S21-2   Relative contributions of the two visual pathways to avian behavior

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Abstract   Birds have two main visual pathways to the telencephalon: the thalamofugal and tectofugal pathways. In the thalamofugal pathway in the chicken (*Gallus gallus*), neurons on each side of the thalamus receive visual afferents from the contralateral retina and project to either the ipsilateral or contralateral Wulst of the telencephalon. These projections are organized asymmetrically: there are more contralateral projections from the left thalamus to the right Wulst than vice versa. This organization is consistent with lateralized visual processing in the Wulst. Since the visual Wulst has reciprocal connections with many telencephalic regions, we suggest that the Wulst is not simply a primary visual area, but also an integration area of the telencephalon. In the tectofugal pathway, each optic tectum (TeO) receives contralateral retinal afferents and then projects to the n. rotundus (Rt) of the thalamus, and, in turn, Rt projects to the ectostriatum in the telencephalon. Contrary to earlier assumptions that TeO projects to only the ipsilateral Rt (via large, myelinated axons), it has now been found that many TeO neurons project bilaterally via small, unmyelinated axon collaterals to the Rt on both sides of the thalamus. Thus, there are two stages of visual transmission in the tectofugal pathway: the first involves rapid transmission to the ipsilateral Rt only and the second involves delayed transmission to both the ipsilateral and contralateral Rt. The significance of these two stages of visual transmission in controlling behaviors is discussed, as well as the differential roles of the two visual pathways in reversal learning and other behavioral controls.

Key words   Thalamofugal pathway, Tectofugal pathway, Visual behavior, Lateralization

1   Introduction

Birds have two main visual pathways, the thalamofugal and tectofugal, which send visual information to the forebrain (Fig. 1). The telencephalic area of the thalamofugal pathway is the visual Wulst, which receives visual input via the nucleus geniculatus lateralis pars dorsalis (GLd) of the thalamus (Deng and Rogers, 1998a). The telencephalic area of the tectofugal pathway, the ectostriatum (E), receives afferents from the nucleus rotundus (Rt) on each side of the thalamus; Rt receives visual inputs via the optic tecta (TeO) (Deng and Rogers, 1998b). Over the past three decades, a great deal of effort has been put into working out how the two pathways are organized and what roles they play in controlling various visually guided behaviors.

Although it is now clear that the tectofugal pathway plays a fundamental role in visual information processing, particularly in birds with pareally-positioned eyes, the function of the thalamofugal pathway and its role in visually guided behavior are still obscure. Here it should also be kept it in mind that, until recently, knowledge of the function of the avian visual pathways has been based largely on investigations of one species, the pigeon, and that that knowledge has been used to explain the visual behavior of other species. Our recent studies have found, however, some clear differences in the organization of visual pathways between the chicken and pigeon (Deng and Rogers, 1998a,

b; Rogers and Deng, 1999). In this paper, I examine the functional organization of visual pathways in the chicken and their role in visual behavior, and then compare them to those in other species of birds.

2   Visual transmission in thalamofugal and tectofugal pathways in the chicken

One important feature of the avian visual system is the complete decussation of optic nerves in the optic chiasm. Therefore, the optic nerves from one eye project completely to the TeO of the tectofugal pathway and the GLd of the thalamofugal pathway on the other side of brain. Although it has long been known that the GLd sends its efferents to both the ipsilateral and contralateral visual Wulst, the TeO has only recently been found to project substantially to the contralateral as well as ipsilateral Rt in the thalamus (Deng and Rogers, 1998a,b). Thus there are bilateral projections in both pathways: the bilateral GLd-Wulst and TeO-Rt projections. Because information from left and right eyes can only be superimposed on the same neural structure by bilateral projections, such an arrangement is essential for binocular processing and intraocular interaction of information. I have now examined the organization of the bilateral projections in the two pathways of the chicken using double labelling methods.

I injected the fluorescent tracer fluorogold into the

visual Wulst or Rt on the one side of brain and rhodamine B isothiocyanate into the other and then examined the labeled neurons by fluorescent microscopy. This showed that the organization of the projections in the thalamofugal pathway is different from that of the tectofugal pathway (Deng and Rogers, 1998b). In the thalamofugal pathway, there are very few bilaterally projecting neurons, which means that GLd neurons project solely to either the ipsilateral or the contralateral visual Wulst and suggests that different kinds of visual information are transmitted by each projection to the Wulst (i.e., transmitted through separate channels). The GLd-Wulst projections are also organized asymmetrically: there are more contralateral projections from the left thalamus to the right Wulst than vice versa (Rogers and Deng, 1999). Given the presence of these asymmetries, the organization of the thalamofugal pathway should enable the left and right Wulst to process different visual information simultaneously. In fact, functional lateralization has been found in the Wulst of chickens (Deng and Rogers, 1997).

