum accessorium; HV, hyperstriatum ventrale, NC, neostriatum caudale; NF, neostriatum frontale; NI, neostriatum intermedium; SAC, stratum album centrale; SGC, stratum griseum centrale; SGFS, stratum griseum et fibrosum superficiale; SP, n. subpretectalis; TeO, tectum opticum.

Neuroanatomical and electrophysiological studies have shown DLP also receives somatosensory and auditory inputs (Wild, 1987; Korzeniewska, 1987; Korzeniewska and Güntürkün, 1990; Wang and Hu, 1990). Gamlin and Cohen (1986) suggested that DLP consists of a visual caudal part (DLPc) and a somatosensory rostral part (DLPr), but more recent studies (Wild, 1987; Korzeniewska, 1987; Korzeniewska and Güntürkün, 1990) have not confirmed the functional distinction between DLPc and DLPr. Furthermore, Korzeniewska and Güntürkün (1990) have found that 29% of the DLP neurones are multimodal units and integrate visual, somatosensory and auditory inputs. Thus, the possible function of the second tectofugal pathway is to integrate information from different sensory modalities and it, therefore, provides capacity for supramodal operations (Güntürkün, 1991).

1.3 STRUCTURAL ASYMMETRY OF THE VISUAL PATHWAYS

1.3.1 Asymmetry of the thalamofugal pathway

1.3.1.1 Asymmetry of the GLd-Wulst projections

Although the thalamofugal visual pathway of the pigeon has been studied extensively (Güntürkün et al., 1993b; also see p. 3-16 for detail), asymmetry of this pathway has been investigated only in the chick (Rogers, 1996). Using horseradish peroxidase, Boxer and Stanford (1985) first reported the presence of asymmetry in the thalamofugal projections to the forebrain, there being a greater number of contralateral projections from the left thalamus to the right Wulst than conversely from the right thalamus to the left Wulst in chicks aged 8 days (Fig. 1.9). This finding has been confirmed by a series of experiments using fluorescent tracers (Fluorogold, FG and True Blue, TB; Rogers and Sink, 1988; reviewed by Rogers, 1995, 1996). In this series of experiments, after injecting FG into the visual Wulst on one side of the forebrain and TB into the visual Wulst on the other side, the GLd neurones labelled on both sides of the thalamus were counted. The ratio of the number of cells labelled contralaterally to the injection site to the number labelled in GLd ipsilateral to the injection site (c/i ratio) revealed the asymmetry. This procedure of calculating the c/i ratio was used to control for variations in the amount of the tracers injected which caused variations between the number of cells labelled both ipsilaterally and contralaterally (Rogers and Sink, 1988; Adret and Rogers, 1989). The results have shown that the c/i ratio obtained after injecting tracer into the right Wulst is significantly higher than that obtained by injecting into the left Wulst (Rogers and Sink, 1988; Adret and Rogers, 1989). The higher right c/i ratio may indicate either a higher number of contralateral

