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Research Report

Cortical connections of the rat lateral posterior thalamic nucleus

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ABSTRACT

Spatial processing related to directed attention is thought to be mediated by a specific cortical–basal ganglia–thalamic–cortical network in the rat. Key components of this network are associative cortical areas medial agranular cortex (AGm) and posterior parietal cortex (PPC), dorsocentral striatum (DCS), and lateral posterior (LP) thalamic nucleus, all of which are interconnected. Previously, we found that thalamostriatal projections reaching DCS arise from separate populations of neurons of the mediorostral part of LP (LPMR). The far medial LPMR (fmLPMR) terminates in central DCS, a projection area of AGm, whereas central LPMR terminates in dorsal DCS, a projection area of PPC. This represents segregated regional convergence in DCS from different sources of thalamic and cortical inputs. In the present study, thalamocortical and corticothalamic projections arising from and terminating in LPMR and neighboring thalamic nuclei were studied by anterograde and retrograde tracing techniques in order to further understand the anatomical basis of this neural circuitry. A significant finding was that within LPMR, separate neuronal populations provide thalamic inputs to AGm or PPC and that these cortical areas project to separate regions in LPMR, from which they receive thalamic inputs. Other cortical areas adjacent to AGm or PPC also

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Abbreviations: ACC, anterior cingulate cortex; AD, anterodorsal thalamic nucleus; AGl, lateral agranular cortex; AGm, medial agranular cortex; AM, anteromedial thalamic nucleus; AV, anteroventral thalamic nucleus; BDA, biotinylated dextran amine; Cg1, cingulate cortex, area1; Cg2, cingulate cortex, area2; CL, central lateral thalamic nucleus; CM, central medial thalamic nucleus; CV, cresyl violet; DCS, dorsocentral striatum; DLG, dorsal lateral geniculate nucleus; fmLPMR, far medial portion of lateral posterior thalamic nucleus, mediorostral part; Fr2, frontal cortex, area 2; FrA, frontal association cortex; HL, hindlimb cortex; ic, internal capsule; LD, laterodorsal thalamic nucleus; LDDM, laterodorsal thalamic nucleus, dorsomedial part; LDVL, laterodorsal thalamic nucleus, ventrolateral part; LP, lateral posterior thalamic nucleus; LPLR, lateral posterior thalamic nucleus, laterorostral part; LPMR, lateral posterior thalamic nucleus, mediorostral part; lPPC, posterior parietal cortex, lateral portion; MD, mediodorsal thalamic nucleus; MDC, mediodorsal thalamic nucleus, central part; MDL, mediodorsal thalamic nucleus, lateral part; MDM, mediodorsal thalamic nucleus, medial part; MO, medial orbital cortex; mPPC, posterior parietal cortex, medial portion; Oc1, occipital cortex, area 1; Oc2L, occipital cortex, area 2, lateral part; Oc2M, occipital cortex, area 2, medial part; Par 1, parietal cortex, area 1; PC, paracentral thalamic nucleus; PF, parafascicular thalamic nucleus; Po, posterior thalamic nucleus; PPC, posterior parietal cortex; PrL, prelimbic cortex; PtPD, dorsal posterior parietal cortex; Re, reuniens thalamic nucleus; Rh, rhomboid thalamic nucleus; RSD, retrosplenial dysgranular cortex; RSGc, retrosplenial granular c cortex; Rt, reticular thalamic nucleus; S1BF, primary somatosensory cortex, barrel filed; S1FL, primary somatosensory cortex, forelimb area; S1HL, primary somatosensory cortex, hindlimb area; VA, ventroanterior thalamic nucleus; VL, ventrolateral thalamic nucleus; VLO, ventrolateral orbital cortex; VPL, ventral posterolateral thalamic nucleus

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demonstrated reciprocal connections with LP or surrounding nuclei in a topographic manner. Our findings suggest that the cortical–basal ganglia–thalamic network mediating directed attention in the rat is formed by multiple loops, each having reciprocal connections that are organized in a precise and segregated topographical manner.

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1. Introduction

The rat lateral posterior thalamic nucleus (LP) is a key component of the neural circuitry for directed attention and its dysfunctional counterpart, contralateral neglect. This circuitry includes cortical, thalamic and striatal components that appear to be organized in functionally compartmented loops, as are known to exist for sensory, motor and limbic functions (Reep and Corwin, 2008). In rats, unilateral lesions of either medial agranular cortex (AGm or Fr2) or posterior parietal cortex (PPC), or disconnection of the axons linking them, produce neglect (Burcham et al., 1997; Corwin and Reep, 1998). This neglect is multimodal, involving visual, auditory and somatic sensory stimuli. Rats with cortical lesions may recover spontaneously or as a result of specific treatments (Corwin and Reep, 1998; Brenneman et al., 2008).