It is also possible that, even though the visual Wulst of the chicken receives visual inputs from the frontal visual field, it is not involved in binocular vision because different visual information is transmitted to each Wulst. Even so, it should be noted that in owls and other birds with frontally-oriented eyes, the thalamofugal pathway is involved

in binocular vision, including stereoscopic depth perception (Nieder and Wagner, 2000).

In contrast to the GLd-Wulst projections, there are many bilaterally projecting neurons (up to 45%) in the TeO which, via their collateral branches of axons, project simultaneously to both the ipsilateral and contralateral Rt. Therefore, after receiving inputs from the contralateral eye, the tectal neurons could send the same information to both the ipsilateral and contralateral Rt via these bilaterally projecting neurons and then to the ectostriatum (E) in each hemisphere. It has been shown that the TeO neurons projecting to the ipsilateral Rt have large, myelinated axons, whereas those projecting bilaterally to both the left and right Rt, and neurons projecting only to the contralateral Rt, have small, unmyelinated axons (Saleh and Ehrlich, 1984). Based on this organization, it has been proposed that visual transmission in the tectofugal pathway of chickens is two-staged. In the first, visual information is transmitted rapidly from each eye to the contralateral hemisphere, and the second transmission is delayed, the information being transmitted slowly to both hemispheres.

It is possible that rapid neural transmission may be used for detecting the stimulus and priming the neuronal activities of the relevant forebrain areas. Then the delayed neural transmission that follows may be used for further
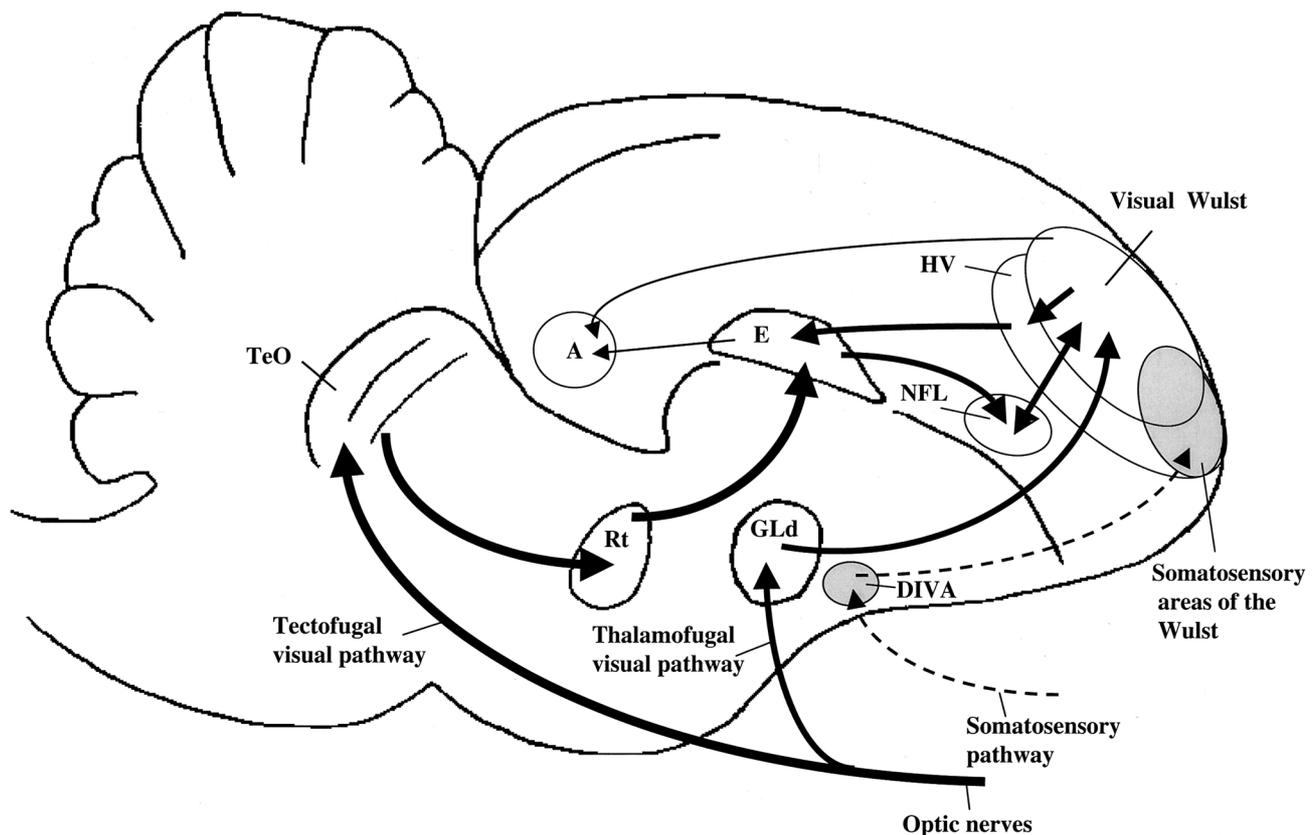
Fig. 1 Schematic view of the two visual pathways and the intratelencephalic connections between them
Note: in the Wulst, the visual area is overlapped with the somatosensory area. Abbreviations: A, archistriatum; E, ectostriatum; DIVA, n. dorsalis intermedius ventralis anterior; HV, hyperstriatum ventrale; NFL, neostriatum frontale, pars lateralis; GLd, n. geniculatus lateralis pars dorsalis; N, neostriatum; Rt, n. rotundus; TeO, tectum opticum.

