CHAPTER 4

Thalamocingulate Connections in the Monkey

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All cortical areas make massive reciprocal connections with the dorsal thalamic nuclei and because the great majority of subcortical inputs to the cortex originate from the dorsal thalamic nuclei, many believe that these thalamocortical inputs are essential for normal cortical functions. Although it remains unclear how they specifically contribute to cortical function, it has been suggested that they operate both as a way station for transmitting information from subcortical regions to the cortex (Sherman and Guillery, 2001) and as an "indirect relay" station for communicating information between different cortical regions (Rouiller and Welker, 2000). Regardless of which of these two modes is operative, the dorsal thalamic nuclei do not merely transfer information to the cortex, but they are an active integrator or modulator of information that is essential for normal cortical function. To this end, it is an essential prerequisite to know the details of the underlying connectivity between the dorsal thalamus and cortex.

The cingulate cortex consists of four major regions (ordered posterior to anterior): posterior cingulate cortex (PCC), retrosplenial cortex (RSC), midcingulate cortex (MCC), and anterior cingulate cortex (ACC; Chapters 1, 3, 13; Vogt, 1993: Vogt *et al.*, 2004, 2005). These four divisions are comprised of more than 20 different cortical areas that lie within the cingulate gyrus and the banks of the adjoining cingulate and callosal sulci in monkeys and humans. Recent anatomical studies using axonal transport methods in monkeys have uncovered a rough picture of thalamocingulate connectivity—each cingulate area has connections with a different set of thalamic nuclei as discussed in this chapter. These thalamic nuclei represent not only associational and midline/intralaminar thalamic nuclei but also parts of the motor and sensory thalamic nuclei. We must bear in mind that many more connections remain to be elucidated for most cingulate areas. For detailed cytoarchitecture and nomenclature of the monkey dorsal thalamus, the reader should consult the textbooks of Jones (1985, 1998) and Steriade *et al.* (1997).

Goals of This Chapter

A long tradition of cortical neurobiology holds the view that essential cortical function is determined to a large extent by its thalamic afferents. Although cingulate cortex plays an important role in intrinsically generated, top-down cognitive processing, thalamic afferents are critical for its roles in memory, nociception, response selection, and visuospatial processing. In this chapter we review the anatomical organization of thalamocortical and corticothalamic projections of the monkey cingulate gyrus. The specific goals of this chapter are as follows:

1. Evaluate thalamic projections of the dorsal and ventral parts of area 23 with retrograde tracers.
2. Demonstrate reciprocal projections to the dorsal thalamus with biotinylated dextran amine (BDA), a marker of anterograde transport, from parts of area 23 and the retrosplenial areas.
3. Describe the differential thalamic inputs to the rostral and caudal cingulate motor areas which are themselves pivotal to defining the midcingulate region.
4. Review the differential thalamic inputs to anterior cingulate areas with an important demonstration of those to area 32.
5. Summarize dorsal thalamic inputs to the entire cingulate gyrus and consider the memory, motor, and visuospatial consequences of these connections to cingulate functions.

Posterior Cingulate Cortex

The PCC consists of areas 23a, 23b, and 23d, which reside at the surface of the caudal posterior cingulate gyrus, area 23c in the ventral bank of the caudal cingulate sulcus, and area 31, which lies dorsal to area 23b (Vogt *et al.*, 1987, 1995, 1997). Areas 23a and 23b are further divided into ventral areas 23a and 23b (areas v23a and v23b), which are located posteroventral to the splenium of the corpus callosum, and dorsal areas 23a and 23b (areas v23a and v23b), which are located dorsal to the corpus callosum (Vogt *et al.*, 2005). Differentiation of these areas is based on findings that show areas v23a/b differ from areas d23a/b in cytoarchitecture, chemoarchitecture, and corticocortical and thalamocortical connectivity (Goldman-Rakic *et al.*, 1984; Morris *et al.*, 1999b; Shibata and Yukie, 2003; Vogt *et al.*, 2005; Yukie, 1995).

These ventrodorsal differences in area 23 are also corroborated by human clinical and neuroimaging studies showing that both areas v23a/b and d23a/b may contribute to spatial memory (Maguire, 2001), but areas v23a/b alone may contribute to other kinds of memory, such as verbal (Rudge and Warrington, 1991) and auditory-verbal memory (Grasby *et al.*, 1993). In addition to subdividing area 23 according to its ventrodorsal characteristics, recent cytoarchitectonic assessment of monkey cortex has demonstrated that the most rostral part of area d23a/b can be subdivided into an area 23d, a dysgranular area transitional to the most caudal part of area 24 (Vogt *et al.*, 2005). Taken together, these studies indicate that the PCC consists of areas v23a, v23b, d23a, d23b, 23d, 23c, and 31.

Area v23b

Retrograde neuronal tracer studies have demonstrated that area v23b receives thalamocortical projections mainly from the anterior thalamic, medial pulvinar, and lateral posterior nuclei as shown in Figure 4.1A-F (Shibata and Yukie, 2003). In the anterior nuclei (Fig. 4.1C), projections originate from the rostral parts of the anteromedial and anteroventral nuclei. In the medial pulvinar nucleus (Fig. 4.1F), projections originate from cells aggregated in patches mainly in the medial part of the nucleus. In the lateral posterior nucleus, however, projections originate from a disparate population of cells. We observed that a large retrograde tracer injection into area v23b labeled many cells mainly in the medial part of the lateralis posterior nucleus (Fig. 4.1E), whereas a small injection restricted to a part of area v23b labeled only a few cells (not illustrated). This suggests that the lateral posterior nucleus may have localized projection fields within area v23b. In addition to these major projections, area v23b receives minor projections from the central latocellular, limitans, reuniens and laterodorsal nuclei, and the dorsal parts of the ventral anterior and lateral nuclei.

Corticothalamic projections from area v23b terminate mainly in the anteromedial, anteroventral, laterodorsal, lateral posterior, and medial pulvinar nuclei as shown in Figure 4.2A-F (Shibata and Yukie, 2003). In the medial pulvinar nucleus (Fig. 4.2F), area v23b terminal projections distribute onto patches, especially in the dorsomedial part of the nucleus. Area v23b also sends minor projections to the limitans nucleus and the dorsal part of the ventral lateral nucleus (Shibata and Yukie, 2003).

Area d23b

Area d23b receives thalamocortical projections from more nuclei than does area v23b as shown in Figure 4.1G-L: the lateral posterior and medial pulvinar nuclei, the central latocellular nucleus, the lateral part of the mediodorsal nucleus, and the dorsal parts of the ventral anterior and lateral nuclei (Shibata and Yukie, 2003). Although area d23b also receives projections from the anteromedial and anteroventral nuclei, these are weaker than those to area v23b and originate mainly from the caudal parts of these anterior nuclei. In addition, area d23b receives minor projections from the laterodorsal, reuniens, and limitans nuclei (Fig. 4.1G-L) (Shibata and Yukie, 2003).

Corticothalamic projections from area d23b terminate mainly in the anteromedial, anteroventral, laterodorsal, lateral posterior and medial pulvinar nuclei, and in the dorsal parts of the ventral anterior and lateral nuclei (Fig. 4.2G-L; Shibata and Yukie, 2003). Projections from area d23b to the anteromedial and anteroventral nuclei terminate mainly in caudal parts of these nuclei. In the medial pulvinar nucleus, the terminal fields of area d23b projections reach as far as the medial border of the lateral pulvinar nucleus (Fig. 4.2L; Shibata and Yukie, 2003). This contrasts with the findings of a previous study (Baleydier and Mauguière, 1985) suggesting that area d23b projections terminated in a restricted region of the dorsal part of the medial pulvinar nucleus. Area d23b also sends minor projections to the limitans nucleus, the central latocellular and lateral nuclei, the dorsolateral part of the mediodorsal nucleus, and the medial part of the lateral pulvinar nucleus (Fig. 4.1G-L).