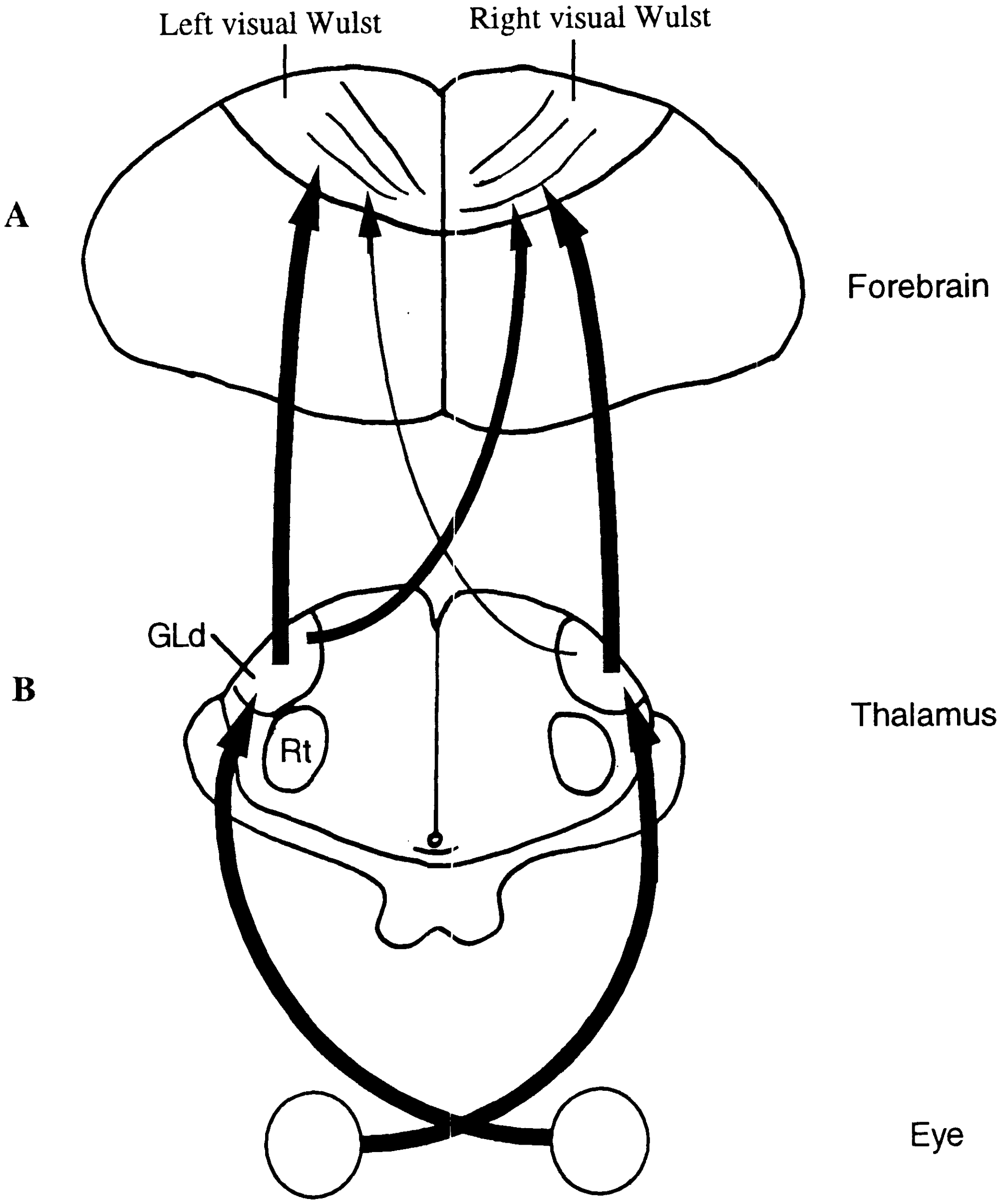

Figure 1.9 A schematic view of the asymmetrical GLd-visual Wulst projections in the chick. A and B are transverse sections of the forebrain and the thalamus respectively. More cells project from the left GLd to the right visual Wulst than vice versa. Abbreviation: GLd, n. geniculatus lateralis pars dorsalis; Rt, n. rotundus. (Redrawn from Adret and Rogers, 1989).

projections to the Wulst from the left GLd or fewer ipsilateral projections to the Wulst from the right GLd. However, it appears that it reflects the former because Box and Stanford (1985) were able to locate the asymmetry in contralateral projections (see also, Rogers and Bolden, 1991). Consistent with the right visual Wulst receiving more contralateral projections than the left Wulst, the synaptic density per unit volume is significantly higher in the right than in the left HA of 2-day-old male chicks (Stewart et al., 1992).

1.3.1.2 Effects of light exposure during embryonic development on the asymmetry in the thalamofugal visual projections

The asymmetry of the thalamofugal projections in the chick is induced by lateralized light stimulation of the right eye from day E17 to hatching on day E21 (E17 or E21, etc. referring to date of incubation, prior to hatching as opposed to poshatching; Rogers and Sink, 1988; Rogers and Bolden, 1991). For most avian species, at all stages of embryonic development, the right eye receives more visual stimulation than the left (Freeman and Vince, 1974; Rogers, 1986, 1995). This is because the embryo is oriented in the egg so that the right eye is positioned next to the shell, whereas the left eye is occluded. During the earlier stages (E3-14) of incubation, the chick embryo lies in a position with its left side and left eye against the yolk sac, and the right eye next to the membranes and shell. Therefore, the right eye may receive relatively more light input, reaching it via the shell and membranes, than the left eye. From day E14 to E17, the embryo is re-oriented so that both eyes are enveloped by the yolk sac. During the later stages of incubation (E17 to hatching on day E21), the yolk sac has shrunk and the head tilts to the left side of the body with the orientation of the embryo being such that the left eye is occluded by the body and the right eye is positioned next to the air sac. The right eye is, therefore, able to receive light input reaching it through the egg shell and membranes. The eyes alternate between open and closed frequently from day E17 but since the eyelid is transparent, the right eye receives light even when the eyelid is closed (Freeman and Vince, 1974; Rogers, 1995).

Although the right eye receives more light exposure than the left during both the earlier and later stages, the asymmetrical light input during the last few days, day E18 and E19 of incubation, is particularly important for development of brain lateralization in the chick. During this period the visual projections to the forebrain are becoming functional in the chick (Rogers, 1995). Visually evoked potentials can be detected in the optic tecta on day E17 and they mature on day E18 (Peters et al., 1958; reviewed by Rogers, 1995). Light evoked potentials can be first recorded from the forebrain on day E19 (Sedlácek, 1967). Also on day E19/20 both the ectostriatal and hyperstriatal regions of the chick forebrain have high levels of metabolic activity as indicated by the amount of uptake of 2-deoxyglucose (Rogers and Bell, 1994).

Rogers and Sink (1988) manipulated the light exposure to the left or right eye of the male chick and they were able to reverse the direction of the structural asymmetry by withdrawing the embryo's head from the egg on day E19/20 of incubation, applying a patch to the right eye and exposing the left eye to light. The eye-patch was removed at hatching, and both eyes received light after hatching. On day 2 posthatching, FG and TB were injected into the left and right visual Wulst separately. Four days later, the chicks were perfused and the GLd-Wulst projections were analysed as discussed previously (p. 29). Control chicks with the left eye occluded, which mimics the normal condition, retained the normal pattern of asymmetry in the GLd-Wulst projections. In the chicks with the right eye occluded (opposite to the normal condition) and with the left eye receiving exposure to light during the last days of incubation, the asymmetry was reversed so that there were more contralateral projections from the right GLd to the left visual Wulst than from the left GLd to the right visual Wulst. After incubated in dark conditions, chicks were found to have symmetry of the thalamofugal projections (Rogers and Bolden, 1991).

Recently, Rogers and Krebs (1996) have investigated the effects of different wavelengths of light on the development of the asymmetry of the thalamofugal projections. Red (peak transmission at 670 nm) and green (peak transmission at 500 nm) lights are as effective as broad-spectrum (white) light in establishing asymmetry in these projections. This lack of wavelength specificity for stimulating the development of asymmetry is consistent with the finding that the thalamofugal pathway is not involved in colour vision (Pritz, et al., 1970; Güntürkün, 1991). Light intensities of around only 100 lux during the sensitive period from day E19/20 to hatching are sufficient to cause the development of this asymmetry (Rogers, 1996).

The asymmetry is apparent after hatching but it is not present in the thalamofugal projections of the chick embryo following light exposure and injection of tracer on day E19/20 (Rogers et al., 1993): True Blue and either Fluorogold or Diamadino Yellow were injected into the left and right visual Wulst of embryos on day E19 and the chicks were allowed to survive for 4 days. Therefore, the development of asymmetry induced by light exposure on day E19/20 before hatching does not become apparent until day 2 posthatching.

The asymmetry in the thalamofugal projections is present in young male chicks during the first three weeks posthatching, after which it disappears (Rogers and Sink, 1988; Rogers, 1991). Female chicks also have asymmetry of the thalamofugal projections but to a lesser degree (Rajendra and Rogers, 1993). The sex differences in the asymmetry of the thalamofugal projections may reflect a role of sex hormones (Rogers, 1996). It has been shown that, after injecting testosterone or oestrogen in slow-release forms into eggs on day E16 and therefore elevating the hormone level until after hatching, no asymmetry develops even if the eggs are incubated with light exposure (Schwarz and Rogers, 1992;

Rogers and Rajendra, 1993). High levels of these hormones appear to promote growth of the GLd projections from both sides of the thalamus and therefore they mask the effects of asymmetrical light stimulation. Thus, the development of the asymmetry in the thalamofugal projections of the chick is modulated by an interaction of the hormonal level and lateralized light input (Rogers and Adret, 1993).

