Anat Embryol (2000) 201:75–84

ORIGINAL ARTICLE

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Organisation of the amygdalo-thalamic pathways in rats

Accepted: 30 June 1999

Abstract This study examines the organisation of the pathways from the amygdala to the thalamus. Amygdaloid nuclei (medial, central, basolateral and olfactory groups) of Sprague-Dawley rats were injected with biotinylated dextran using stereotaxic coordinates and their brains were then aldehyde-fixed and processed using standard methods. We have three major findings. First, the amygdala has a distinct set of projections to particular nuclei of the thalamus. The thalamic nuclei with the heaviest amygdaloid terminations include the zona incerta, the mediodorsal and the midline nuclei. Second, nuclei of different amygdaloid groups project to the thalamus in slightly different patterns. For example, some groups of nuclei project to the thalamic reticular nucleus (e.g. medial, olfactory) whilst others do not (e.g. central, basolateral). Thus, there is a certain amount of heterogeneity within the amygdaloid projections to the thalamus. Third, when we compare our results on the amygdalo-thalamic pathways to the many previous descriptions of the thalamo-amygdaloid pathways, we note that they are largely out of register. In other words, some of the thalamic nuclei that project to a given group of amygdaloid nuclei do not necessarily receive a projection back from that same amygdaloid nucleus. Hence, there is no substrate for a strong feed-back relationship between the thalamus and the amygdala, as there has been shown for other centres of the brain (e.g. between the thalamus and neocortex).

Key words Rat · Biotinylated dextran · Dorsal thalamus · Amygdala

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Introduction

We have been interested in the general organisation of subcortical afferents that reach the dorsal thalamus, having described already those that arise from the ventral thalamus – thalamic reticular nucleus (Coleman and Mitrofanis 1996; Kolmac and Mitrofanis 1997) and the zona incerta (Power et al. 1999) - and from many nuclei of the brainstem (Kolmac and Mitrofanis 1998; Kolmac et al. 1998). In this study, we describe the organisation of afferents from the amygdala, a major subcortical centre of the forebrain thought to be responsible for generating the appropriate emotional reaction in response to a given sensory stimulus (Turner and Herkenham 1991).

The dorsal thalamus has been described as the "gateway" to the neocortex, since most inputs that reach the neocortex from the sensory periphery (e.g., retina, cochlea, skin) or from other brain parts (e.g., brainstem, cerebellum) do so after passing through the dorsal thalamus. The dorsal thalamus is made up of distinct nuclei that can be grouped into either first-order, higher-order or intralaminar/midline nuclei. First-order nuclei receive much of their "primary drive" from usually one peripheral or subcortical source (e.g., dorsal lateral geniculate and ventral lateral nuclei) and project to one or two cortical areas; higher-order nuclei, for the most part, receive their primary drive from particular cortical areas (layer V cells) and then project back to these cortical (e.g., posterior thalamic and lateral posterior nuclei) and the intralaminar/midline nuclei are generally driven by many sources including the cerebellum, spinal cord, basal ganglia and brainstem and project to more widespread areas of cortex (e.g., paraventricular, rhomboid, parafascicular and central-lateral nuclei; see Jones 1985; Guillery 1995; Sherman and Guillery 1996; Steriade et al. 1997).

The amygdala, as with the dorsal thalamus, can be divided up into distinct functional groups of nuclei also. In general, four groups are recognised – central, medial, basolateral, olfactory – with each having largely distinct

patterns of connections (de Olmos et al. 1985). For example, the central nucleus has rich interconnections with many of the distinct nuclei of the brainstem (Hopkins 1975; Kretteck and Price 1978; Otterson 1981; Davis 1992; Fallon and Ciofi 1992; Jia et al. 1992), the medial nucleus interconnects with the olfactory bulb, hypothalamus and preoptic area (Kretteck and Price 1978; Veening 1978; Kevetter and Winans 1981; Luiten et al. 1983; Wong et al. 1993), the olfactory nuclei have connections with olfactory bulb, cerebral cortex, hypothalamus (de Olmos 1972; Scalia and Winans 1975; Kretteck and Price 1977 1978), and the basolateral complex connects heavily with the cortex (Kretteck and Price 1977; Sripanidkulchai et al. 1984), hypothalamus (Petrovich et al. 1996) and basal forebrain (Kretteck and Price 1977). In addition to these connections, each of these amygdaloid nuclei, particularly the medial, olfactory and basolateral groups, have been shown to project to the dorsal thalamus (Kretteck and Price 1977; 1978; Nitecka et al. 1979; Ottersen and Ben-Ari 1979; Turner and Herkenham 1991). The organisation of an amygdaloid projection back to the thalamus, however, has received little if any attention previously.

The major aim of this study was to explore the patterns of projections from the amygdala to the thalamus in rats. In general, the basic questions posed here are: (1) which thalamic nuclei receive a heavy input from the amygdala? (2) which amygdaloid nuclei form these projections to the thalamus? and (3) are these amygdalothalamic projections in register with the previously described thalamo-amygdaloid projections? Overall, the results generated should provide insights into whether the amygdala is in a strong position to influence the activity of different thalamo-cortical pathways through its connections with the dorsal thalamus.

Materials and methods

Subjects

Sprague-Dawley rats of either sex were used (250–300 g; *n*=33). Prior to use, they were kept in a 12 h light/dark cycle and had access to food and drink ad libitum. All of the following experimental procedures were approved by the Animal Ethics Committee of the University of Sydney.