Retrosplenial Areas 29 and 30

Retrosplenial areas 29 and 30 are located in the dorsal bank of the caudal callosal sulcus (Vogt *et al.*, 1987, 1997, 2005; Morris *et al.*, 1999b). Area 29 occupies the lateral part of the bank, whereas area 30 occupies the medial part, adjoining area 23a. Retrosplenial areas 29 and 30 are hypothesized to have a pivotal role in memory access (Chapter 13; Vogt *et al.*, 1997); however, definitive functional studies in monkeys are still lacking, because monkey area 29/30 is small and difficult to access experimentally.

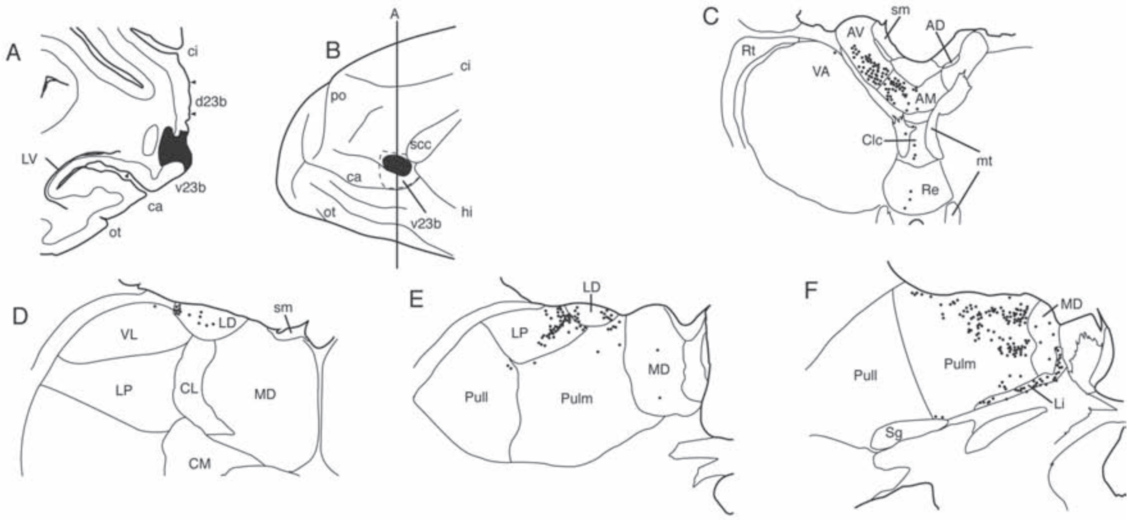
Most of the thalamocortical projections to area 30 originate from the anteroventral nucleus as shown in Figure 4.1M-R (Shibata and Yukie, 2003). The projections to area 30 arise mainly from the rostral and caudodorsolateral parts of the anteroventral nucleus. Projections to area 29 originate exclusively from the dorsolateral part of the anteroventral nucleus and the entire anterodorsal nucleus (Fig. 4.1S-X).

Corticothalamic projections from area 30 terminate mainly in the mid-rostrocaudal parts of the anteromedial and anteroventral nuclei (Fig. 4.2M-R). Projections from area 30 to the medial pulvinar, laterodorsal, and ventral lateral nuclei are much sparser than those from areas v23b and d23b. After injection of tritiated amino acids into area 30, Morris *et al.* (1999a) observed labeled terminals in the anteroventral, anterodorsal, laterodorsal, and lateral posterior nuclei. However, this widespread labeling may be because their injection involved the adjoining area 23. Since most thalamocortical projections are generally reciprocated by corticothalamic projections (e.g., Steriade *et al.*, 1997), it logically follows that area 29 may also project mainly to the anterodorsal nucleus and some parts of the anteroventral nucleus. However, the definitive targets of corticothalamic projections from area 29 remain unknown.

Midcingulate Area 24´

The MCC consists of areas 24a´, 24b´, and 24c´. Areas 24a´ and 24b´ are located on the medial gyral surface, whereas area 24c´ is on the ventral bank of the cingulate sulcus (Chapter 3; Vogt *et al.*, 1997, 2005). Areas 24a´/b´

WGA-HRP injection into area v23b



WGA-HRP injection into area d23b

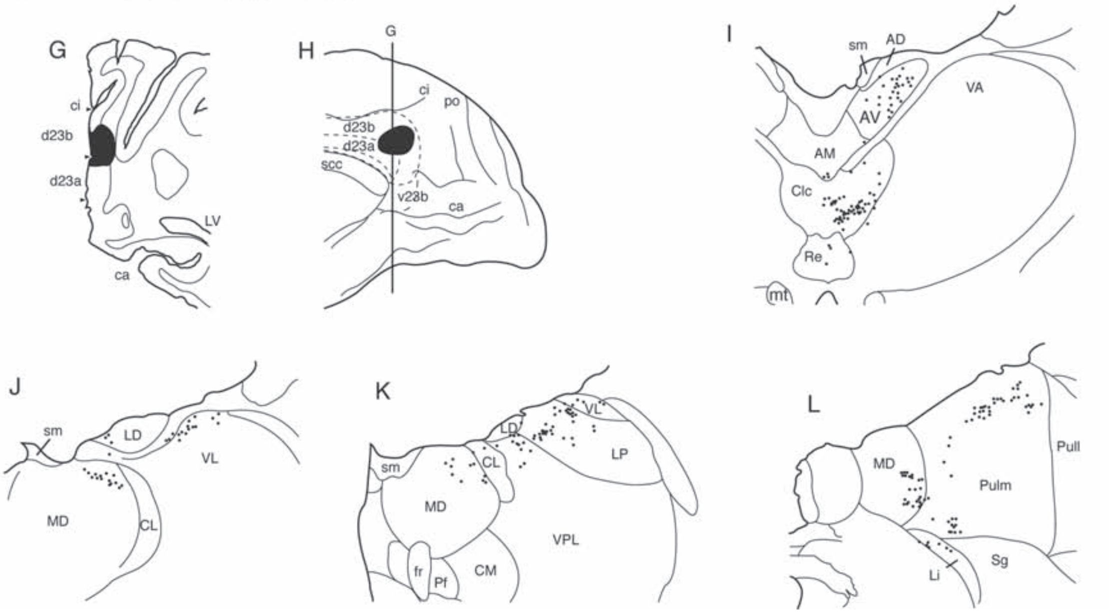


Fig. 4.1 Diagrams of the distribution of retrogradely labeled cells (one dot/labeled neuron) in the dorsal thalamus following injections of retrograde tracers involving area v23b (A-F), area d23b (G-L), area 30 (M-R), and area 29 (S-X). In S-X, the DY injection site and DY-labeled cells are shown in black, whereas the CTb-injection site and CTb-labeled cells are shown in gray. A, G, M, S, and T depict injection sites in drawings of brain sections cut in a transverse plane. B, H, N, and U indicate the rostrocaudal level of the injection site viewed from the medial aspect of the hemisphere. C-F, I-L, O-R, and V-X (arranged in rostrocaudal order) depict the distribution of labeled cells in dorsal thalamic nuclei. Modified from Shibata and Yukie (2003).