This structural asymmetry in the chick's thalamofugal pathway does not appear to be strain-specific, since it has been revealed in two strains of domestic chick (Boxer and Stanford, 1985; Rogers and Sink, 1988) and also a strain of feral chick (Adret and Rogers, 1989). So far, there have been no investigations of possible asymmetry in the organization of the thalamofugal visual projections in any other avian species.

1.3.2 Asymmetries of the tectofugal pathway

The structural asymmetries of the tectofugal pathway have been investigated only in the pigeon (reviewed by Rogers, 1996; Güntürkün, 1997b).

1.3.2.1 Morphological asymmetries of the optic tectum

By measuring the soma size of tectal neurones in cross-sections of the optic tectum of the pigeon, significant left-right differences have been shown (Melsbach et al., 1991; Güntürkün, 1997c). In the SGFS (layers 2-12 of Cajal's numerical system, see p.20 for detail), a retinorecipient layer of the left tectum, the cells are significantly larger than those in the SGFS of the right tectum. By contrast, the deep layers (SGC, SAC and SGP, i.e. layers 13-15 of Cajal's Numerical system) of the right tectum, particularly SGC, have larger cell bodies than those of the left tectum (Güntürkün, 1997c). In the deeper layers, cells of the right tectum also have more dendrites than those of the left tectum (Güntürkün et al., 1989). Therefore, the neurones in layers SGC, SAC and SGP of the right tectum have a larger surface area than those of the left tectum. Güntürkün (1997c) has suggested that the asymmetry of the soma size in SGC is linked to the left and right difference of tectal projections to the Rt, as described in the next section.

Since there is no sex effect on these morphological asymmetries of the tectal neurones (Güntürkün, 1997c), it seems that sex hormones may not play a role in these morphological asymmetries of the pigeon.

1.3.2.2 Asymmetry of the tecto-Rt projections

The asymmetry in the tectofugal pathway is present also in the ascending projections from the tecta to Rt on each side of the brain (Güntürkün, 1997a; Fig. 1.10). After injecting the fluorescent tracer, Rhodamine B isothiocyanate (RITC), into the left or right Rt, Güntürkün et al. (1995) counted the labelled neurones in SGC of the optic tectum on both sides of the brain. From the number of labelled neurones, a bilateral index (BI) was calculated for each animal using the formula: $BI=n_{ipsi} - n_{contra} / n_{ipsi} + n_{contra}$, where n_{ipsi} is the number of the labelled neurones in the optic tectum ipsilateral to the injection side of Rt and n_{contra} is the number of the labelled neurones contralateral to the injection side of Rt. The BI value is between +1 (completely ipsilateral) and -1(completely contralateral), with 0 representing symmetrical projections. A significant difference between the BI value for the left and right Rt was found (the mean left BI was 0.38 and the right BI was 0.61; Güntürkün, 1997b). Therefore the left Rt receives equal numbers of afferents from both the ipsilateral and contralateral tecta. The right Rt receives mainly ipsilateral tectal projections. In other words, it has been shown that the right tectum sends more contralateral projections to the left Rt than the left tectum to the right Rt (Güntürkün, 1997a; Fig. 1.10). Thus, the left Rt and ectostriatum receive visual information from both eyes equally but the right Rt and ectostriatum receive input from mainly the left eye (Fig. 1.10).