Tracer injections

Rats were anaesthetised after an intraperitoneal injection of ketamine (100 mg/kg) and Rompun (10 mg/kg). Biotinylated dextran [10 kDa; 10% in phosphate-buffered saline (PBS); Molecular Probes, Ore., USA)] was injected, via iontophoresis (10–15 µA for 20 min; 6 s on, 6 s off), into the following nuclei using stereotaxic coordinates (Paxinos and Watson 1986): central amygdaloid nucleus (*n*=7), medial amygdaloid nucleus (*n*=8), anterior cortical nucleus (*n*=5), amygdalo-hippocampal transition area (*n*=2), basolateral amygdaloid nucleus (*n*=7) and the basomedial amygdaloid nucleus (*n*=4). After surgery, the rats were allowed to recover for 7 days and were then anaesthetised deeply with Nembutal (sodium pentobarbitone: 60 mg/ml). The animals were perfused trans-cardially with PBS (0.1 M; pH 7.4), followed by 4% buffered formaldehyde. After removal of the brains, they were post-fixed in the same fixative for 1 h, and immersed in PBS with the addition of 20% sucrose until the block sank. The brains were then cut using a freezing microtome into coronal sections at a thickness of 50 µm and stored in PBS. In general, every second section was processed for dextran detection. Sections were washed in PBS with the addition of 0.5% Triton (Sigma, Mo., USA) for 1 h and then incubated in the avidin-biotin-peroxidase complex (1:120; Sigma, Mo., USA) for 4 h at room temperature. Next, sections were reacted in a nickel-TRIS buffered saline (NTBS) - 3,3'-diaminobenzidine tetrahydrochloride (DAB; Sigma, Mo., USA) solution (Clemence and Mitrofanis 1992). Sections were then mounted onto gelatinised slides, air-dried overnight, counterstained with neutral red, dehydrated in ascending alcohols, cleared in Histoclear, and coverslipped using DPX.

Analysis

Coronal sections were drawn with reference to the atlases of Paxinos and Watson (1986) and/or Swanson (1992) and the injection sites and the anterogradely labelled terminals were plotted with the use of a camera lucida. Drawings and plots were then scanned onto a computer graphics program and the schematic diagrams shown in Figs. 3–6 were constructed.

Results

Injection site and tracer

In this study, biotinylated dextran was used as anterograde tracer for several reasons. It provides discrete injection sites with little spread from the focal point (see Fig. 1). Further, dextran has not been reported to be transported trans-synaptically or to be taken up by intact

Abbreviations for figures *ACo* Anterior amygdaloid nucleus · *AN* anterior thalamic nucleus · *AHIA* Amygdaloid hippocampal transitional area · *BLA* basolateral amygdaloid nucleus · *BLP* basolateral posterior amygdaloid nucleus · *BMA* basomedial anterior amygdaloid nucleus · *BMP* basomedial posterior amygdaloid nucleus · *CeA* central amygdaloid nucleus · *CL* central lateral nucleus · *CM* central medial nucleus · *cp* cerebral peduncle · *CPu* caudate-putamen complex · *cZI* caudal sector zona incerta · *DAB* 3,3, diaminobenzidine tetrahydrochloride · *dLGN* dorsal lateral geniculate nucleus · *dMGN* dorsal division medial geniculate nucleus · *dZI* dorsal sector zona incerta · *fr* fasciculus retroflexus · *G* gustatory thalamic nucleus · *GP* globus pallidus · *Hb* Habenula · *IAM* interoanteriormedial thalamic nucleus · *ic* internal capsule · *LD* laterodorsal thalamic nucleus · *LP* lateral posterior nucleus · *MD* mediodorsal thalamic nucleus · *MeA* medial amygdaloid nucleus · *ml* medial lemniscus · *mt* mammillothalamic tract · *NTBS* nickel tris base saline · *ot* optic tract · *PBS* phosphate-buffered saline · *Pc* paracentral thalamic nucleus · *pc* posterior commissure · *Pir* Piriform area· *Pf* parafascicular nucleus · *PMCo* posterior medial cortical amygdaloid nucleus · *Po* posterior thalamic nucleus · *Pt* parataenial thalamic nucleus · *Pv* paraventricular thalamic nucleus · *R* thalamic reticular nucleus · *Re* reuniens thalamic nucleus · *Rh* rhomboid thalamic nucleus · *rZI* rostral sector zona incerta · *scp* superior cerebellar peduncle · *sm* stria medullaris · *Spf* subparafascicular thalamic nucleus · *STN* subthalamic nucleus · *VL* ventrolateral thalamic nucleus · *vLGN* ventral lateral geniculate nucleus · *VM* ventromedial thalamic nucleus · *vMGN* ventral division medial geniculate nucleus · *VPL* ventral posterior lateral nucleus · *VPM* ventral posterior medial nucleus · *vZI* ventral sector zona incerta

