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Review

Thalamotelencephalic organization in birds☆

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Abstract

Investigation of thalamo-telencephalic connections reveals correspondences between the avian and mammalian thalamic subdivisions (which may or may not mean true homologies). Based mainly on hodological comparisons, the avian thalamus possesses the principal anatomical and functional subdivisions characteristic for mammals. The current review is focused on a comparative analysis of intralaminar, midline and mediodorsal nuclei. There is evidence for matching subdivisions in the case of midline thalamic and mediodorsal nuclei within the avian dorsal thalamic zone, whereas such correspondence is evident, if less complete, in the case of the intralaminar nuclei. Thalamic connections are also relevant to the debated issue of the avian 'prefrontal' cortex. From the current study it is suggested that the prefrontal analogue regions of the bird may spread across the rostrocaudal extent of telencephalon, the rostral nidopallial/mesopallial region (formerly known as medial neostriatum/hyperstriatum) being one subdivision, receiving direct input from the paraventricular thalamic nucleus homologue of midline thalamic region (the medial juxtaventricular region of the nucleus dorsomedialis posterior). Hodological evidence from the current study and other reports argues for the possibility that the area corticoidea dorsolateralis might be hodologically comparable to the cingulate cortex, receiving input from a mediodorsal thalamic-relevant subdivision (lateral subdivision of nucleus dorsomedialis anterior, and medial aspect of nucleus dorsolateralis pars medialis), which also projects on the caudal nidopallium close to (but not coextensive with) the nidopallium caudolaterale, another potential analogue of avian prefrontal cortex. The rostral dorsolateral aspect of nucleus dorsomedialis anterior thalami and the dorsal aspect of nucleus dorsolateralis pars medialis are partially comparable to the mammalian intralaminar nuclei, sharing connections to non-limbic 'corticoid' areas (the Wulst), and the reticular thalamic nuclei.

Keywords: Diencephalon; Avian brain; Prefrontal cortex; Cingulate cortex; Intralaminar nuclei; Midline nuclei; Mediodorsal nucleus

Contents

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1. Introduction

The dorsal thalamus of vertebrates has long been envisaged as a relay station interposed between subtelencephalic and telencephalic brain centres. An increasing body of data pertaining to the anatomical composition, parcellation, connectivity and functional responses of thalamic subdivisions suggests that these nuclei participate in regulatory circuits that are far more elaborate than previously thought. Basic divisions of the thalamus comprise the rostral lemnothalamus (equivalent to the dorsal tier of Redies et al. [30]), receiving predominantly lemniscal afferents, and the caudal collothalamus (equivalent to the intermediate and ventral tiers [30]), receiving input from the midbrain roof [5]. According to the main telencephalic output regions, the thalamus is subdivided into specific sensory relay nuclei, in particular those of the somatosensory pathway ('sensory thalamus'), basal ganglia-related nuclei ('motor thalamus'), and anterior, intralaminar/midline and mediodorsal nuclear groups ('limbic thalamus'). Such categorization can only be made by gross simplification. However, we used these simplified categories for a comparative overview of the main thalamotelencephalic connections in mammals and birds. First, parts of the intralaminar thalamus also have extensive connections to non-limbic cortical regions. Secondly, the present review it is not intended to cover the nuclei of special senses (vision, hearing, taste sensation).

The sauropsid brain branched off from the common ancestor about 300 million years ago and has attained its peak in extant birds. Despite this early divergence from the mammalian forms, there are remarkably well traceable homologies between the two vertebrate classes, particularly in the subtelencephalic regions. Even within the telencephalon, the subpallial structures such as the septum or caudate-putamen can be correlated with their avian counterparts with reasonable certainty. The most profound difference is found in the development and organization of the pallium. Birds lack the layered cortex and neurons having a pyramidal-like morphology, so typical of the mammalian brain. However, the pallial structures overlying the striatum and pallidum are capable of processing elaborate sensory, motor, associative and motivational information. One key element of such processing – and a potential point of departure for a correlative study – is the organization of thalamic input. In reptiles, the partly ipsilateral and partly bilateral thalamocortical projection originates from the dorsolateral anterior nucleus, and reaches different parts of the dorsal cortex, representing sensorimotor cortex [16]. In mammals the thalamic 'gate' is essential for most cortical operations and this is expected to be the case also with birds. The present review attempts to summarize the main findings pertinent to the avian thalamotelencephalic pathways, and, in particular, to elaborate on the issue of the intralaminar, midline and mediodorsal thalamic connections. In this paper we followed the recently revised avian nomenclature [32], giving the old terms in brackets when necessary.

2. Somatosensory thalamus

Concerning somatosensory relay, a direct sensory thalamocortical pathway is absent in amphibians, i.e. the lemnothalamus having specific sensory nuclei may appear in reptiles [41]. By contrast to mammals, where the 'dorsalizing' tendency in vertebrate pallial development brought about a concentration of somatosensory thalamocortical projection in the dorsal pallium (neocortex), birds have more diffuse projections extending to both dorsal and ventral pallial fields [1]. The main thalamotelencephalic somatosensory pathways arise from the caudal nucleus dorsolateralis posterior (DLPc) and the nucleus dorsalis intermedius ventralis anterior (DIVA), and terminate in both the rostral Wulst and the caudal and intermediate nidopallium (neostriatum) [12]. The same dorsal thalamic nuclei were found also to receive input from the gracile, cuneate and external cuneate nuclei, as well as the tractus descendens trigemini [18,42,43]. Also, the nucleus uvaeformis (Uva) of songbirds has multiple afferent and efferent connections which make this nucleus an equivalent of the DLPc of the pigeon [44]. It has been suggested that the DLP, with its multiple inputs from different sensory modalities would be hodologically similar to the nucleus ventromedialis thalami of teleost fish and to the posterior complex of mammalian thalamus [18]. The caudal DLP–DIVA complex is a likely equivalent of the ventrobasal nuclei: ventralis posteromedialis (VPM) and ventralis posterolateralis (VPL). Furthermore, a special region of disputed origin (nucleus basorostralis, former nucl. basalis) receives the ascending terminals arising from the trigeminal system [10,47].

3. Motor thalamus

Thalamic relay plays an essential part in the generating of motor patterns and, particularly, in monitoring one's own actions (corollary discharge) [37]. The ventral tier nuclei of mammals, nucl. ventralis anterior (VA) and nucl. ventralis lateralis (VL) participate in the pallido-thalamo-pallial loop, relaying basal ganglia output to the frontal cortex, in particular primary motor, supplementary, premotor and cingulate motor areas. Functionally related motor areas of the frontal cortex and VA/VL have convergent projections to specific regions of the dorsal striatum [23]. The abundance of reciprocal connections between the VA/VL nuclei and different areas of the motor cortex suggests that the ventral tier nuclei (and the mediodorsal nucleus) of mammalian thalamus also have a role in the mediation of information flow between cortical circuits [24]. Although it is likely that the basic elements of basal ganglia organization had already been present in ancestral tetrapods, the general Bauplan being shared by all extant tetrapods including anamniotes [22], a major step forward must have been an extensive development of pallial connections in stem amniotes [31].

Birds share the key features of basal ganglia organization with those of mammals, including the existence of