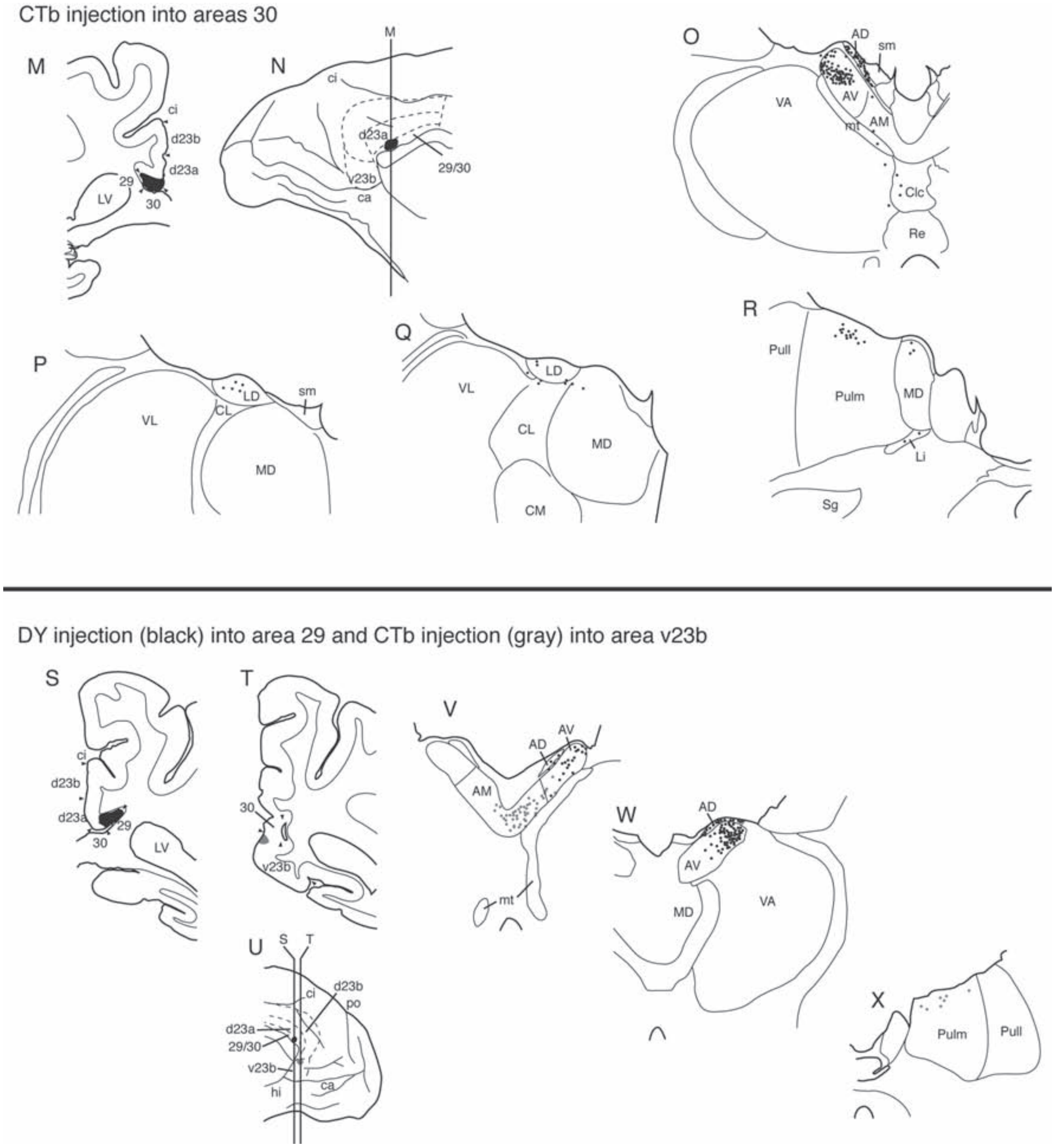


Fig. 4.1 (*Continued.*)

are further subdivided into posterior (areas p24a´/b´) and anterior parts (areas a24a´/b´) on the basis of cyto- and chemoarchitectonic differences (Vogt *et al*., 2003). Area 24c´ can be further subdivided along its caudorostral axis into areas 24d, p24c´, and a24c´. These three subareas with their fundal extensions may correspond, respectively, to the lower trunk and leg representation region of the caudal cingulate motor area, the upper trunk and arm representation region of the caudal cingulate motor area, and the rostral cingulate motor area (Chapter 5; Dum and Strick, 1991; He *et al*., 1995; Vogt *et al*., 2005). However, some discrepancies remain relating the anatomical parcellation of the cingulate motor areas to the precise delineation of their somatotopic maps. Some authors define the caudal cingulate motor area as the ventral cingulate motor area, which corresponds to our caudal cingulate motor area, and dorsal cingulate motor area (Dum and Strick, 1991; Dum and Strick, 1993; Takada *et al*., 2001). The latter area, however, may be the part of medial area 6 that extends into the dorsal bank of the cingulate sulcus (Dum and Strick,1993; He *et al*., 1995; Vogt *et al*., 2005), rather than part of the MCC.