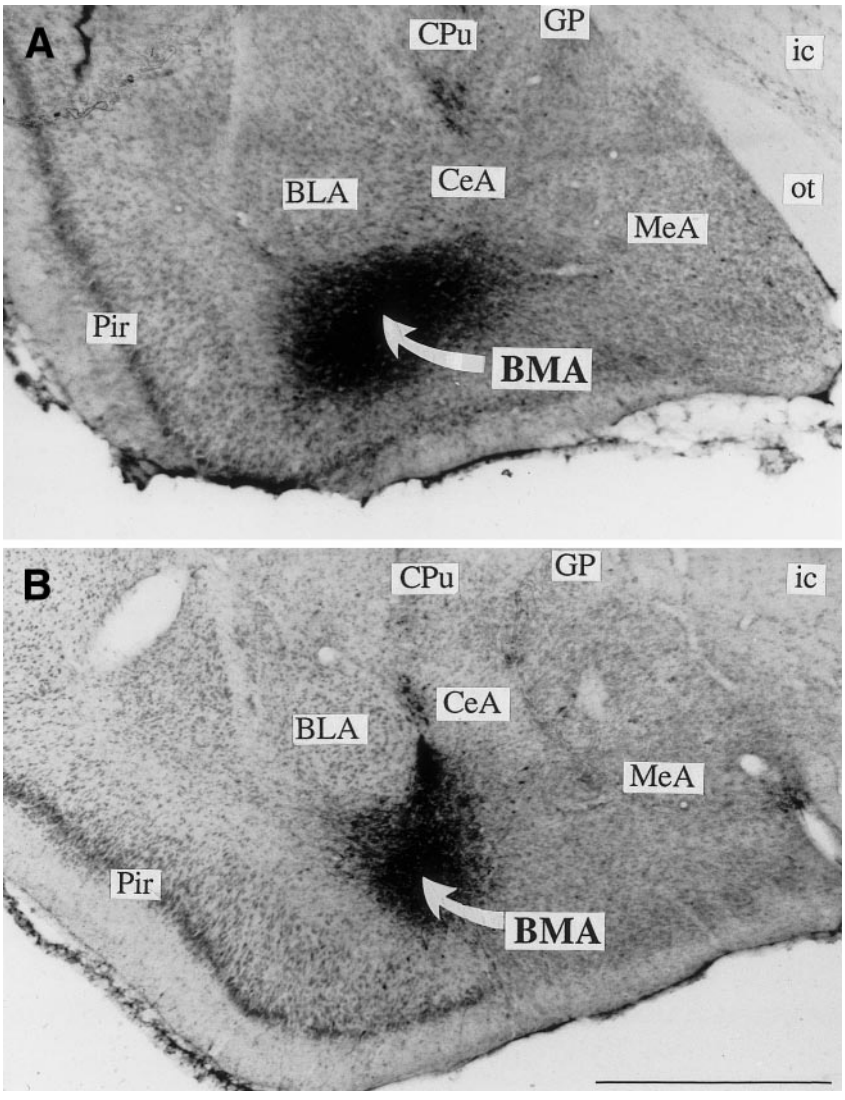

Fig. 1 A, B Examples of biotinylated dextran injection sites into the amygdala of the rat. In these cases (injections into BMA), as in all the others considered in this study, the injection site was discrete and limited to the targeted nucleus. *Arrows* indicate the focal point of the injection site within the BMA (two injections into the same nucleus are shown for comparison). Both **A** and **B** are of coronal sections; dorsal to top, and lateral to left. Sections were counterstained with neutral red. *Bar* 1 mm

and/or damaged axons of passage (Rajakumar et al. 1993; Coleman and Mitrofanis 1996; Kolmac and Mitrofanis 1997). Finally, this tracer yields strong and consistent terminal-like labelling in the thalamus after amygdaloid injections (Fig. 2).

General

The amygdaloid complex is made up of four major groups of nuclei (see de Olmos et al. 1985). These are the central, medial, basolateral and olfactory nuclei. The medial and central groups are each made up of a single nucleus, and these were injected with dextran. The basolateral and olfactory groups, on the other hand, are each made up of four and three nuclei respectively; in these cases, two nuclei of each group were injected. We thought that this series of injections would provide a worthwhile portrait of the organisation of the amygdalo-thalamic pathways. Results from the different injections into the same amygdaloid nuclei were very similar.

Organisation of the amygdalo-thalamic pathways

The morphology of the labelled terminals in the thalamus after dextran injections into the different amygdaloid nuclei appeared very similar in all cases (Fig. 2). For example, the labelled terminals seen in the zona incerta (Fig. 2A,B) were very similar in morphology and organisation to those seen in the mediodorsal thalamic nucleus (Fig. 2C,D). The labelled terminals were in the form of fine fibres with small swellings or boutons (arrows, Fig. 2). Although the morphology of labelled terminals was similar in the different thalamic nuclei, the distribution of these terminals across the thalamus was rather different.

Central amygdaloid nucleus

Figure 3 shows a series of schematic diagrams depicting the pattern of anterograde labelling seen in the thalamus after a dextran injection into the central nucleus. After

