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Topological relation of chick thalamofugal visual projections with hyper pallium revealed by three color tracers

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Abstract

In birds, there are two visual projections from retina to higher pallium, i.e., tectofugal and thalamofugal pathways. The latter one is lateralized in chick and suggested to be involved in visually evoked social behavior, like recognition of novelty, predator, and conspecific animals. We wanted to establish functionally relevant topological connection map between thalamic nuclei and hyperpallium apicale (HA) and carried out tracing study with three color fluorescent tracers. The tracers were serially injected in HA either along with the medial–lateral (M–L) or anterior–posterior (A–P) axis. We found that M–L axis and A–P axis in HA were transferred into the dorsal–ventral axis and the medial–lateral axis, respectively within the nucleus geniculatus lateralis pars dorsalis (GLd). In another word, the medial part of nucleus dorsolateralis anterior thalami pars lateralis (DLLv) projected to anterior part of HA and the ventral part of nucleus dorsolateralis anterior thalami pars lateralis pas ventralis (DLLd) projects to lateral HA. This result suggests that thalamus would process information in parallel through each subnuclei and elaborate coordination among them in relation to topological map presented in higher pallium.

Keywords: Avian thalamofugal visual pathway; Retrograde tracer; Topology; Wulst; Thalamus; Social behavior, Asymmetry; Chick

1. Introduction

Neuroethological study of avian social behavior has attracted researchers in various disciplines with a hope to make a comparative study of development of social communication in animal kingdom. Chick has been used in developmental study because of easy access for experimental manipulation of embryo, and as the consequence the knowledge about molecular landmark of developing nervous system has been accumulated (Puelles et al., 2000), which allows us to find a universal design of nervous system as well as species-specific divergent (Reiner et al., 2004). Now, a genome project of chick is completed (Wallis et al., 2004) and this situation is also promoting us to neuroethological study of chick. We have studied the asymmetry of chick visual pathway (Koshiba et al., 2002, 2003), since visually guided behavior is suitable to investigate the development of social communication triggered by imprinting or learning of familiar or unfamiliar subjects just after hatching (Rogers

Abbreviations: 4Di10ASP, 4-(4-(didecylamino)styryl)-*N*-methylpyridinium iodide; A–P, anterior–posterior; DiI, 1,1′-dioctadecyl-3,3,3′,3′-tetramethylindocarbocyanine perchlorate; DIVA, nucleus dorsalis intermedius ventralis anterior; DLA, dorsolateral anterior salami; DLAda, rostral part of DLA; DLAlr, nucleus dorsolateralis anterior thalami pars lateralis rostralis; DLAmc, nucleus dorsolateralis anterior thalami pars magnocellularis; DLL, nucleus dorsolateralis anterior thalami pars lateralis; DLLv, nucleus dorsolateralis anterior thalami pars lateralis pars ventralis; DLLd, nucleus dorsolateralis anterior thalami pars lateralis pars dorsalis; DS, decussatio supraoptica; E(number), embryonic-day after starting incubated; FG, Fluorogold; GLd, nucleus geniculatus lateralis pars dorsalis; HA, hyperpallium apicale; LdOPT, nucleus lateralis dorsalis nuclei optici principalis thalami; LFB, lateral forebrain bundle; M–L, medial–lateral; NF, nidopallium frontale; P(number), postnatal-day after hatching; PB, phosphate buffer; PBS, phosphate buffer saline; PFA, paraformaldehyde; SPC, nucleus superficialis parvocellularis; TMS, tractus septopallio-mesencephalicus

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and Andrew, 2002). There are two visual pathways, thalamofugal and tectofugal pathways. A series of evidence suggest that tectofugal pathway is quite similar between birds and mammals, but thalamofugal pathway is different especially in lateral-eye birds like chick and pigeon compared with frontal-eye birds like owl and mammals as well (Nguyen et al., 2004). In lateral-eye birds, thalamofugal pathway is more important for lateral view than for frontal view (Gunturkun and Hahmann, 1999), but in chick frontal view is also captured by each eye (Rogers and Andrew, 2002). Two important restrictions, however, make the chick thalamofugal pathway attractive (Rogers and Andrew, 2002). First, in chick visual information from two eyes is completely crossed at the level of retinofugal pathways and most of thalamofugal projections run to ipislaterally and send some contralateral fibers to visual Wulst (a multilayered eminentia of the rostral roof of the avian telencephalon), so each hemisphere differentially received the information from each eye. Second, the left hemisphere is more concerning the visual acuity, on the other hand, the right hemisphere the global special cognition. Thus, each thalamofugal pathway from each eye is processing quite different information. This anatomical segregation will offer an opportunity to more easily investigate the relationship between complex behavior and neuronal circuits.