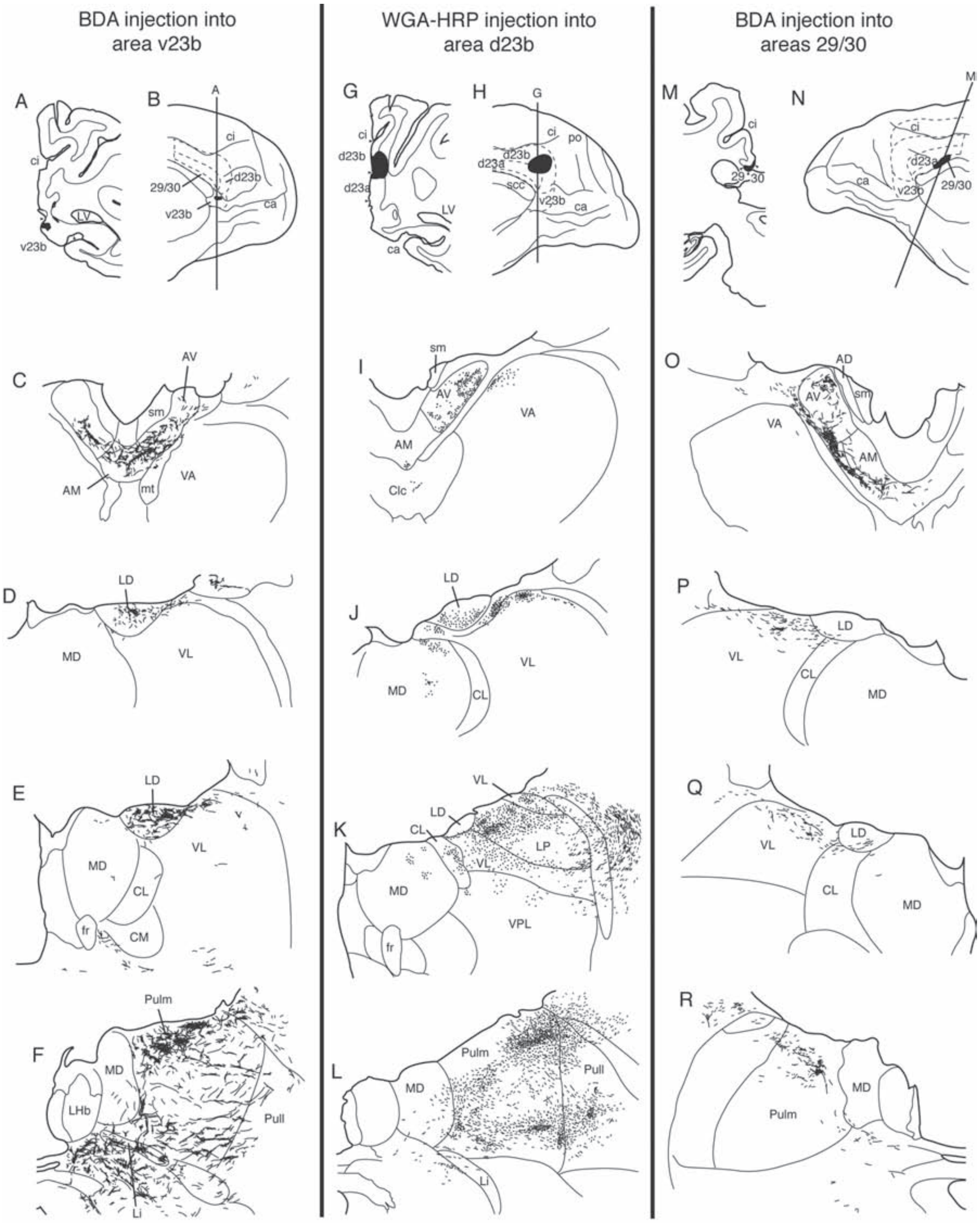


Fig. 4.2 Diagrams of the distribution of anterogradely labeled fibers (lines) and terminals (dots) in the dorsal thalamus, following injections of BDA into area v23b (A-F), WGA-HRP into area d23b (G-L), and BDA into area 30 (M-R). A, G, and M depict injection sites in a transverse plane. B, H, and N indicate the rostrocaudal level of the injection site viewed on the medial surface. C-F, I-L, and O-R are in rostrocaudal order and depict the distribution of labeled fibers and terminals in the dorsal thalamic nuclei. Modified from Shibata and Yukie (2003).

The caudal and rostral cingulate motor areas are anatomically characterized by the direct projections to primary motor cortex (Dum and Strick, 1991; Morecraft and Van Hoesen, 1992; Muakkassa and Strick, 1979) and spinal cord (Biber *et al.*, 1978; Dum and Strick, 1991; Hutchins *et al*, 1988; Luppino *et al.*, 1994; Murray and Coulter, 1981). The caudal cingulate motor area is involved in execution of voluntary movements, whereas the rostral cingulate motor area is involved in selection of these movements (Procyk *et al.*, 2000; Shima *et al.*, 1991; Shima and Tanji, 1998; Tanji *et al.*, 2002). These issues are thoroughly considered in Chapter 5. Thalamocortical connections of the forelimb representation regions within caudal (area p24c´) and rostral cingulate motor areas (area a24c´) have recently been analyzed (Hatanaka *et al.*, 2003). However, those of other regions within the caudal and rostral cingulate motor areas (e.g., area 24d) and the cingulate gyral areas 24a´/b´ have not yet been studied in detail.

Area p24c´

Thalamic projections to the forelimb representation region in the caudal cingulate motor area, which largely corresponds to area p24c´, have recently been analyzed using retrograde tracers. Hatanaka *et al.* (2003) showed that these projections originate primarily from the oral and caudal parts of the ventral lateral nucleus, the oral part of the ventral posterolateral nucleus, and the transitional region between the caudal part of the ventral lateral nucleus and the oral part of the ventral posterolateral nucleus as shown in Figure 4.3A-E. Other prominent afferents also originate from the central lateral nucleus and the centre médian-parafascicular nucleus, especially from the dorsal region of its pars media (Fig. 4.3C-F). Minor projections originate from the parvicellular part of the ventral anterior nucleus, the medial part of the ventral lateral nucleus, and the mediodorsal nucleus (Fig. 4.3). Cells in the ventral lateral nucleus that project to area p24c´ appear to receive projections from the cerebellum (Dum and Strick, 1993; Hatanaka *et al.*, 2003). Corticothalamic projections from area p24c´ may terminate mainly in the caudal part of the ventral lateral nucleus (McFarland and Haber, 2002; Van Hoesen *et al.*, 1993).

Area a24c´

Thalamic projections to the forelimb representation region of the rostral cingulate motor area within area a24c´ originate predominantly from the parvicellular part of the ventral anterior nucleus, the oral part of the ventral lateral nucleus, the caudalmost part of the mediodorsal nucleus, and the intralaminar nuclei (i.e., central lateral nucleus and centre médian-parafascicular nucleus) as shown in Figure 4.4 (Hatanaka *et al.*, 2003). Projections from the ventral anterior and ventral lateral nuclei to the rostral cingulate motor area terminate in layers I, III, and V (McFarland and Haber, 2002). Some projections also originate from the medial part of the ventral lateral nucleus (Fig. 4.4A-D; Hatanaka *et al.*, 2003).

The corticothalamic projections from area a24c´ appear to terminate mainly in the rostral part of the ventral anterior nucleus (McFarland and Haber, 2002; Van Hoesen *et al.*, 1993). Area a24c´ also projects to the caudoventral part of the parvicellular division of the mediodorsal nucleus (Erickson and Lewis, 2004).

As described above, the thalamocortical connections of areas p24a´/b´ and a24a´/b´ are yet to be definitively characterized. Our preliminary unpublished data, however, indicate that these areas may connect mainly with the anterior, midline, and medial pulvinar nuclei, rather than the ventral anterior/lateral nuclei. Other areas in the gyral as well as sulcal cortex within the MCC may also project to the ventral anterior nucleus (Erickson and Lewis, 2004), although details of this projection remain to be described.

Anterior Cingulate Cortex

The ACC is located around the genu of the corpus callosum and is distinguishable structurally and functionally from MCC (Vogt *et al.* 1997, 2004). The ACC consists of areas 24, 32, and 25. Area 24 is further divided into areas 24a and 24b on the gyral surface around the genu of the corpus callosum and area 24c in the dorsal bank of the rostral cingulate sulcus. Area 32 lies rostral to areas 24a and b, whereas area 25 lies ventral to the genu.

The ACC, especially areas 32 and 25 and the subgenual areas 24a/b, may modulate emotion, mood state, and visceromotor functions in humans (Blood *et al.*, 1999; Drevets, 2000; Drevets *et al.*,, 1997; Kondo *et al.*, 2003; Mayberg *et al.*, 2000; Simpson *et al.*, 2001a, 2001b). Although the specific functional roles played by each area are largely unknown, areas 24, 32, and 25 may be involved in different aspects of these functions. This view is supported by anatomical studies in monkeys demonstrating different subcortical projections from areas 24, 32, and 25 to autonomic control centers including the bed nucleus of the stria terminals, hypothalamus, periaqueductal gray, and parabrachial nucleus (An *et al.*, 1998; Chiba *et al.*, 2001; Freedman *et al.*, 2000; Öngür *et al.*, 1998).

Area 24

Thalamocortical projections to areas 24a-c originate mainly from the rostral part of the ventral anterior nucleus and from midline and intralaminar nuclei

