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ASYMMETRIC CROSS-HEMISPHERIC CONNECTIONS LINK THE RAT ANTERIOR THALAMIC NUCLEI WITH THE CORTEX AND HIPPOCAMPAL FORMATION

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Abstract—Dense reciprocal connections link the rat anterior thalamic nuclei with the prelimbic, anterior cingulate and retrosplenial cortices, as well as with the subiculum and postsubiculum. The present study compared the ipsilateral thalamic-cortical connections with the corresponding crossed, contralateral connections between these same sets of regions. All efferents from the anteromedial thalamic nucleus to the cortex, as well as those to the subiculum, remained ipsilateral. In contrast, all of these target sites provided reciprocal, bilateral projections to the anteromedial nucleus. While the anteroventral thalamic nucleus often shared this same asymmetric pattern of cortical connections, it received relatively fewer crossed inputs than the anteromedial nucleus. This difference was most marked for the anterior cingulate projections, as those to the anteroventral nucleus remained almost entirely ipsilateral. Unlike the anteromedial nucleus, the anteroventral nucleus also appeared to provide a restricted, crossed projection to the contralateral retrosplenial cortex. Meanwhile, the closely related laterodorsal thalamic nucleus had almost exclusively ipsilateral efferent and afferent cortical connections. Likewise, within the hippocampus, the postsubiculum seemingly had only ipsilateral efferent and afferent connections with the anterior thalamic and laterodorsal nuclei. While the bilateral cortical projections to the anterior thalamic nuclei originated predominantly from layer VI, the accompanying sparse projections from layer V largely gave rise to ipsilateral thalamic inputs. In testing a potentially unifying principle of anterior thalamic – cortical interactions, a slightly more individual pattern emerged that reinforces other evidence of functional differences within the anterior thalamic and also helps to explain the consequences of unilateral interventions involving these nuclei. **© 2017 The Authors. Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).**

Keywords: Contralateral, Corticothalamic, Hippocampus, Interhemispheric, Thalamocortical, Thalamus.

INTRODUCTION

Reciprocal connections between the thalamus and cortex underlie numerous brain functions. Attention has naturally focussed on the dense, ipsilateral thalamocortical projections, which are often complemented by return thalamic inputs from deep cortical layers (Deschenes et al., 1998; Sherman, 2007). In addition to these ipsilateral connections, there are both indirect and direct pathways that provide inter-hemispheric communication between the thalamus and contralateral cortex. One indirect pathway involves the commissural fibers that connect corresponding cortical areas across the two hemispheres. There are, in addition, direct connections that link the thalamus with the cortex in the opposite hemisphere. Their prevalence remains uncertain, however, as the lack of a description of a particular crossed thalamic-cortical connection does not confirm its absence, with many papers leaving this information unspecified.

The current study focussed on the rat anterior thalamic nuclei (ATN). The ATN comprise three principal nuclei, the anteromedial (AM), anteroventral (AV), and anterodorsal (AD) nucleus, along with a fourth nucleus in the rodent, the interanteromedial nucleus (IAM) (Swanson, 1992). We also included the laterodorsal (LD) nucleus as it displays clear hodological similarities with the ATN (van Groen and Wyss, 1990a, 1992b; Shibata, 1996, 2000; van Groen et al., 2002b). These combined nuclei have important roles in human episodic memory and rodent spatial memory (Sutherland and Rodriguez, 1989; Aggleton and Sahgal, 1993; Taube, 1995; Byatt and Dalrymple-Alford, 1996; Aggleton & Brown, 1999; Harding et al., 2000; Vertes et al., 2001; Warburton et al., 2001; van Groen et al., 2002a;

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Abbreviations: AD, anterodorsal thalamic nucleus; AM, anteromedial thalamic nucleus; a-p, anterior-posterior; AV, anteroventral thalamic nucleus; BDA, biotinylated dextran amine; Cg, cingulate cortex; DY, diamidino yellow; FB, fast blue tracer; FG, fluorogold tracer; HPC, hippocampus; IAD, interanterodorsal thalamic nucleus; IAM, interanteromedial thalamic nucleus; LD, laterodorsal thalamic nucleus; LP, lateral posterior thalamic nucleus; M2, secondary motor cortex; MD, mediodorsal thalamic nucleus; PL, prelimbic cortex; PoS, postsubiculum; PT, parataenial thalamic nucleus; RSC, retrosplenial cortex; RSD, dysgranular retrosplenial cortex; RSG, granular retrosplenial cortex; Sm, stria medullaris of the thalamus; SUB, subiculum; V1, primary visual cortex; V2, secondary visual cortex; VA, ventral anterior thalamic nucleus; VL, ventrolateral thalamic nucleus; WGA-HRP, horseradish peroxidase-conjugated wheat germ agglutinin.

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Aggleton et al., 2010; Clark and Taube, 2012; Jankowski et al., 2013).