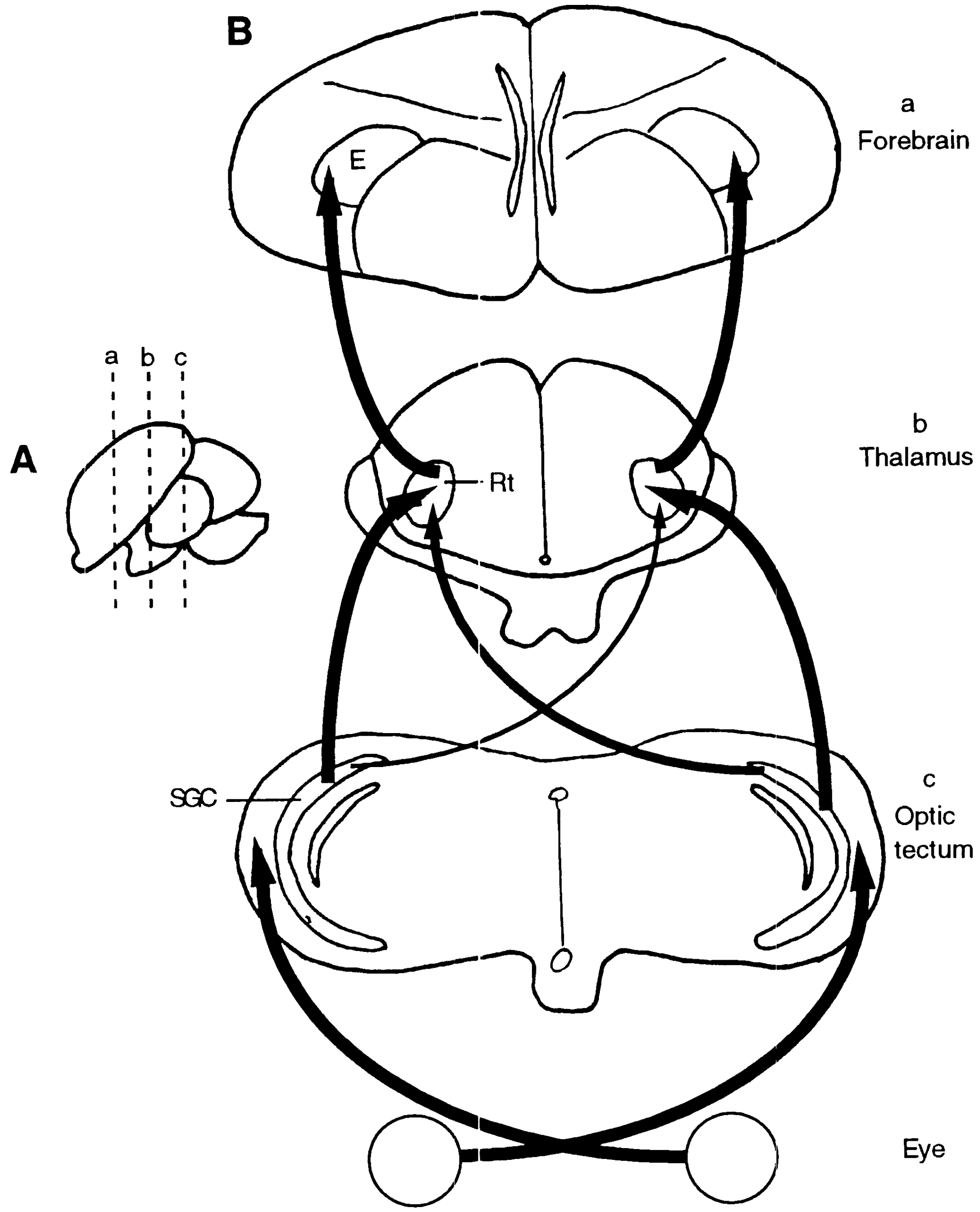

Figure 1.10 Schematic view of the asymmetrical tecto-rotundal projections in the pigeon. A is a schematic drawing of the brain showing the sectioning plates (dashed line) of the section of brain shown in B (a, b and c). B presents the visual projections from layer SGC of the optic tectum to Rt on the both sides of the thalamus. In turn, Rt projects to ipsilateral ectostriatum (E) of the forebrain. Note that there are more tectal projections from right tectum to the left Rt than vice versa. Abbreviation: SGC, stratum griseum centrale. (Based on Güntürkün, 1997a.)

The asymmetry of the tecto-Rt projections has been confirmed by recording the visual responses of the rotundal neurones to a flashing light. It was found that the left Rt has more neurones responding to the ipsilateral presentation of the flash than has the right Rt (left Rt had twice as many as right Rt), although the same number of visual responsive neurones was recorded in both the right and left Rt (Güntürkün, 1997a).

Thus, structural asymmetries exist in both the tectofugal and contralateral pathways of the birds. In view of the fact that the structural asymmetry of the thalamofugal pathway has been investigated only in the chick and the structural asymmetry of the tectofugal pathway has been investigated only in the pigeon, it is now most important that the possibility of asymmetry in the two visual pathways be examined in a single species. The research conducted for this thesis examined both visual pathways in the chick.

1.3.2.3 Effects of light exposure

As described for the chick, prior to hatching, the head of the pigeon embryo is turned so that the left eye is occluded by the body, while the right eye is close to the translucent shell and thus exposed to the light (Güntürkün, 1993). This lateralized light stimulation also affects asymmetry of the tectofugal pathway. When pigeons were incubated in the dark and thereafter reared in the nest by their parents, there were no morphological asymmetries in the retinorecipient tectal layers 2-7 (the numerical system, see p.20). When pigeons were incubated with light exposure (only the right eye receiving the light), they had the usual asymmetry in that cell body sizes in layers 2-7 of the left tectum were larger than those in the same layers of the right tectum (Güntürkün, 1993). Güntürkün (1997a,c) has suggested that neurotrophins may play a key role in the development of the morphological asymmetry of tectal neuronal size. It is possible that lateralized light stimulation of the embryo leads to a higher level of activity on the right ganglion cells of the retina of the right eye and a greater amount of neurotrophin release in the left tectum compared to the right tectum. In turn, these neurotrophins may cause enlargement of the soma size of neurones in the superficial retinorecipient layers. It should be noted that soma sizes of retinal ganglion cells are the same in both left and right retinae (Güntürkün, 1997c). Therefore, light stimulation before hatching does not affect the neurones in the retinal ganglion cell layer.

1.4 FUNCTION LATERALIZATION OF THE AVIAN BRAIN

Consistent with asymmetry of the visual pathways, functional lateralization has been found in visually guided behaviours. Visual lateralization was first discovered in the chick brain by unilateral treatment of the protein synthesis inhibitor, cycloheximide (Rogers and Anson, 1979). Since then, visual lateralization has been found in many avian species using a variety of behavioural tests (reviewed in Rogers, 1995, 1996; Güntürkün, 1997 a, b). Avian visual lateralization, therefore, has been used as a model to study the neural mechanisms of brain lateralization. A summary of the extensive literature on functional lateralization in the chick brain will follow.

1.4.1 Functional lateralization revealed by unilateral treatment of the forebrain hemispheres

1.4.1.1 Food/non-food categorization (Pebble-floor task)

By administering cycloheximide into the left, right or both hemispheres of 2-day-old chicks and testing these chicks binocularly during the second week of life posthatching, Rogers and Anson (1979) revealed that the left hemisphere is dominant for controlling a visual performance on the "pebble-floor task". This task requires the chick to find grains scattered on a background of pebbles stuck to a perspex floor. Untreated, control chicks learn to categorize food from pebbles (non-food) within 60 pecks; they peck mostly at the grain and avoid pebbles in the last 20 pecks. Unilateral cycloheximide treatment of the left hemisphere on day 2, as well as cycloheximide treatment of both hemispheres, prevents the chick from categorizing grain from pebbles and the treated chicks continue to peck at random in the last 20 pecks. By contrast, cycloheximide injection into the right hemisphere is without effect.

This effect of cycloheximide treatment is not caused directly by its inhibition of ribosomal protein synthesis, but indirectly by raising the level of glutamate and aspartate in the amino acid pools of the forebrain (Hambley and Rogers, 1979). Howard et al. (1980) injected glutamate unilaterally into the right or the left forebrain hemisphere and found that this treatment mimics the action of cycloheximide. The results showed that glutamate treatment of the left hemisphere or both hemispheres, but not the right hemisphere, impairs performance of the pebble-floor task. Thus, only the left forebrain hemisphere is involved in categorizing grain (food) from the pebbles (non-food) in the chick.