binocular information processing, including information used for perceiving depth and analyzing details of visual targets. Consistent with this interpretation, binocular neurons have been found in both the Rt and E of the zebra finch, and information from both eyes interacts in these binocular cells (Schmidt and Bischof, 2001).

3 Telencephalic connections of the telencephalic visual areas

The visual Wulst receives inputs not only from GLd, but also from a large number of connections with other telencephalic areas (Deng and Rogers, 2000). The visual Wulst has dispersed reciprocal connections with the ipsilateral neostriatum frontale, pars lateralis (NFL), the ipsilateral neostriatum intermedium, the ipsilateral dorso-lateral neostriatum (including neostriatum caudale, pars lateralis), and also the bilateral archistriatum (A) (Deng and Rogers, 2000). The visual Wulst, moreover, occupies only a part of the Wulst. The Wulst, as a heterogeneous structure, also receives inputs from other modalities, such as somatosensory and auditory signals (Deng and Wang, 1992, 1993); in fact, the rostral somatosensory area of the Wulst overlaps with the visual area in the pigeon (Fig. 1; Deng and Wang, 1992). It is particularly interesting that the somatosensory inputs interact with visual information on single neurons located in the overlapping areas (Deng and Wang, 1993). All of the evidence supports our hypothesis that the Wulst is not simply a primary visual area but also a telencephalic integration area (Deng and Wang, 1993; Deng and Rogers, 1997), which could explain why the Wulst is particularly important for some cognitive functions and complex behaviors, such as reversal learning.

In contrast to the Wulst, the ectostriatum (E) is specialized for processing visual information only. The core region of E, which receives inputs from Rt, projects to its belt/surrounding neostriatum area; and this region, in turn, projects mainly to NFL, the dorsolateral portion of the tempero-parieto-occipital area (TPO), the lateral portion of the neostriatum intermediale (NIL) and, in a few efferents, to the NCL and A (Husband and Shimizu, 1999; Alpár and Tömböl, 2000). Through these connections, the visual information may be processed in the target areas. For example, Delius et al. (1984) have found that lesions of a lateral telencephalon region, including the NFL and TPO, impair pattern discrimination in the pigeon. Apart from the reciprocal connections with the surrounding neostriatum found in the chicken, however, no other direct reciprocal connections with any telencephalic areas have been found in birds (Husband and Shimizu, 1999; Alpár and Tömböl, 2000).

Some telencephalic areas, such as the NFL and A, receive projections from both the Wulst and E (Fig. 1). It is possible that visual information from both the tectofugal and thalamofugal pathways interacts in the NFL and A, an interaction that may play a role in some cognitive functions. Moreover, although the Wulst does not project directly to the E, it does project to the HV (Hyperstriatum ventrale;

Alpár and Tömböl, 1998). Since the HV projects to E, the Wulst could modulate visual processing in the E via indirect Wulst-HV-ectostriatum connections (Fig. 1). In fact, the visual Wulst has an excitatory influence on flash-evoked responses in the E of the zebra finch (Engelage and Bischof, 1994). Such indirect connections are the neural basis for coordinating the two pathways in controlling visually guided behavior.

4 Roles of two visual pathways in visually guided behavior

The thalamofugal and tectofugal pathways not only have different organization but also differential roles in visual processing and in controlling visually guided behavior. Lesions of the Rt and E cause severe deficits of simple color, visual intensity and pattern discrimination, but similar lesions of the GLd and Wulst have no or little effect on the performance of these tasks (Bessette and Hodos, 1989). However, lesions of the Wulst impair some cognitive functions, such as food versus non-food categorization (Deng and Rogers, 1997), sun-compass associative learning (Budzynski et al., 2002) and reversal learning (Benowitz and Lee-Teng, 1973).