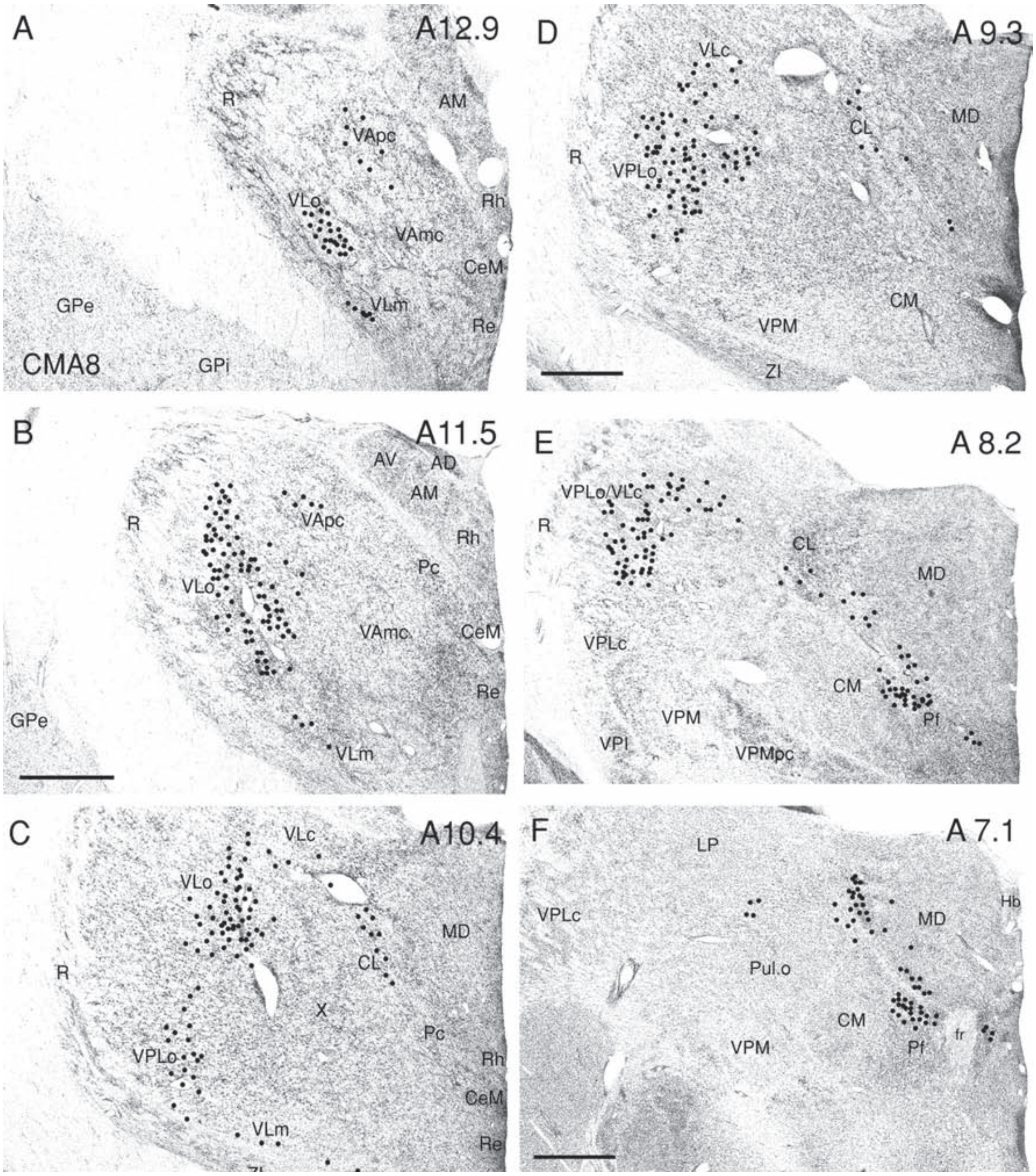


Fig. 4.3 Retrogradely labeled cells (dots) plotted onto Nissl-stained sections following an injection of BDA into the forelimb representation region of the caudal cingulate motor area within area 23c. Numbers on the right upper corner of each panel denote the distance from the external auditory meatus. Modified from Hatanaka *et al.* (2003).

(i.e., the central densocellular, central superior lateral, central lateral, parafascicular, and limitans nuclei) (Vogt *et al.*, 1987). The parvicellular division of the ventral anterior nucleus projects to area 24b, terminating in patches within layers I, III, and V (McFarland and Haber 2002). The medial pulvinar nucleus projects to areas 24a-c, terminating in layers III and IV (Romanski *et al.*, 1997). This projection mainly terminates in area 24b. Minor projections originate from parts of the mediodorsal nucleus (the caudalmost part of the densocellular subnucleus and the peripheral part of the parvicellular subnucleus) (Vogt *et al.*, 1987); the dorsomedial part of the anteromedial nucleus; and other parts of midline and intralaminar nuclei,

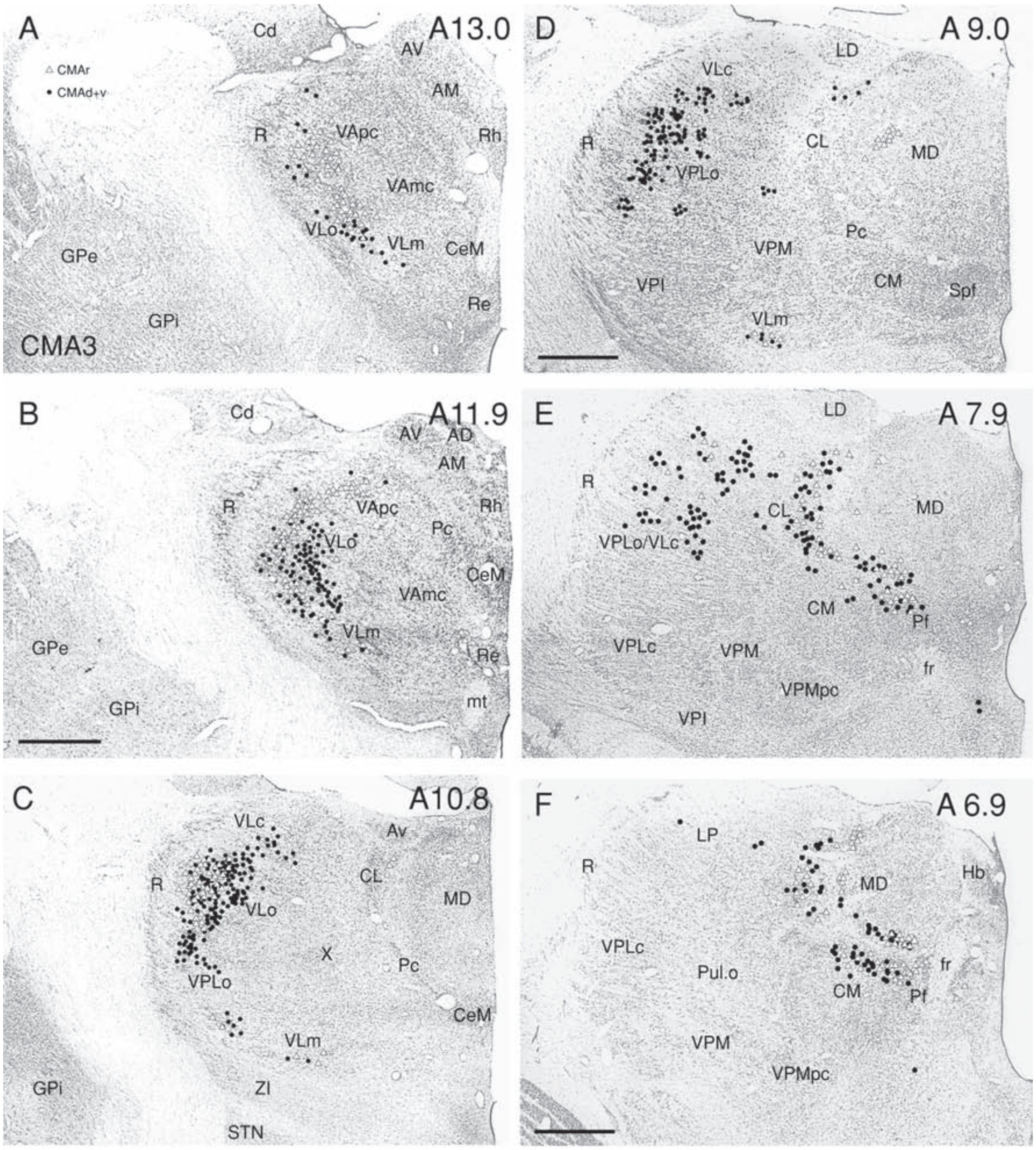


Fig. 4.4 Retrogradely labeled cells plotted onto Nissl-stained sections. Dots represent labeled cells following an injection of WGA-HRP into the forelimb representation region of the rostral cingulate motor area in area 24c′. Triangles represent labeled cells, following an injection of BDA involving the forelimb representation regions of both the caudal cingulate motor area and ventral bank of the cingulate sulcus. Numbers on the right upper corner of each panel denote the distance from the external auditory meatus. Modified from Hatanaka ***et al***. (2003) with permission.

such as the paraventricular, parataenial, central latocellular, central inferior, and reuniens nuclei (McFarland and Haber 2002; Romanski *et al*., 1997; Vogt *et al*., 1987). The differential thalamocortical projections to anterior cingulate area 24a, area 24b, and area 24c have not been comprehensively studied.