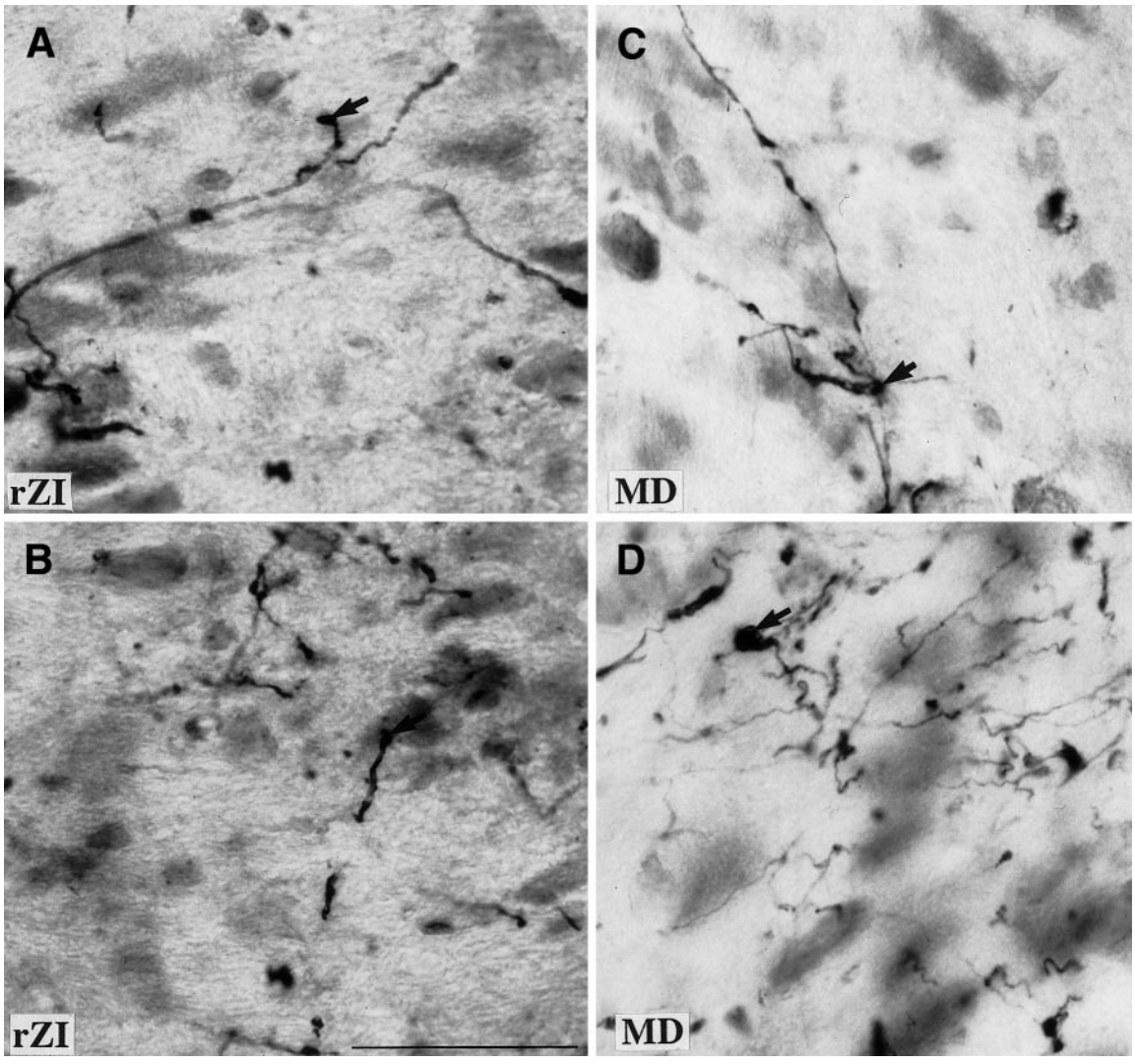

Fig. 2 A–D Examples of anterogradely labelled terminals in the thalamus after injections of biotinylated dextran into the rat amygdala. **A, B** Show labelled terminals seen in the rostral sector of the zona incerta (*rZI*) after an injection into the central nucleus of the amygdala. **C, D** Show labelled terminals in the mediodorsal thalamic nucleus (*MD*) after an injection into the amygdalo-hippocampal transition area. Note that the morphology of the labelled terminals in each nucleus after both injections was very similar. *Arrows* point to small labelled boutons. *Bar* 50 µm

this injection, as with others into the central nucleus, anterogradely labelled terminals were distributed in a number of thalamic nuclei. These terminals appeared in small, distinct regions in the medial part of the mediodorsal nucleus, rostral sector of the zona incerta and the paraventricular nucleus of the midline group. Fewer labelled fibres were seen in the rhomboid nucleus of the midline group, the ventral sector of the zona incerta and in the ventral regions of the gustatory nucleus (Fig. 3).

Medial amygdaloid nucleus

The pattern of anterograde labelling resulting from an injection of dextran into the medial nucleus is shown in Fig. 4. Other dextran injections into medial nucleus revealed similar patterns. Zones of rich anterograde labelling were seen in the medial lip of the rostral reticular nucleus, the rostral sector of the zona incerta, the ventromedial nucleus, the central-medial/paracentral nucleus and subparafascicular nucleus of the intralaminar group and in small isolated patches of the posterior thalamic nucleus. A few labelled terminals were also seen in the nucleus reuniens of the midline group and in the dorsal and caudal sectors of the zona incerta.

Olfactory amygdala

The olfactory amygdala injected in this study were the anterior cortical nucleus and the amygdalo-hippocampal transition area. Labelling patterns in the thalamus after injections into each of these nuclei were very similar