Recently, I have collaborated with L.J. Rogers in an investigation of the roles played by the two pathways in pattern reversal learning by *c-fos* (an early immediate gene) expression. Chickens were trained to search for food in paper cones (length 25 mm, diameter 10 mm) that were printed with black and white checked patterns or toned simply grey without a pattern. During the training period of 5 trials a day for 4–5 days, the patterned-cones contained grains for reward (positive stimuli) and the grey cones none (negative stimuli). Once the chicken had learned this discrimination, it was exposed to reversal, in which the grey cones were filled with grains (now positive) and the patterned cones empty (negative). After only 15 trials (3 re-training sessions, each of 5 trials), the chickens learned the reversed association of the visual stimuli. After completing this relearning task, the *c-fos* expression in the brain was examined by immunohistochemistry.

Preliminary results revealed no *c-fos* immunoreactive neurons in the GLd or Wulst of control chickens. There was, however, a strong *c-fos* expression in the TeO, and also weak expression in the E and Rt. In contrast to the controls, many *c-fos* immunoreactive neurons were found in the GLd and Wulst in the chickens subjected to reverse learning, and also many in the Rt and E. There was, however, no clear difference between control and reverse learning birds in *c-fos* expression in the TeO.

This outcome suggests that the TeO may be activated by general visual stimuli. It is possible that this non-specific activation of the TeO is suitable for monitoring environmental changes; but the Rt and E may be involved in this function also, at a lower level. Since an obvious increase of *c-fos* expression was found in Rt and E after re-

Table 1   Comparison of functions of the telencephalic visual areas of the thalamofugal and tectofugal pathways (based on lesion studies)

Visually guided behaviors	Lesions in the Wulst	Lesions in the Ectostriatum

Simple visual tasks:
    Brightness discrimination
    Pattern discrimination
    Color discrimination
	No or little impairment (pigeon, Pritz et al., 1970; Reley et al., 1988)	Severe impairment (pigeon, Hodos and Karten, 1970; Bessette and Hodos, 1989)

Visual acuity	Reduction in the lateral visual field (pigeon, Güntürkün and Hahmann, 1999)	Reduced in the frontal visual field (pigeon, Güntürkün and Hahmann, 1999)

Psychophysical tasks:
    Intensity-difference threshold
    Size threshold
    Line orientation threshold
	Minor but stable impairment (pigeon, Hodos et al., 1986; Pasternak and Hodos, 1977)	Elevation of threshold (pigeon, Hodos et al., 1988; Mulvaneny, 1979)

Complex and cognitive function: Pattern-reverse learning	Marked deficits (Bobwhite quail, Stettner and Schultz, 1967; chicken, Benowitz and Lee-Teng, 1973; pigeon, Macphail 1976)	(Ectostriatum may also be involved in pattern-reverse learning based on the recent c-fos repression study in chickens)
Color-reverse learning	Marked deficits (pigeon, Shimizu and Hodos, 1989)	Impaired (pigeon, Chaves and Hodos, 1998)
Matching-to-sample performance	Marked deficits (pigeon, Pasternak, 1977)	
Sun-compass associative learning	Deficits (pigeon, Budzynski et al., 2002)	No deficits (pigeon, Budzynski et al., 2002)
Food vs non-food categorization	Deficits (chicken, Deng and Rogers, 1997)	No deficits (chicken, Deng and Rogers, 1997; pigeon, Watanabe, 1992)
Recognition of individual conspecifics	No deficits (pigeon, Watanabe, 1992)	Deficits (pigeon, Watanabe, 1992)

verse learning, the tectofugal pathway is involved in its visual processing. This is consistent with lesioning studies in pigeons, which have shown that lesions of both the Rt and E impair color-reverse learning (Chaves et al., 1993; Chaves and Hodos, 1998). Chaves et al. (1993) also found that lesioning in the GLd of the thalamofugal pathway has no effect on color-reverse responses in the pigeon, even though the Wulst is crucial for both color- and pattern-reverse learning in all avian species studied. They suggested that the Wulst receives visual inputs required for color-reverse learning through the tectofugal pathway, but not thalamofugal afferents (Chaves et al., 1993; Chaves and Hodos, 1998). Our present experiment provides clear evidence that the GLd is involved in reverse learning, at least in pattern-reverse learning.

Based on evidence for the organization of the visual pathways and the behavioral studies described above, I suggest that the tectofugal pathway is responsible for detail analysis of the visual stimulus. Without doubt, visual processing in this pathway is also important in higher cognitive function. The thalamofugal pathway, in particular the Wulst, may be otherwise important for some cognitive functions and controlling other complex behaviors. For example, lesions of the E but not the Wulst impair discrimination of color, visual intensity and pattern. Lesions of the Wulst also impair some cognitive functions. The tectofugal pathway may well be responsible for monitoring changes in environment; further activation in that pathway and the turning-on of the thalamofugal pathway may be followed up for further analysis of visual targets and controlling relevant behaviors. Thus, interaction between the two pathways seems necessary for controlling visually guided behavior, particularly for those visual functions involved in higher cognition.

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