Only a few previous studies have definitively demonstrated the corticothalamic projections of area 24. The projections from areas 24a and 24b to the mediodorsal nucleus have been shown to originate from the superficial and deep aspects of layer VI (Giguere and Goldman-Rakic, 1988; McFarland and Haber, 2002).

Furthermore, area 24b also projects to the medial pulvinar nucleus (Romanski *et al.*, 1997). After injections of tritiated amino acids into the ACC, Yeterian and Pandya (1988) observed numerous densely labeled terminals in the magno- and parvicellular subnuclei of the mediodorsal nucleus, the ventral anterior nucleus, the anteromedial nucleus, midline nuclei (central latocellular, central intermedial, and paraventricular nuclei), and intralaminar nuclei (central superior lateral, centre médian-parafascicular, and limitans nuclei). However, this extensive terminal labeling may be because the injections involved the rostral parts of the midcingulate cortex or area 32 (Yeterian and Pandya 1988).

Area 32

Area 32 has been reported to receive massive thalamocortical projections from the mediodorsal nucleus as shown in Figure 4.5 (Bachevalier *et al.*, 1997; Barbas *et al.*, 1991; Giguere and Goldman-Rakic, 1988; Goldman-Rakic and Porrino, 1985; Ray and Price, 1993; Vogt *et al.*, 1987). The retrograde tracing study of Bachevalier *et al.* (1997) revealed that projections from the mediodorsal nucleus are topographically organized such that the posterior and ventral parts of area 32 receive projections from the dorsal part of the magnocellular subnucleus, whereas the anterior and dorsal parts of area 32 receive projections from the dorsal part of the parvicellular subnucleus. A similar topography was also reported by Ray and Price (1993). These thalamocortical projections to area 32 terminate as patches in layers III and IV (Giguere and Goldman-Rakic, 1988; McFarland and Haber, 2002; Russchen *et al.*, 1987). Area 32 also receives projections from the medial pulvinar nucleus, intralaminar nuclei (paracentral, central superior, central superior lateral, parataenial, centre médian-parafascicular, limitans, and suprageniculate nuclei), midline nuclei (paraventricular, central densocellular, central intermediate, central inferior, central latocellular, and reuniens nuclei), magnocellular part of the ventralis anterior nucleus, and anterior nuclei (mainly the anteromedial nucleus) (Fig. 4.5; Barbas *et al.*, 1991; Romanski *et al.*, 1997).

One primary thalamic target of area 32 projections is the mediodorsal nucleus (Giguere and Goldman-Rakic, 1988; Russchen *et al.*, 1987). The projections to the mediodorsal nucleus originate from the superficial part of layer VI, and, to a lesser extent, the superficial part of layer V in area 32 (Giguere and Goldman-Rakic, 1988), and terminate mainly in the magnocellular subnucleus (Chiba *et al.*, 2001; Giguere and Goldman-Rakic, 1988; Russchen *et al.*, 1987). However, the precise terminal fields of this projection have not been demonstrated by anterograde tracing methods. Area 32 also projects to the anteromedial, (Xiao and Barbas, 2002a), paraventricular, parataenial, reuniens, medial pulvinar, and limitans nuclei (Chiba *et al.*, 2001). More precise anterograde tracing studies are required to determine the exact corticothalamic terminal fields of area 32 within these thalamic nuclei.

Area 25

Area 25 receives thalamic projections mainly from the magnocellular subnucleus and the dorsal part of the parvicellular subnucleus of the mediodorsal nucleus, the medial pulvinar nucleus, and the central densocellular and parataenial nuclei (Bachevalier *et al.*, 1997; Romanski *et al.*, 1997; Vogt *et al.*, 1987). Minor projections also originate from the anteromedial, reuniens, central superior lateral, parafascicular, and limitans nuclei (Vogt *et al.*, 1987).

Previous anterograde tracing studies demonstrated that area 25 projects strongly to the dorsomedial part of the magnocellular subnucleus of the mediodorsal nucleus, the parataenial nucleus, and the medial pulvinar nucleus (Freedman *et al.*, 2000; Romanski *et al.*, 1997). Projections from area 25 to the anterior thalamic nuclei were not observed by Freedman *et al.*, (2000), whereas projections to the anteromedial and/or interanteromedial nucleus were confirmed by other authors (Chiba *et al.*, 2001; Xiao and Barbas, 2002a), indicating that area 25 projections to the anterior thalamic nuclei may be topographically organized. Area 25 also provides minor projections to other midline nuclei such as the paraventricular and reuniens nuclei (Freedman *et al.*, 2000).

Overall Organization of Thalamic Connections of the Cingulate Gyrus

We have reviewed the thalamic connections of some areas of the monkey cingulate gyrus, showing that each area studied has connections with a specific set of dorsal thalamic nuclei (Fig. 4.6). For instance, previous studies have clearly demonstrated the following reciprocal projections: posterior cingulate area v23b connects with the anterior, medial pulvinar, and lateral posterior nuclei; whereas area d23b connects with the anterior, medial pulvinar, mediodorsal, ventral anterior, ventral lateral, and midline nuclei. Retrosplenial areas 29 and 30 connect mainly with the anterior nuclei. The cingulate motor areas within the MCC connect mainly with the ventral anterior, ventral lateral, ventral posterolateral, intralaminar, and mediodorsal nuclei. Anterior cingulate area 24 mainly connects with the mediodorsal, ventral anterior, ventral lateral, intralaminar, and midline nuclei. Areas 32 and 25 connect with the mediodorsal, anterior, medial pulvinar, midline, and intralaminar nuclei. However, few studies have definitively demonstrated specific thalamic connections of posterior cingulate areas 23a, 23c, 23d, and 31; midcingulate areas 24a´ and 24b´; and anterior cingulate areas