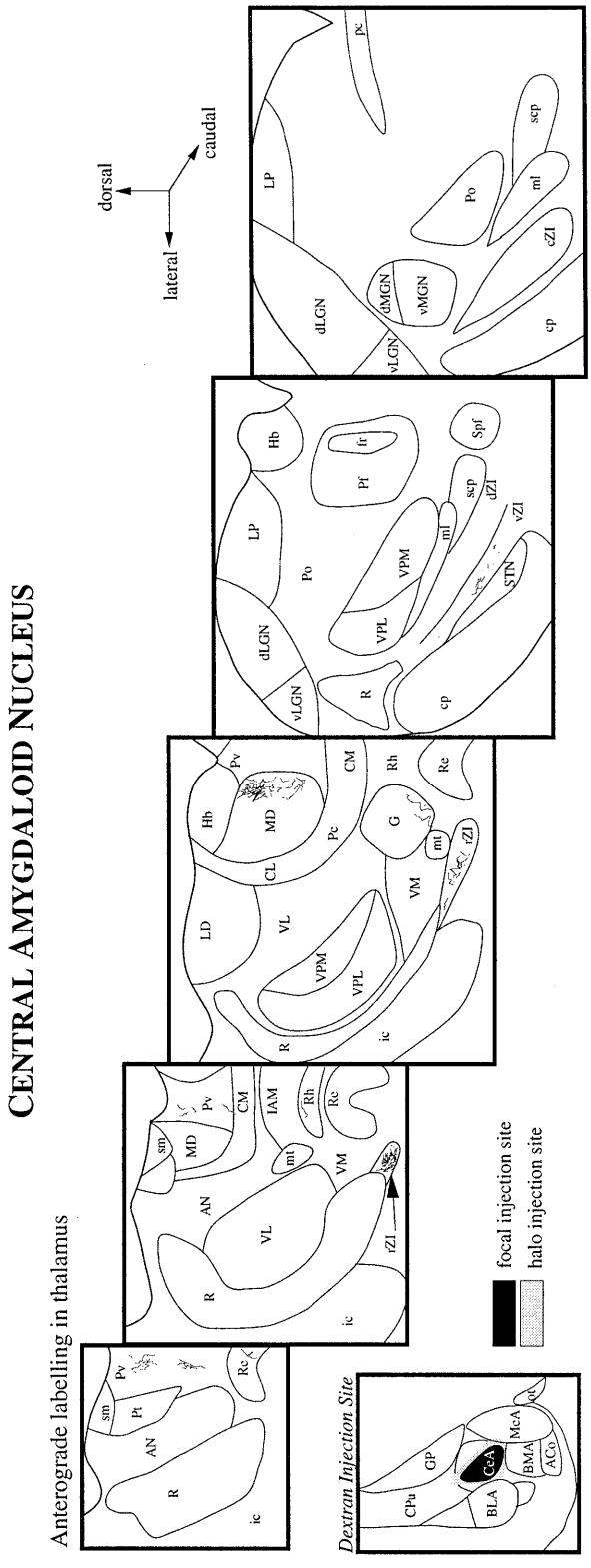

Fig. 3 Schematic diagrams of the distribution of anterogradely labelled terminals in the rat thalamus after an injection of biotinylated dextran into the central nucleus of the amygdala (injection site shown). Labelled axons in the thalamus with boutons were drawn; labelled axons of passage (thicker and with no boutons) were not drawn. Sections were approximately 200 µm apart. Nuclear borders were determined after Nissl counterstaining

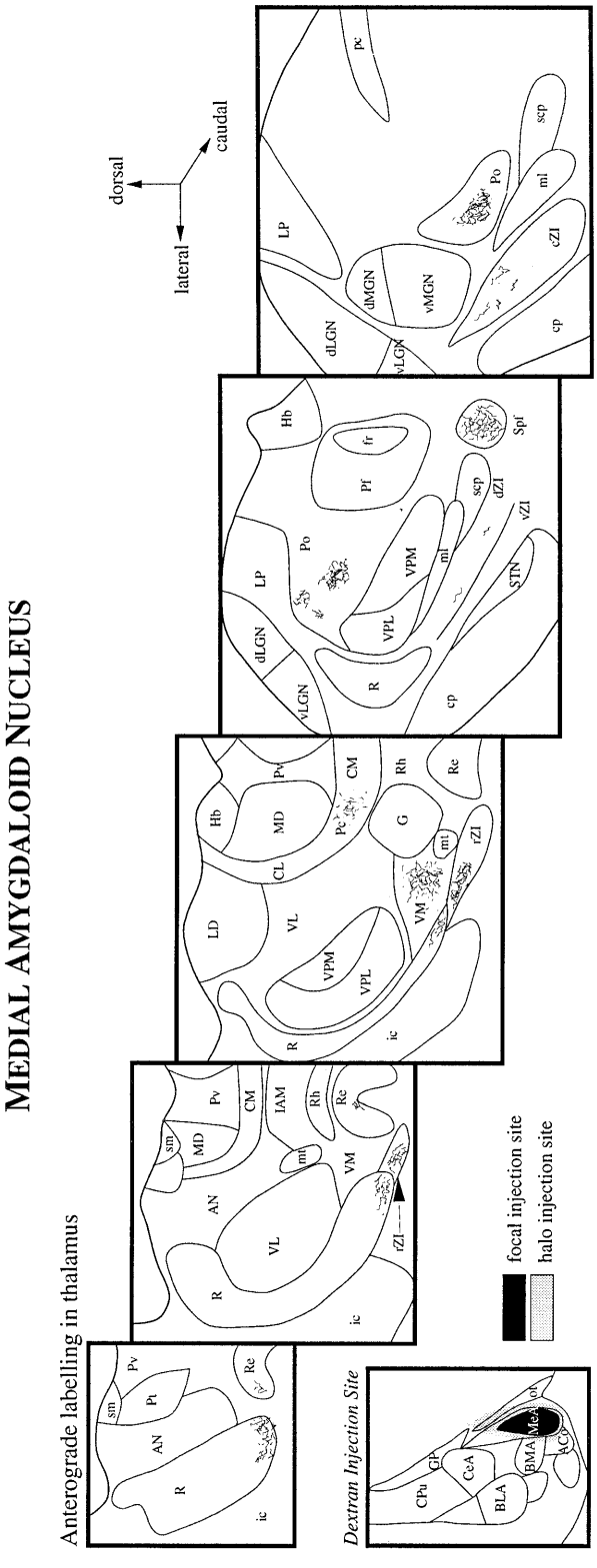

Fig. 4 Schematic diagrams of the distribution of anterogradely labelled terminals in the rat thalamus after an injection of biotinylated dextran into the medial nucleus of the amygdala (injection site shown). Labelled axons in the thalamus with boutons were drawn; labelled axons of passage (thicker and with no boutons) were not drawn. Sections were approximately 200 µm apart. Nuclear borders were determined after Nissl counterstaining