To begin with, we need a solid anatomical data of the central nervous system related to visually guided social behavior. The extensive studies pioneered by Karten and Dubbeldam (1973) and Karten and Hodos (1970) revealed the existence of subnuclei in the region of the nucleus geniculatus lateralis pars dorsalis (GLd) (Boxer and Stanford, 1985; Deng and Rogers, 1998; Medina et al., 1997; Miceli et al., 1990; Miceli and Reperant, 1982; Remy and Gunturkun, 1991; Watanabe, 1987). The nuclei in GLd can be categorized into three groups in terms of ipsi- and contralateral connections with HA (Deng and Rogers, 1998). However, there is ambiguity among the published literature. First, the age of experimental animal is different from each report. Second, the tracer dye is different (see caution by Gunturkun et al., 1993, Deng and Rogers, 1999) and the precise injection site is not consistent among the reports and not systematically studied. Further, the relative location of stained nuclei is not well defined in the schematic drawings to summarize the tracing study in most publications. Therefore, we need to establish a map showing the connection between thalamic nuclei and HA by ourselves using the same neonatal animals for behavior study. We therefore, started tracing studies of the topological map using multi-color tracers at the same time and tried to reconstitute the three dimensional map based on multi-color slice image. Thereby, we could reveal new dimension of thalamus-HA connection in more convincing way.

2. Materials and methods

2.1. Animals and light regulation

Fertilized chick eggs (white leghorn) purchased from a local distributor (Nakamura egg farm, Gifu), were incubated in a dark incubator at 37.7 °C until the embryonic day 19–20 (E19-20), exposed to light (200–300 lux, from a tungsten light bulb) during the final 3 days of incubation, and hatched. To avoid the complexity in brain anatomy because of sex difference, we used only males. All the animal experiments were approved and performed under the ethical regulation of experimental animals in National Institute of Neuroscience, NCNP. In this manuscript, we followed the recommendation of revised nomenclature for avian telencephalon according to Reiner et al. (2004).

2.2. Tracing studies

Under anesthetization by 100 μl of 15% Nembutal (Dainihon Pharmaceutical) in sterile distilled water, tracer dyes were injected into birds brain on day 2 post-hatching

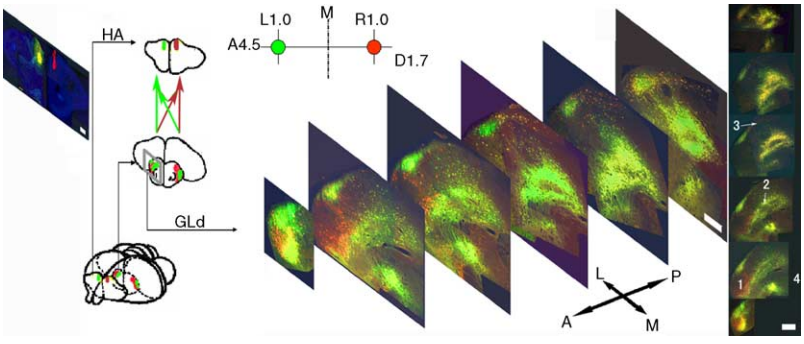

Fig. 1. Reconstitution of thalamic nuclei revealed by two color tracers injected in vivo. Injection point was 4.5 mm anterior (A4.5) from the reference, the intersection of skull suture, 1.0 mm left or right (L1.0 or R1.0) and 1.7 mm deep (D1.7) (see the scheme). The thalamic region (GLd) was focused (boxed by a rectangle) and the fluorescent images from this region were serially aligned along the A–P axis as well as M–L axis as shown. The same serial figures were separately aligned as the insert shown in the right side of the figure (the bottom image is corresponding to the most anterior image). The number 1, 2, 3, and 4 mark the region assigned as DLAlr, medial part of DLL, SPC, and LFB, respectively (see more detail in the text and Figs. 3 and 4). The colored arrows indicate the direction of neuronal projection of thalamofugal pathway in the scheme [scale bar is 0.5 mm].