The ATN have numerous reciprocal connections with the cortex and hippocampal formation, the latter involving subicular regions (van Groen and Wyss, 1990a, 1990b; Shibata, 1993; Shibata and Kato, 1993; van Groen et al., 1999; Van Groen and Wyss, 2003; Shibata and Naito, 2005; Wright et al., 2010). Where it has been specified, ATN projections to rat frontal and cingulate areas remain ipsilateral, while the corresponding ATN afferents more often appear bilateral in origin (Dekker and Kuypers, 1976; Swanson and Cowan, 1977; Kaitz and Robertson, 1981; Seki and Zyo, 1984; Oda, 1997; Shibata and Naito, 2005). Nonetheless, weak anterior thalamic projections to the contralateral cortex have been described in primates (Dermon and Barbas, 1994), suggesting it would be premature to exclude the possibility of such projections in the rat. There is also disagreement over whether all cortical projections to the rat AM and AV nuclei are bilateral (Seki and Zyo, 1984; Oda, 1997; Shibata and Naito, 2005).

Both anterograde and retrograde tracers helped to determine whether the apparently asymmetric pattern of bilateral (thalamic afferents) and ipsilateral (thalamic efferents) connections is a general feature of the anterior and laterodorsal thalamic nuclei. We also analyzed the laminar origin of the corticothalamic projections to ATN in both hemispheres in light of current ideas about lamina distinctions (Sherman, 2016). In addition to neocortical regions, we also analyzed the reciprocal ATN connections with the subiculum and postsubiculum, in light of the importance of the hippocampal formation for ATN function.

EXPERIMENTAL PROCEDURES

Animals

A total of 32 adult male Lister Hooded rats (weight 290-350 g, Harlan Laboratories, United Kingdom) were examined for this study. All procedures were approved by the appropriate ethics committee at Cardiff University and followed the UK Animals (Scientific Procedures) Act (1986).

Surgical procedures

All surgeries were performed under an isoflurane-oxygen mixture. The animals were first anesthetized and then placed in a stereotaxic frame. The tracer injection coordinates were partly guided by a stereotaxic brain atlas (Swanson, 1992), corrected by the weight of the animal as well as by comparisons with previous tracer injections.

Choice of tracer

A total of 37 neuroanatomical tracer injections were analyzed as we injected two tracers in five of the animals (Table 1). Typically in the cortex, we used the anterograde tracer *biotinylated dextran amine* (BDA) to map corticothalamic pathways and the retrograde tracer *fast blue* (FB) to map the thalamocortical pathways. In one case the retrograde tracer *fluorogold* (FG) was used since that particular injection (in postsubiculum) required the tracer deposit to cover a larger area (which from our experience is a feature of FG). The 3 kD version of BDA was predominantly used in this study, which can also be transported in the retrograde direction (Fritzsch, 1993; Kaneko et al., 1996; Medina et al.,

Table 1. Table of all anterograde and retrograde tracer injections analyzed. Layers indicated in the third column indicate the center of the tracer deposit and do not exclude potential involvement of other layers. Those regions and layers in parenthesis indicate weak involvement in the injection site

Case #	Target (tracer)	Injection site
Retrograde injections in cortex		
187#9	FB	PL/Cg, layers III/V
187#3	FB	PL/Cg, layers III/V
186#4	FB	PL/Cg (M2), layers III/V
188#3	FB	Cg, layer V
64#6	FB	RSC, layers I-VI
172#27	FB	RSC, layers I-V (M2, V2)
172#28	FB	RSC, layers I-V (M2)
77#26	FB	RSC, layers I-V (V2)
64#3	FB	RSC, layers I-V (VI), M2/V2
196#18	FG	PoS/V2/RSC
Anterograde injections in cortex		
199#9	BDA (3kD)	Cg, layers II-VI (M2)
199#10	BDA (3kD)	Cg, layers II-VI (M2)
199#11	BDA (10kD)	Cg, layers III-VI
187#9	BDA (3kD)	RSC, layers V/VI
186#4	BDA (3kD)	RSC, layers II-V
188#5	BDA (3kD)	RSC, layer V
182#3	BDA (3kD)	SUB (V1/2/PoS)
182#4	BDA (3kD)	SUB (V1/2)
WGA-HRP injections in cortex		
88#1	WGA-HRP	PL, layers V/VI
88#2	WGA-HRP	PL, layers III/V
82#2	WGA-HRP	SUB/HPC
Retrograde injections in the anteroventral and anteromedial thalamic nuclei		
88#5	FB	AV
42#2	DY	AV
198#2	FB	AM (IAD, HPC)
41#5	DY	AM
45#11	FB	AV/AM
Retrograde injections centered in, but not restricted to, the anterior thalamic nuclei		
88#6	FB	AV/VA
41#5	FB	AV/AD (AM, VA)
45#11	DY	AM (PT)
42#2	FB	AM (PT)
191#9	FB	AV (AD, VL, AM)
198#4	ctb	AV (AM, PT)
Retrograde injections centered in, but not restricted to, the laterodorsal thalamic nucleus		
191#10	FB	LD (LP, HPC)
196#19	FG	LD (VA-VL)
WGA-HRP and BDA injections centered in, but not restricted to, specific anterior thalamic nuclei		
28#8	WGA-HRP	AV/VA/AD/AM (HPC)
37#4	WGA-HRP	AV (AD, AM, HPC)
183#12	BDA (3kD)	AV (AD, AM, VA, PT)

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