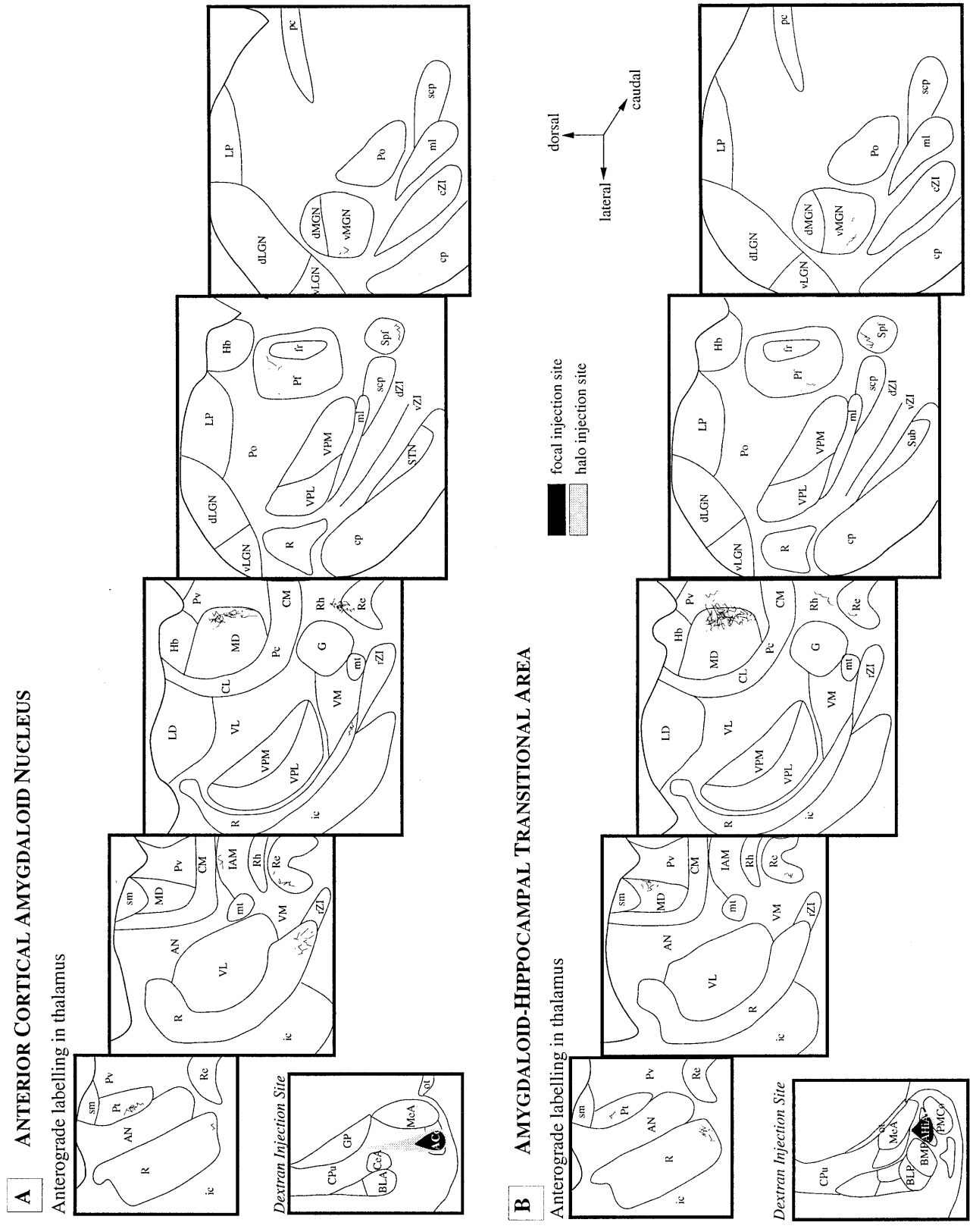

Fig. 5 Schematic diagrams of the distribution of anterogradely labelled terminals in the rat thalamus after injections of biotinylated dextran into the anterior cortical (**A**) and the amygdalo-hippocampal transitional area (**B**) nuclei of the olfactory amygdala (injection sites shown). Labelled axons in the thalamus with boutons were drawn; labelled axons of passage (thicker and with no boutons) were not drawn. Sections were approximately 200 µm apart. Nuclear borders were determined after Nissl counterstaining