1.4.1.2. Control of attack and copulation

Unilateral injection of cycloheximide and glutamate into the brain hemispheres has also revealed marked lateralization in controlling attack and copulation behaviour in the chick (Howard et al., 1980; Rogers, 1986; Bullock and Rogers, 1986). After injecting cycloheximide or glutamate into the left or right hemisphere of the chick on day 2 posthatching, attack and copulation levels were measured in the second week of life using standard hand-thrust tests (Howard et al., 1980; the detail of hand-thrust tests based on Andrew (1966) will be described in Chapter 7, p.195). Cycloheximide and glutamate treatment of the left hemisphere elevates attack and copulation responses, similar to the effect of the testosterone treatment. However, cycloheximide and glutamate treatment of the right hemisphere is without effect (Howard et al., 1980; Zappia and Rogers, 1983; Rogers, 1986; Bullock and Rogers, 1986). Rogers (1980) suggested that the left hemisphere, or pathways associated with it, normally inhibits attack and copulation in the untreated chicks and that glutamate treatment removes this inhibition. According to this hypothesis, the right hemisphere activates attack and copulation behaviour. In fact, the role of the right hemisphere in activating attack and copulation has been confirmed by monocular testing of testosterone-treated chicks (see below, p.47).

1.4.1.3 Auditory habituation

Auditory habituation was measured by presenting a novel, banging sound to a food-deprived chick while feeding. Unilateral treatment of glutamate (25 µl of 100mM) or cycloheximide (20 µg in 25µl saline), which spread through the whole forebrain hemisphere including visual and auditory areas, revealed lateralization of auditory habituation learning in the chick (Rogers and Anson, 1979; Howard et al., 1980). Cycloheximide and glutamate treatment of the left hemisphere was found to slow auditory habituation to the same extent as bilateral treatment, whereas the same treatment of the right hemisphere was completely without effect on auditory habituation (Rogers and Anson, 1979; Howard et al., 1980).

1.4.1.4 Imprinting memory and passive avoidance learning

Functional lateralization during recall of imprinting memory has also been investigated by unilateral treatment of glutamate (Johnston and Rogers, in press). Chicks were imprinted by exposure to a stuffed hen or a box for 140 min on day 2 posthatching. Then, glutamate was injected into the right or left hemisphere 1, 3 or 6 hours after training, and recall of the imprinting memory was tested 8 hours after training (Johnston and Rogers, in press). Glutamate treatment of the right hemisphere prevented recall of imprinting memory, whereas the same treatment of the left hemisphere had no effect. Therefore, the left and right hemispheres have different roles in the formation or recall of imprinting memory as also shown by Cipolla-Neto et al. (1982).

The lateralization of memory formation of a passive avoidance learning task has also been revealed by unilateral injection of glutamate into the left or right hemisphere (Patterson et al., 1986). Chicks were trained to peck at a bead coated with methyl anthranilate (a bitter tasting substance). If the chick was able to recall the bitter taste of the bead, it would avoid pecking at a similar dry bead when it was presented 24 hours later. If the chick was injected with glutamate into the left medial hyperstriatum ventrale 5 minutes before training, it pecked at the bead. After a similar injection of glutamate into the right medial hyperstriatum ventrale, the chick avoided the bead. Therefore, glutamate treatment of the left medial hyperstriatum ventrale, but not the right medial hyperstriatum ventrale, causes amnesia. However, injection of glutamate into the right lateral neostriatum, but not the left lateral neostriatum, produces amnesia. This demonstrates that different regions of the left and right hemispheres encode memory of the task, or are involved in recall of the memory

1.4.2 Visual lateralization revealed by monocular testing

Functional lateralization can be revealed not only by unilateral treatment of the hemisphere with cycloheximide or glutamate but also by monocular testing of visually guided behaviours using temporary occlusion of one or the other eye. As reviewed above (p.2), the complete decussation at the optic nerves in the chiasm leads to retinal afferents to the contralateral optic tectum and the contralateral GLd of the thalamus only. Also, many avian species (including the chick and pigeon) have laterally placed eyes and, therefore, a narrow binocular visual field (22^0 in the pigeon, Martin, 1994; 11^0 in the chick, Jahnke, 1984). Furthermore, 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). Therefore, the neural structures linked to one eye may act as an independent unit and process different visual information from the neural structures linked to the other eye.

Andrew et al.(1982) first coined the terms 'left eye system (LES)' and 'right eye system (RES)': LES refers to the neural structures fed by the left eye and RES refers as the neural structures fed by the right eye (Andrew, 1988; Vallortigara and Andrew, 1994). This highlights the differential processing of the LES and RES. Although the main input of each eye might go to its contralateral hemisphere (as usually assumed in the monocular studies), it must be kept in mind that there are bilateral inputs from each eye to the forebrain visual regions and there is asymmetry in the organization of these projections. This aspect of the LES and RES will be considered in the Chapter 9 General Discussion (p.250).

By means of monocular testing, many functional lateralizations of LES and RES have been shown in different behavioural tasks using the chick and the pigeon (Andrew et al., 1982; Andrew and Brennan, 1983, 1985; Andrew, 1988, 1991; Vallortigara and Andrew, 1991, 1994; Rogers, 1996; Güntürkün, 1997a). Here only lateralization of performance on the pebble-floor task, social recognition and topographical information processing will be reviewed.

1.4.2.1 Function of the right eye system (RES)

1.4.2.1.1 Food/non-food categorization

Consistent with the results obtained by unilateral treatment of the hemispheres with cycloheximide or glutamate, left-hemisphere lateralization of food/non-food categorization has also been demonstrated by monocular testing of the chick. In the first or second week posthatching, with occlusion of the left eye and therefore using only the right eye, chicks categorize as rapidly as control tested binocularly (i.e., in the same number of pecks). However, with occlusion of the right eye and therefore using only the left eye, chicks are unable to categorize grain from pebbles as rapidly as chicks using either the right eye only or both eyes (Mench and Andrew, 1986; Zappia and Rogers, 1987). Furthermore, Vallortigara and Andrew (1991) have reported that RES is also used to discriminate a familiar ball (a ball with a horizontal bar on the face) from an unfamiliar ball with a large modification (a ball having no bar at all or having a horizontal white stripe around the entire circumference; this will be discussed in detail on p.46).