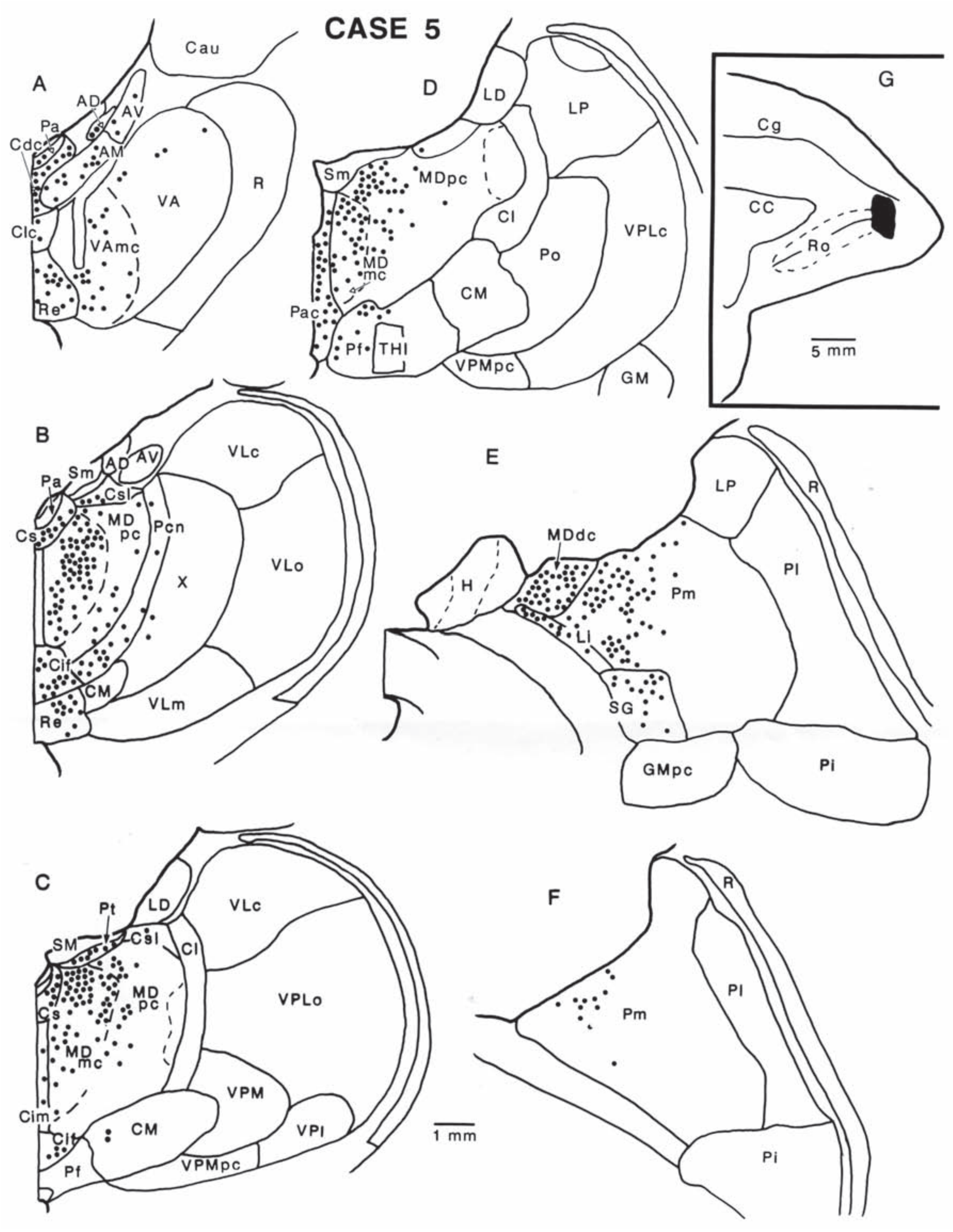


Fig. 4.5 Drawings of the distribution of retrogradely labeled cells (dots) following an injection of HRP into the rostral part of area 32. Reproduced from Barbas *et al.* (1991) with permission.

24a, 24b, and 24c. Bearing in mind the paucity of data about many cingulate areas, we describe the overall patterns of the primary connections between the main thalamic nuclear groups and the four major divisions of the cingulate gyrus as shown in Figure 4.6.

The anterior thalamic nuclei connect mainly with the PCC, RSC, and ACC; and the ventral nuclei connect mainly with the PCC and MCC. The mediodorsal nucleus connects mainly with the PCC, MCC, and ACC; and the medial pulvinar mainly connects with the PCC and ACC. The midline and intralaminar nuclei connect with virtually all cingulate gyrus areas.

Functional Implications of Thalamocingulate Connections

Vogt and colleagues (1997, 2004; Chapters 1 and 13) have suggested that the posterior cingulate areas 23 and 31 participate in visuospatial processing, the retrosplenial areas 29 and 30 in memory access, the midcingulate area 24′ in response selection, and the anterior cingulate areas 24, 32, and 25 in affect regulation. As we described above, each of these cortical areas receives inputs from a specific set of thalamic nuclei, which integrate and/or modulate information received from the cingulate, as well as from other cortical areas and subcortical structures. This implies that information processing in a given cingulate cortical area may be modulated by subcortical and/or indirect cortical inputs through the thalamus. Thalamic projections to the cingulate cortical areas are largely reciprocated by corresponding corticothalamic projections that provide inputs to a specific set of thalamic nuclei. Some components of the corticothalamic inputs may convey feedback information to the dorsal thalamus, whereas other components may convey feed-forward information

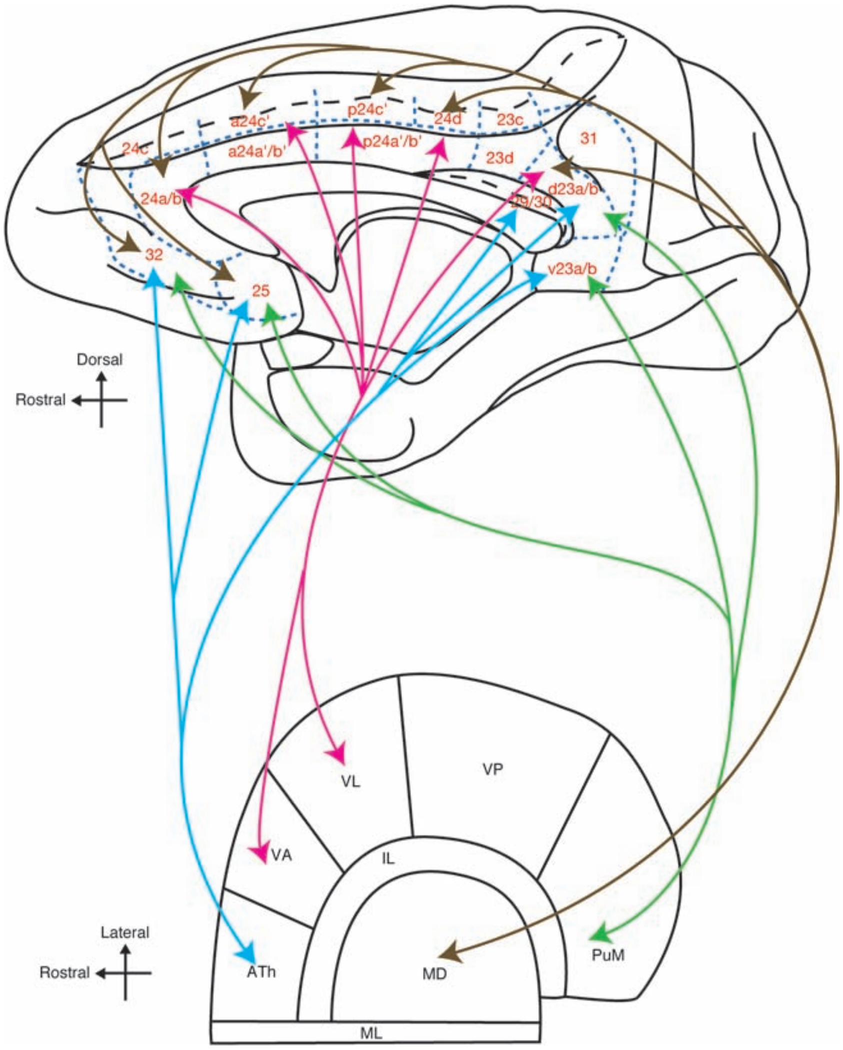


Fig. 4.6 Summary of major connections between dorsal thalamic nuclei and cingulate areas. Cingulate areas are shown in the medial view of the hemisphere, whereas the dorsal thalamic nuclei are shown in the section cut at a horizontal plane. The connections of the midline/intralaminar nuclei are not depicted, because these thalamic nuclei connect virtually with most parts of the cingulate gyrus, except for retrosplenial areas 29 and 30. The lateral posterior nucleus is included in the medial pulvinar nucleus (cf, Steriade *et al*., 1997). Dotted lines indicate approximate borders of each cingulate area (Chapter 3; Vogt *et al*., 2005). Dashed lines indicate the fundi of the cingulate and callosal sulci.

through the thalamus to other cortical areas. Given the tight inter-relationship between the thalamus and cingulate cortex, it is understandable that the information flow between the dorsal thalamus and cingulate cortex is essential for cingulate cortical functioning. However, the functional relationship between each thalamic nucleus and specific cingulate cortical areas is known only to a limited extent.