Nucleus LP is reciprocally connected with AGm and PPC, as well as with visual areas occipital cortex, area 1 (Oc1), occipital cortex, area 2, lateral part (Oc2L) and occipital cortex, area 2, medial part (Oc2M) (Sukekawa, 1988; Reep et al., 1994; Reep and Corwin, 1999; Sefton et al., 2004), and these cortical areas are themselves interconnected (Reep et al., 1990, 1994, 1996; Vandevelde et al., 1996; Reep and Corwin, 1999).

Thalamic nucleus LP also projects to dorsocentral stratum (DCS), a site where corticostriatal projections from AGm and PPC converge (Erro et al., 2002; Cheatwood et al., 2003; Reep et al., 2003; Cheatwood et al., 2005). The DCS is an essential node in the circuitry for directed attention. Unilateral lesions of DCS produce neglect that does not recover spontaneously or after treatment with a dopamine agonist, in contrast to neglect resulting from cortical lesions (Van Vleet et al., 2000, 2002, 2003a, 2003b). The main input from LP to DCS has been shown in retrograde tracing studies to arise from the far medial portion of rostral LP, fmLPMR (Erro et al., 2002; Cheatwood et al., 2003). Recently, we found using anterograde tracing that fmLPMR projects to the matrix compartment of central DCS and to the dorsal periphery of DCS (Kamishina et al., 2008). In contrast, central LPMR projects only to the dorsal periphery of DCS. The laterorostral part of LP (LPLR) and other thalamic nuclei surrounding LP project sparsely to dorsolateral and dorsomedial regions of the striatum but do not project to DCS. Thus, fmLPMR, the portion of LP that projects to AGm, also projects to central DCS, a major target of AGm. Double anterograde fluorescent labeling confirmed that axons from fmLPMR intermingle with axons from AGm, thus raising the possibility that they synapse on common medium spiny striatal output neurons (Cheatwood et al., 2005). In a parallel manner, central LPMR projects to PPC and to the dorsal periphery of DCS, a major target of PPC, suggesting that terminals from central LPMR and PPC may also converge on single medium spiny striatal neurons. The dorsal periphery of DCS receives input from fmLPMR, central LPMR, and PPC. All three of these inputs terminate in segregated foci, but it is not known if there is overlap among foci from these different sources. These findings indicate that DCS is a region of convergence for thalamostriatal and corticostriatal projections from regions that are themselves interconnected, and that there is some topographic separation of inputs from different thalamic and cortical sources.

The significant differences within LP regarding thalamostriatal projections to DCS suggest that there may also be differences with regard to the topography of thalamocortical and corticothalamic projections involving LP, AGm, and PPC. Such differences would have functional implications for the operation of the circuitry for directed attention. Corticothalamic projections are known to promote synchronized oscillatory activity that is thought to underlie the coherent action of large groups of thalamic neurons (Contreras et al., 1996; Jones, 2001), and thalamocortical neurons exert a powerful effect on cortical neurons through convergent, synchronous activation (Bruno and Sakmann, 2006). Corticothalamic projections influence the occurrence of tonic versus burst firing of thalamocortical neurons (Sherman, 2001). In general, layer V neurons provide an excitatory driving function to thalamic neurons, whereas layer VI neurons exert a modulatory influence through their effect on the tonic versus bursting mode of thalamic neurons (Sherman, 2001; Cudeiro and Sillito, 2006; Sherman and Guillery, 2006; Sherman, 2006). However, corticothalamic relationships are unknown at the structural or functional level for inputs to the rat LP from AGm and mPPC (medial PPC), and the topography of thalamocortical relationships between LP and AGm and PPC is not well mapped. For example, although it has been shown that LP projects to AGm and PPC, do these projections arise from separate groups of neurons in LP? If so, are these populations of neurons segregated or intermingled? These two possibilities represent divergent ways in which information could be distributed from LP to the cortex. Similarly, because we know that fmLPMR is the source of input to DCS, particularly to its central part, it is of interest to determine which corticothalamic projections reach fmLPMR. In light of these questions, we sought to determine with greater precision the topography of projections from LP to AGm and PPC. In addition, we mapped the reciprocal projections from these cortical areas to LP, and observed how these related to projections from neighboring cortical areas.

2. Results

2.1. *Thalamocortical projections*

Terminal labeling patterns from thalamus to cortical areas were examined by injecting the anterograde axonal tracer 10k

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