RES superiority for food/non-food categorization has been shown also in adult pigeons (Güntürkün and Kesch, 1987). In a grain-grit discrimination test, which is similar to the pebble-floor task, 30 grains are mixed with 1000 pebbles resembling the grains in shape, size and colour and the adult pigeons are allowed to peck at the grain/pebble mixture for 30 seconds. By calculating the number of grains consumed by the pigeons, it has been shown that pigeons using the right eye consume more grains than those using the left eye. Thus, in both the chick and pigeon, the RES is dominant for food/non-food categorization. This RES dominance has also been revealed in visual discrimination tests using artificial patterns as the stimuli (Güntürkün, 1985; Güntürkün and Kischkel, 1992).

1.4.2.1.2 Retention of visual discrimination learning

In the pigeon RES dominance has also been demonstrated for memory retention and memory recall of a discrimination task (von Fersen and Güntürkün, 1990). Von Fersen and Güntürkün (1990) trained pigeons under binocular conditions to discriminate 100 different visual patterns (positive stimuli) from 625 similar (negative) stimuli and then tested them under either binocular or monocular conditions for memory retention. Under monocular conditions, the pigeons using the right eye had significantly higher retention performance than those using the left eye. However, the pigeons using the left eye had scores only just above chance level. Similar results have been obtained in young chickens (average age of 9 days posthatching with the range of 2-22 days old; Gaston and Gaston, 1984). The chicks were trained binocularly to discriminate patterns (a positive stimulus, a cross, from a negative stimulus, a triangle) and then they were tested binocularly or monocularly for memory retention. Chicks using the right eye showed excellent retention of the discrimination, as did the binocular ones, whereas chicks using the left eye demonstrated virtually no memory recall of the task. Thus, it appears that the birds can access the circuits that learn or consolidate memory for these visual discrimination tests only through the RES.

1.4.2.2 Function of the left eye system (LES)

1.4.2.2.1 Processing of topographical information

The LES has been shown to have an advantage in processing of spatial or topographical information. This was first observed in a visual habituation task given to chicks by Andrew (1983). A novel, violet bead was introduced into the home cage of the chick from below floor level; the chick pecked at the bead but, after repeated presentations, it became habituated to the stimulus and ceased to peck at it. Once habituation had been established, the bead was introduced from above. Dishabituation occurred only when the bead was viewed in the left visual field, but not in the right visual field (Andrew, 1983; Andrew, 1988). In another experiment, the procedure was reversed so that the bead was first presented from above and then, after habituation, introduced from below. Again, the dishabituation occurred only when the chick used the left eye. Thus, only the LES responds to a change in spatial cues.

Rashid and Andrew (1989) later confirmed that only the LES is able to use topographical features for orientation. They trained chicks to find food buried under sawdust at a particular spot within a large tray. The chicks could use either proximal cues (coloured patterns marked on the walls of the tray or two small bottles between and beyond the areas where the food was hidden) or distal visual cues (features on the floor and walls of the laboratory external to the tray) to locate the buried food. The chicks were tested monocularly without food being buried and the relation of the two sorts of visual cues was either kept the same as in training or was separated by rotating the tray through 180^0. The chicks were tested from day 7 to day 14 posthatching. From day 9 posthatching, chicks using the left eye used an efficient search strategy in that they concentrated search in the two areas indicated by either the proximal or the distal cues. Chicks using the right eye searched at random over the entire tray. Therefore, the LES is better in guiding orientation than the RES. However, on day 8, chicks using the RES are able to search in the expected location of the food although they attended only to the distal cues and not to the proximal cues.

1.4.2.2.2 Individual social recognition

The LES of the chick is also more capable of recognition of conspecific individuals (Vallortigara and Andrew, 1991,1994; Vallortigara, 1992). Vallortigara and Andrew (1991) tested 3-day-old chicks in a task in which they were given a choice between a familiar and an unfamiliar companion. They were tested either binocularly or monocularly. The apparatus was a runway with a familiar companion (cagemate) and an unfamiliar chick placed in small compartments at either end of the runway. The tested chick was placed in the centre of the runway. During a 6 minute test period, the time spent in each third of the runway (two ends and one centre) was scored. Male and female chicks, tested binocularly, made different choices: males chose to stay with the unfamiliar stimulus and females chose to stay with the cagemate. The chicks tested using the LES also made clear choices, the same as the binocular chicks. However, when tested using the RES, chicks made no clear choice, staying equal time with the cagemate and the stranger. Therefore, chicks using the LES recognise conspecific individuals, whereas those using the RES do not.

Experiments using an artificial model partner confirmed these findings (Vallortigara and Andrew, 1991). After being reared with a model partner (a red table-tennis ball with a horizontal white bar on one face) for the first two days after hatching, male chicks were given, on day 3 posthatching, a runway choice test between the familiar model and an unfamiliar ball with the white bar rotated by 45^0 or 90^0. The male chicks tested using the LES chose the familiar ball but avoided the unfamiliar object with a rotation of the bar to vertical. If the unfamiliar ball had only a small transformation (a ball with an oblique bar at 45^0), the LES chick chose the novel ball. Thus, when using the LES the chick is able to detect even minor differences between familiar and unfamiliar stimuli. When the chicks were tested using the RES, they chose at random between the familiar ball and the ball with an oblique bar at 45^0 or one with a vertical bar. The RES chicks chose the familiar ball only when required to choose between it and a ball with no bar at all or with a horizontal white stripe around the entire circumference. Thus, using the RES, the chick responds only to large changes, which would indicate a change in a category rather than a detail. This result is consistent with those of the pebble-floor task in that the RES categorizes food from non-food (Mench and Andrew, 1986; Zappia and Rogers, 1987).