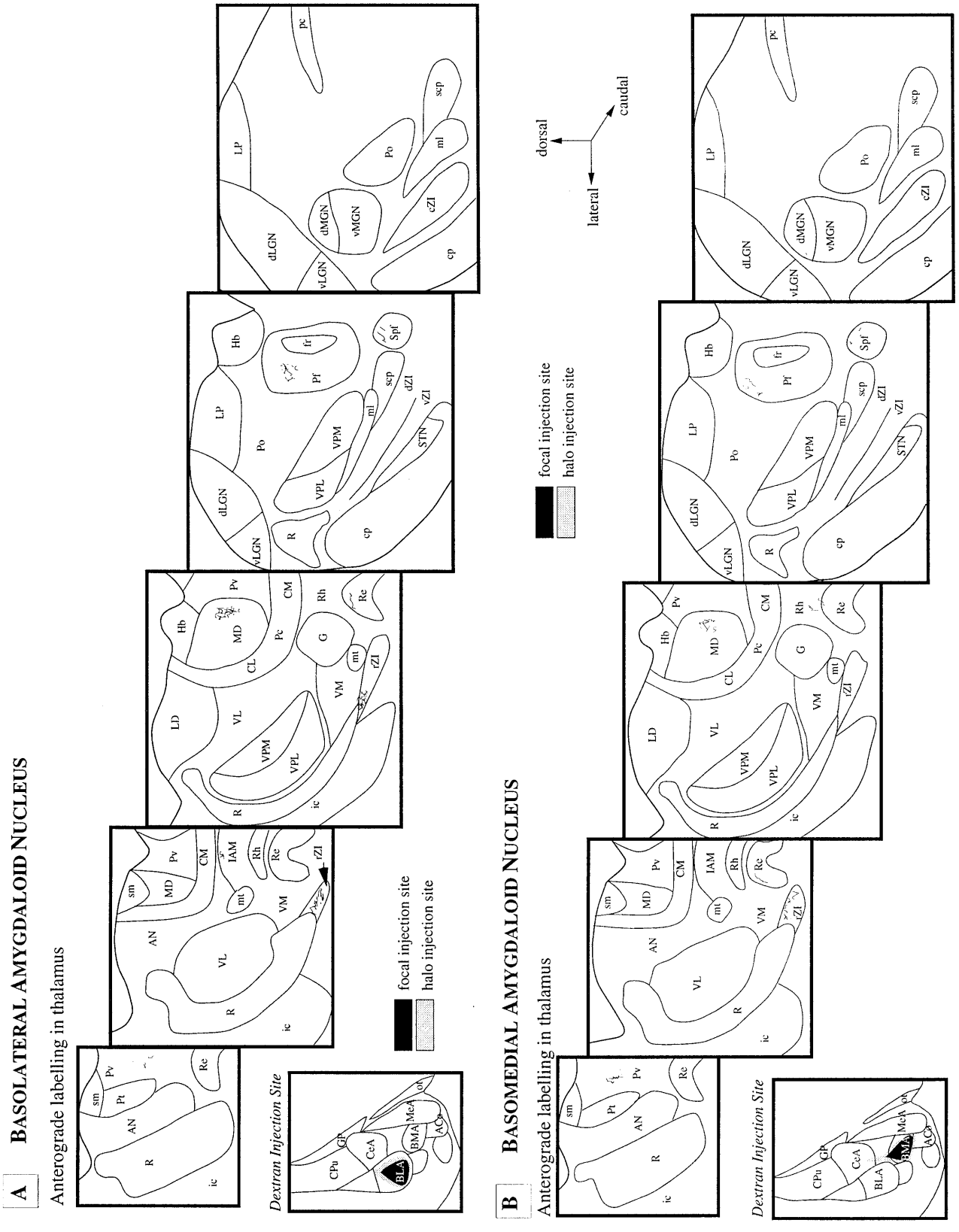

Fig. 6 Schematic diagrams of the distribution of anterogradely labelled terminals in the rat thalamus after injections of biotinylated dextran into the basolateral (**A**) and the basomedial (**B**) nuclei of the basolateral complex (injection sites shown). Labelled axons in the thalamus with boutons were drawn; labelled axons of passage (thicker and with no boutons) were not drawn. Sections were approximately 200 µm apart. Nuclear borders were determined after Nissl counterstaining

(Fig. 5A,B). In general, many labelled terminals were seen in the medial regions of the mediodorsal nucleus and in various nuclei of the midline group, including the paraventricular, parataenial, rhomboid and reuniens nuclei. Labelled terminals were also seen in the medial lip of the rostral reticular nucleus, the parafascicular and subparafascicular nuclei of the intralaminar group and in the ventral division of the medial geniculate nucleus. Other regions of the thalamus were usually devoid of labelled terminals.

Basolateral complex

In this study, we made injections into the basolateral and basomedial nuclei of the basolateral complex (Fig. 6). After injections into each of these nuclei, many labelled terminals were found in the medial regions of the mediodorsal nucleus; a few labelled terminals were seen within various midline (e.g. paraventricular, rhomboid and interanteromedial) and intralaminar (e.g. parafascicular, subparafascicular) nuclei (Fig. 6). In addition, the basolateral injections yielded many labelled terminals within the rostral sector of the zona incerta (Fig. 6).

Discussion

This study has three major findings:

1. The amygdala sends a well-defined projection to distinct nuclei of the greater thalamus.
2. There are some differences in the projections patterns of the different amygdaloid nuclei to the thalamus.
3. When comparing our results on the amygdalo-thalamic pathway to the many previous descriptions of the thalamo-amygdaloid pathways, we note that they are, for the most part, not in register with one another.

Each of these findings will be discussed separately below.

Organisation of a well-defined amygdalo-thalamic pathway

The present study shows that, rather than "blanket" all of the thalamus with terminations, the amygdala is very particular regarding its terminations within the thalamus (see also McDonald 1985; Russchen et al. 1987; Kretteck and Price 1977). In essence, the amygdala has a discrete and precise set of projections to distinct nuclei of the thalamus, a feature that was not clear from previous studies since none had focussed specifically on the amygdalo-thalamic pathway. We show that the thalamic nuclei with the heaviest amygdaloid projections include the mediodorsal nucleus, various midline nuclei (eg, paraventricular, parataenial) and the zona incerta (rostral sector). Thus, rather than have a very global effect on thalamic, and hence cortical activity, the amygdala may be in a position to influence particular thalamo-cortical pathways and therefore particular functional areas of neocortex.