Previous studies in monkeys and humans suggest that the anterior thalamic nuclei are important for various memory functions. Lesions involving the anterior nuclei cause moderate recognition and associative memory impairments in monkeys (Aggleton and Mishkin, 1983a). Interestingly, glucose utilization in the anterior nuclei increases during the performance of spatial working memory tasks (Friedman *et al.*, 1990). Clinical studies in humans have shown that infarctions involving the right anterior thalamus result in visuospatial memory impairment, whereas those involving the left anterior thalamus result in verbal memory impairment (Clarke *et al.*, 1994; Ghika-Schmid and Bogousslavsky 2000; Graff-Radford *et al.*, 1990). These facts suggest that the anterior thalamic nuclei are important for visuospatial and auditory-verbal memory processes, possibly making substantial contributions to visuospatial and verbal-auditory functions (e.g., Yukie, 1995) of posterior cingulate area 23, especially area v23b, and memory access functions of retrosplenial areas 29 and 30 (e.g., Friedman *et al.*, 1990). In addition to memory functions, the anterior nuclei may be involved in emotion and motivation, as shown by human clinical and imaging studies (George *et al.*, 2001; Ghika-Schmid and Bogousslavsky, 2000; Tasker and Kiss, 1995). These anterior thalamic functions may correlate with affect regulation functions inherent to areas 32 and 25 (George *et al.*, 2001; Xiao and Barbas, 2002b).

The mediodorsal nucleus is considered to make important contributions to the posterior cingulate visuospatial, midcingulate response selection, and anterior cingulate affect functions. The parvicellular subnucleus of the mediodorsal nucleus may transmit spatial information to the PCC for visuospatial functioning and to the MCC for skeletomotor functioning, since damage involving this subnucleus causes spatial memory impairment (Isseroff *et al.*, 1982). This subnucleus may also provide to area 24 information relevant for short-term memory (Fuster and Alexander, 1973). On the other hand, the magnocellular subnucleus of the mediodorsal nucleus may provide to areas 32 and 25 information relevant for olfaction and autonomic regulation (Benjamin and Jackson, 1974; Yarita *et al.*, 1980). The densocellular subnucleus may provide somatosensory and somatomotor information to the rostral cingulate motor area (area a24c′), since anatomical data, as described above, indicate that the rostral cingulate motor area receives spinal and cerebellar inputs via the densocellular subnucleus. Other subnuclei may also transmit motor information related to eye movement, because the distribution of mediodorsal nucleus neurons that connect with frontal and supplementary eye fields may also overlap with those that connect with the posterior cingulate and cingulate motor areas (Huerta and Kaas, 1990; Huerta *et al.*, 1986; Stanton *et al.*, 1988). In addition to the transmission of spatial, somatosensory, and motor information, the mediodorsal nucleus may provide information related to mood state, which is consistent with findings from human imaging studies showing increased blood flow and metabolism in the left medial thalamus (including the mediodorsal nucleus) in patients with major depressive and bipolar disorders (Drevets, 2000).

Posterior cingulate areas v23b and d23b and anterior cingulate areas 32 and 25 receive inputs from the medial pulvinar nucleus. This nucleus may provide multimodal sensory, visuomotor, and visual memory information to these cortical areas (Grieve *et al.*, 2000; LaBerge and Buchsbaum, 1990; Robinson and Cowie, 1997; Roland *et al.*, 1987; Romanski *et al.*, 1997).

Projections from the midline and intralaminar nuclei may transmit information related to the arousal state substantially to all the areas of the cingulate region (Paus, 2001). Some of these projections may also transmit memory information, because the hippocampal formation is reported to project to the central latocellular and paraventricular nuclei (Aggleton *et al.*, 1986; Aggleton and Mishkin, 1983b). In human imaging studies, blood flow changes in the midline thalamic nuclei correlate with those in the ACC, implicating the midline nuclei in the regulation of arousal related changes in anterior cingulate activity (Paus, 2001). The intralaminar nuclei may also provide information related to eye movement (Schlag and Schlag-Rey, 1984). The contribution of the intralaminar nuclei to the pain processing in the cingulate gyrus is considered in detail in Chapter 14.

It is well known that the ventral anterior nucleus and the oral part of the ventral lateral nucleus receive input from the basal ganglia, whereas the ventral posterolateral nucleus and the caudal part of the ventral lateral nucleus receive input from the cerebellum (e.g., Steriade *et al.*, 1997). The termination of inputs from the basal ganglia and cerebellum appears to overlap with the cells originating projections to the rostral and caudal cingulate motor areas, respectively (Hatanaka *et al.*, 2003). Thus, the projections from these parts of the ventral thalamic nuclei may constitute pathways that transmit motor information mainly to the MCC. This issue and the relationship with the cingulate-basal ganglia-thalamic circuitry are discussed in detail in Chapter 28.

Future Neuroanatomical and Human Imaging Directions

It is gradually becoming clear that each cingulate area receives specific information from the dorsal thalamic nuclei to process visuospatial memory, response selection, and affect regulation functions. To understand better the functional correlates of each cingulate area and dorsal thalamic nucleus, it is necessary to obtain more complete pictures of thalamocortical connections underlying these distinct functions. At present, only parts of these connections have been studied in detail. Future studies should analyze the thalamocortical connections of each area more comprehensively by using sensitive retrograde and anterograde tracers. When analyzing the thalamocortical connections of cingulate motor areas, electrophysiological identification prior to the injection is essential (Hatanaka *et al.*, 2003). Furthermore, when targeting each dorsal thalamic nucleus with tracer injections, magnetic resonance and ultrasonic imaging of monkey brains prior to or during injection will greatly aid in restricting the tracer injection site to a specific thalamic nucleus (e.g., Tokuno *et al.*, 2000, 2002; Xiao and Barbas, 2002a).

These proposed experiments will provide more complete pictures of the distribution of cells that originate corticothalamic projections and the distribution of thalamocortical projection terminals in each cingulate cortical area. It remains unknown whether neurons of an individual thalamic nucleus provide axonal branches to different cortical areas or whether different populations of thalamic neurons project to different cortical areas. Likewise, it is not known whether individual neurons within a specific cingulate area provide collaterals to several thalamic nuclei or whether different populations of neurons within a cingulate cortical area project to different thalamic nuclei. Information obtained from future anatomical studies that address these issues will provide further insight into the structural and functional relationship between the dorsal thalamic nuclei and cingulate cortical areas, and will help us better understand normal and altered states of these intriguing regions of the cerebral cortex.

There is growing interest in the circuitry of the human cerebral cortex and many studies show joint activation of cortex and thalamus. Although the resolution of the methods employed by diffusion tensor imaging and functional correlation studies is not as high as that of histological methods employed by monkey studies, the latter studies can provide direction and guides for hypothesis testing in human studies. Indeed, as the resolution of human imaging improves, it may eventually be possible to evaluate activation in thalamic sectors, if not nuclei, and the present findings and similar observations should prove useful to guide such work.

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