The advantage of the LES for recognition of individuals has also been shown in a social pecking test (Vallortigara, 1992). After being reared in pairs for two days, chicks were tested on day 3 by combining two cagemate pairs, each pair unfamiliar with the other pair, and all four chicks being tested either binocularly or monocularly. The number of pecks towards the cagemate and two strangers was recorded for each chick and social recognition was measured in terms of pecks at the cagemate versus those at the strangers. When tested binocularly or using the LES, the chicks treated the cagemate and strangers differently, pecking more at strangers. However, when using the RES, the chicks treated the cagemate and strangers similarly and pecked at the familiar and the unfamiliar chicks at random. Again, only the left eye system is involved in individual recognition.

In summary, functional lateralization of the two eye systems has been established. The RES is specialised to attend to selected properties of a stimulus and then to assign the stimulus to a category, e.g, categorizing food from non-food, or chicks from non-chicks. The LES responds to the detailed properties of the stimulus, an ability which is crucial for recognition of individuals (Vallortigara and Andrew, 1991, 1994). The LES is also specialised for processing spatial and topographical information (Rashid and Andrew, 1989; Andrew, 1991).

1.4.2.3 Attack and copulation

Laterality for controlling attack and copulation can be demonstrated not only by unilateral injection of cycloheximide or glutamate (see p.39) but also by monocular testing. Rogers et al. (1985) tested copulation responses of testosterone-treated chicks. The chicks were tested monocularly using the standard hand-thrust tests. When chicks were tested using the LES, they displayed high levels of copulation, as expected following the testosterone treatment (Andrew, 1966). When the chicks were tested monocularly using the RES, they performed at the lower levels of copulation characteristic of untreated controls. Similar results have also been obtained for attack behaviour (Bradshaw and Rogers, 1992; Rogers, 1995). Taking into account the results from both monocular tests as summarized above, and from unilateral treatment of cycloheximide or glutamate showing that injection of glutamate into only the left hemisphere (received mainly from the right eye) elevated copulation and attack responses, it is possible that the LES (right hemisphere) activates attack and copulation and the RES (left hemisphere) suppresses these behaviours (Bradshaw and Rogers, 1992; Rogers, 1995).

1.4.3. Lateralized eye use

Visual lateralization can also be revealed by recording lateralized eye use in chicks tested binocularly. Chicks have been reported to view different stimuli with preferential use of one eye and preferential eye-use shifts from one eye to the other depending on the stimulus being viewed and the age of the chick (Andrew, 1991; Andrew and Dharmaretnam, 1993; Dhamaretnam and Andrew, 1994). For example, chicks use the right eye to view a hen or human on day 8, but the left eye to look at the same stimuli on day 10 and 11 (Andrew and Dharmaretnam, 1993; Dhamaretnam and Andrew, 1994; Workman and Andrew, 1989). The right eye is also used preferentially by a testosterone-treated chick when it circles a model during courtship (Workman and Andrew, 1986).

Lateral asymmetries have been observed in the responses of chicks to novel-coloured objects (Regolin and Vallortigara, 1996). Using food reinforcement, chicks were trained to peck on a small coloured (red or green) box. During testing, the chicks were presented with a familiar (training) and an unfamiliar (different colour) box. The position of the two boxes (on the left or right side) was changed at random. The chick pecked more frequently at the novel box when it was placed on the right side than on the left side. This lateral asymmetry is also age-dependent, with a maximum lateral bias occurring at day 4 and day 11.

Lateralized eye use by binocular chicks has also been determined in visual discrimination tasks. Vallortigara (1989) trained two-week-old chicks in a colour discrimination task using food reinforcement. The chicks performed better when the reinforced coloured disc was placed on the right side with respect to the chick's body than when it was placed on the left. This result is consistent with right eye specialisation for using object features for categorizing stimuli, as discussed previously. Lateralization of position learning was also shown by training young chicks to locate a food source using positional cues (Vallortigara et al., 1988). In this test, the positive box (food reward) was placed against the wall facing the entrance of the test cage, whereas the negative box was placed either on the right or the left side against the wall. Male chicks learned better when the negative box was placed on the left wall.

Recently, by video analysis of the chicks' behaviour during the same learning task using colour or spatial cues, Vallortigara et al. (1996) have determined the eye preferences used to view the stimuli. Using a spatial cue, chicks learned better when the positive box was placed on the left side, which was associated with turning the head to the right to allow lateral viewing by the left eye. Using a colour (object feature) cue, chicks learned better when the positive stimulus was placed on its right side, a strategy which was associated with turning the head to the left to allow lateral viewing by the right eye. Thus, the visual lateralization observed in binocular chicks during simultaneous visual discrimination learning is consistent with the finding that the left eye system attends to the spatial components of stimuli, whereas the right eye system uses object features to assign stimuli to categories (Vallortigara and Andrew, 1994).

1.4.4 Effect of light on functional lateralization

The effect of light exposure of the embryo on the functional lateralization of the grain/pebble categorization (pebble-floor) task and also attack and copulation has been investigated in the chick (Rogers, 1995, 1996). Chicks hatched from eggs incubated in darkness during the last stages of incubation lack visual lateralization for these behaviours at the population level in that there is no difference between the group of chicks given glutamate treatment in the left hemisphere and those given glutamate treatment in the right hemisphere (Rogers, 1982; Zappia and Rogers, 1983; Rogers and Krebs, 1996). However, as little as 2 hours of light exposure on day E19/20 of incubation is sufficient to establish these particular visual lateralizations (Rogers, 1982).

Consistent with the effect of light exposure of the embryo on the structural asymmetry of the thalamofugal pathway of the chick, the direction of functional lateralization for the above behaviours is reversed by manipulating the light exposure prior to hatching (Rogers, 1990). By withdrawing the embryo's head from the egg on day E19/20 of incubation, an eye-patch could be applied on the left or right eye. When the left eye was occluded by the eye-patch, mimicking the natural condition, the same direction of lateralization for pebble-floor performance, attack and copulation was shown as in chicks hatched from un-operated eggs exposed to light before hatching. Glutamate treatment of the left hemisphere on day 2 posthatching prevented or retarded categorization of pebbles from grains and elevated attack and copulation, whereas treatment of the right hemisphere had no effect. In contrast, when the right eye of the embryo was occluded by the eye-patch, leaving the left eye exposed to light (the reverse of the natural condition), the direction of functional lateralization was reversed. Glutamate treatment of the right hemisphere impaired pebble-floor performance and elevated attack and copulation, but treatment of the left hemisphere had no effect. This experiment provides clear evidence for the role of light in determining the direction of particular forms of functional lateralization in the chick brain.