This relationship that the thalamus shares with the amygdala is very similar to the one that it shares with the basal forebrain and with the brainstem, at least in terms of patterns of connections. Both the basal forebrain and brainstem, for example, appear to target particular thalamic nuclei with their projections. For instance, different centres of the basal forebrain (e.g. nucleus of the diagonal band, substantia innominata, nucleus basalis) have restricted terminations within the midline (e.g. parataenial, rhomboid), intralaminar (e.g. central-lateral, paracentral), zona incerta, reticular, gustatory and mediodorsal nuclei (see Kolmac and Mitrofanis 1999), whilst different brainstem nuclei target the zona incerta, reticular, lateral posterior, intralaminar (e.g. parafascicular, central-lateral) and midline (e.g. reuniens, intermedialanterior) nuclei for innervation (see Kolmac and Mitrofanis 1998; Kolmac et al. 1998). For the most part, these thalamic nuclei are the same as those targeted by the amygdala. Thus, the reticular nucleus, midline, intralaminar, zona incerta and mediodorsal nuclei can be viewed as thalamic nuclei transmitting functionally diverse subcortical information to the neocortex. The first-order (except for medial geniculate nucleus) and higher-order (except for the mediodorsal and posterior thalamic nuclei) nuclei are largely devoid of these subcortical projections.

Distinct amygdaloid groups have different patterns of projections with the greater thalamus

Our results indicate that there are some distinct differences in the patterns of projections to the thalamus from the different amygdaloid groups. For instance, no thalamic nucleus receives a projection from all amygdaloid groups, although some receive a projection from most (e.g. mediodorsal, midline, zona incerta), whilst other thalamic nuclei receive a projection from only one or two (e.g. posterior thalamic, reticular). This finding would suggest that even among the amygdaloid groups projecting to the thalamus, there appears to be some heterogeneity. Although the patterns of projection from nuclei of different amygdaloid groups are different, the patterns of projection from nuclei within the same groups are very similar; that is, the basolateral and basomedial nuclei of the basolateral group had similar projections as do the anterior cortical and the amygdalo-hippocampal transition area of the olfactory group. This would suggest that nuclei within the same functional group of amygdaloid nuclei may impart a similar influence on the activity of the thalamus.

Comparison between the amygdalo-thalamic and thalamo-amygdaloid pathways: are they out of register?

Many previous studies have documented the organisation of the thalamo-amygdaloid pathway and it would be

Table 1 Organisation of the thalamo-amygdaloid pathways in rats [thalamo-amygdaloid results taken from Kretteck and Price (1978), Veening (1978) Otterson and Ben-Ari (1979), Nitecka et al (1979), Le Doux et al (1988), Turner and Herkenham (1991); amygdalo-thalamic (reciprocal) results taken from the present study]

Amygdaloid nucleus	Thalamic origins	Reciprocal?
Central	Ventroposterior	–
	Medial geniculate	–
	Midline	√
	Intralaminar	–
Medial	Medial geniculate	–
	Mediodorsal	–
	Midline	–
	Intralaminar	√
Basolateral	Ventroposterior	–
	Medial geniculate	–
	Lateral posterior	–
	Mediodorsal	–
	Midline	√
	Intralaminar	√
Olfactory	Medial geniculate	√
	Midline	√
	Intralaminar	√

useful to compare these projections with the amygdalo-thalamic projections described in this study. Table 1 shows the thalamic projections to each amygdaloid group reported by previous studies. These results, taken together with ours, indicate that only a minority of the thalamo-amygdaloid pathways to the different amygdaloid nuclei are reciprocated by a projection back from these nuclei. Indeed, only the midline and intralaminar, and to a lesser extent the medial geniculate, nuclei seem to have strong reciprocal relationships with the different nuclei of the amygdala. The other nuclei, namely the ventroposterior, lateral posterior and mediodorsal nuclei seem to not receive afferents back from the amygdala. Thus, except for the classical "non-specific" midline and intralaminar nuclei, there does not appear to be a strong feed-back relationship between the thalamus and the amygdala. The significance of this unusual and rather particular relationship is not clear at present. It remains to be determined which one of these pathways, thalamo-amygdaloid or amygdalo-thalamic, is in fact the feed-forward pathway, and which one the feed-back.

At this point, some comment on reciprocal thalamic projections with other brain centres should be made. Perhaps the best-described and most precise set of reciprocal connections that the thalamus has is with the neocortex. For these connections, there is no thalamic nucleus that does not receive a projection back from the cortical area(s) it projects to, although the cortico-thalamic projections do tend to be a little more widespread than the corresponding thalamo-cortical projections (see Steriade et al. 1997). For the brainstem, a slightly different organisation is apparent. Most brainstem nuclei have rich projections to several dorsal thalamic (particularly the intralaminar and midline groups) and ventral (reticular nucleus and zona incerta) nuclei; these same brainstem nuclei receive a projection back from the zona incerta only (see Kolmac and Mitrofanis 1997; Kolmac et al. 1998). Thus, on the one hand, some centres have strong reciprocal connections with the thalamus (e.g., neocortex), whilst other centres have weak reciprocal connections (e.g., brainstem). The amygdala's relationship with the thalamus appears to lie somewhere in between these two extremes, although leaning more towards weak reciprocity.

Conclusions

On the whole, the present results indicate that the amygdala might be in a position to influence particular thalamo-cortical pathways, particularly those involved in emotion, memory and viscero-sensation (see review by Jones 1985), by its rather specific targeting of various thalamic nuclei (e.g. mediodorsal, midline, zona incerta).

Acknowledgements We thank Sharon Spana for technical assistance. The grant sponsor was NHMRC of Australia, grant no. 990255.

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