However, not all forms of functional lateralization in the chick are dependent on light exposure during the last stages of incubation. Recently, Andrew et al. (in preparation) have found that LES and RES differences of choice between a familiar and an unfamiliar ball (with a vertical bar) independent of light exposure before hatching. Eggs were incubated in the dark or under light from day 17 to hatching. After hatching, the chicks were reared with a red ball (with a horizontal bar) and they were given a choice test between the familiar ball and an unfamiliar ball (with a vertical bar) on days 3, 4 and 5. The lateralization of the choice was clear in chicks hatched from eggs incubated in the dark on days 3 and 4. Choice was made by the LES dark-incubated chicks but not by their RES counterparts. In this case, it appeared that light exposure reduced the LES/RES difference.

The period of sensitivity to light has been investigated also by means of both unilateral glutamate treatment (Rogers, 1990) and monocular testing (Rogers, 1997). A similar procedure of manipulating light exposure and glutamate treatment (described in the last paragraph) has been performed posthatching on chicks hatched from eggs incubated in darkness (Rogers, 1990). After hatching the chicks were kept undisturbed in darkness until early on the first day and at this time the right eye was occluded and the left eye was exposed to light for 24 hours. Then, unilateral treatment of the hemispheres with glutamate on day 2 demonstrated that the direction of lateralization for the controlling of attack and copulation was reversed but not that for lateralization of performance of the pebble-floor task. When the monocular exposure to light was performed on day 3 posthatching after the chicks had been kept in darkness, there was no longer a difference between the attack and copulation scores of chicks injected with glutamate in the left or right hemisphere. Therefore, for the lateralization of control of attack and copulation, the sensitive period for the effect of light exposure extends to day 1 but it has ended by day 3 posthatching (Rogers, 1990, 1991). Given that monocular occlusion on either day 1 or day 3 posthatching has no effect on the normal direction of functional lateralization on pebble-floor performance, the sensitive period for the effect of light exposure on pebble-floor performance is over by day 1 posthatching (Rogers, 1990, 1991).

Recently, Rogers (1997) confirmed this finding by manipulating light exposure before and after hatching in combination with monocular testing. If the eggs were exposed to light for 24 hours on day E17 of incubation and, after hatching, the right eye of these chicks was occluded by an eye patch for 24 hours on day 1, the chicks using the RES performed better than those using the LES on the pebble-floor task. Therefore, occlusion of the right eye on day 1 posthatching did not reverse the direction of lateralization. If the chicks were hatched from eggs incubated in the dark and their right eye was occluded (left eye exposed to light) for 24 hours on day 1 posthatching, they did not show any functional lateralization of pebble-floor performance (i.e., they performed the same as normal chicks incubated in the dark exposed to light at hatching). These results confirm that the sensitive period ends on day 1 posthatching.

In the pigeon, also, light stimulation prior to hatching is essential for establishing the visual lateralization for grain-grit discrimination in adulthood (Güntürkün, 1993). Pigeons hatched from eggs incubated in darkness have no difference between the left and right eyes in performance of this task, whereas pigeons hatched from eggs which have been exposed to light (196 lux) throughout the incubation period have better performance with the RES than the LES. Because the pigeon is an altricial species whereas the chick is precocial, the sensitive period to light may extend posthatching. In fact, recently, Manns and Güntürkün (1996) have found that visual lateralization in the pigeon can be reversed by occluding the right eye of the pigeon for 10 days beginning on either day 1 or day 7 posthatching. After occluding the right eye and exposing the left eye to light during early life posthatching, pigeons using the left eye perform better in the grit-grain discrimination task than those using the right eye. However, occlusion of the left eye over the same period of development enhanced the usual right eye advantage on this task. Reversal of functional lateralization is correlated with reversal of the morphological asymmetries in the optic tectum. After right eye occlusion, the soma sizes of the neurones in layers 2-7 of the right tectum are larger than those in the left tectum (Manns and Güntürkün, 1996).

1.5 An Overview of this Thesis

As discussed, although basic knowledge of the visual pathways in the chick has been established during the last two decades, the detailed pattern of the organization of these pathways is still unclear (Güntürkün, 1991). This is particularly true for the bilateral projections from GLd to the Wulst and from the optic tectum to Rt. The primary aim of this thesis is to investigate the organization of the two visual pathways in the chick and their contributions to lateralization of visual function. To perform this research it was first necessary to establish the sensitivity of various retrograde tracers (rhodamine B isothiocyanate, RITC, Fluorogold, FG, and True Blue, TB) for the two sets of projections in the chick (Chapter 3). By double-labelling procedures, the first detailed study of the organization of the bilateral GLd-visual Wulst (Chapter 4) and the bilateral tecto-Rt (Chapter 5) projections in the chick was carried out.

There has been no previous research of lateralization of the tecto-Rt projections in the chick. Given the differences in organization of the visual systems of the chick and pigeon, as has been discussed, it was considered to be important to investigate asymmetry of both visual pathways within the one species. Therefore, the relatively new and more sensitive tracer, RITC, was used to investigate the structural asymmetry of both the GLd-visual Wulst in the chick (Chapter 4). It was then used to see whether there is asymmetry in the tecto-Rt (Chapter 6) projections of the chick.

Because it has been shown that the asymmetry of the thalamofugal projections in the chick, and also asymmetry in the size of tectal neurones in the pigeon, are induced by unilateral light exposure before hatching, it was important to investigate whether light exposure during incubation also plays a role in the development of the tectofugal projections in the chick (Chapter 6).

Behavioural studies of lateralization were also conducted. By localized injection of glutamate into the left or right forebrain visual areas, it was possible to investigate the relevant contributions of the two visual pathways to functional lateralization on certain visual tasks (Chapter 7). Monocular testing was used to investigate the LES/RES differences in social recognition between familiar versus unfamiliar chicks. Although many forms of functional lateralization are induced by unilateral light exposure before hatching, not all of forms of lateralization are dependent on light exposure of the embryo. Therefore, the effect of light exposure on lateralized social recognition was investigated (Chapter 8).