

Somatosensory system

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Summary

The most widely studied aspect of the somatosensory system in metatherian (marsupial) mammals is that of the trigeminal pathway, in particular the pathway concerned with the whiskers, and this is reflected in the content of this chapter.

The structure and innervation of the mystacial vibrissae, or whiskers, on the snout has been described in a number of Australian species. Broadly speaking, the structure and afferent innervation is similar to that of eutherians and the American opossum. Receptors include Merkel cells and lanceolate, lamellated and free nerve endings. Intervibrissal pelage hair in several species is innervated by lanceolate and free nerve endings.

Muscle spindles in limb muscles have been well described in the brush-tailed possum (*Trichosurus vulpecula*) and resemble those of eutherian species, as do Golgi tendon organs. Three types of receptors have been identified in the joint capsules of the kowari (*Dasyuroides byrnei*): Ruffini corpuscles, lamellated corpuscles and free nerve endings. Lamellated corpuscles resembling Pacinian corpuscles are present in the interosseous region of the legs of macropods, and response properties suggest that they are responding to ground-borne vibration.

Little detailed information is available for the inputs of peripheral mechanoreceptors via the dorsal root ganglia to the dorsal column nuclei, although the medullary course and projection patterns of cervical roots in the brush-tailed possum and the potoroo (*Potorous tridactylus*) are reported to be similar to those of eutherians. In the brush-tailed possum, projections of the dorsal column nuclei have been shown to cross contralaterally in the medial lemniscus to innervate the posterior nuclear group (Po) and the ventroposterolateral nucleus (VPL) in the thalamus.

The only species for which a systematic description of the trigeminal brainstem nuclei exists is the tammar wallaby

(*Macropus eugenii*). These nuclei, innervated by the central processes of the trigeminal ganglion cells comprise principalis and the spinal subnuclei (oralis, interpolaris and caudalis). Patches of succinic dehydrogenase (SDH) and cytochrome oxidase (CO) activity, thought to correlate with the mystacial vibrissae, are present in all nuclei except oralis, although they are less clear than in rodents. These patches are clearer in the brush-tailed possum.

The somatosensory thalamus of Australian diprotodont species is well differentiated, in contrast to some other marsupial species. The ventroposteromedial nucleus (VPM) and VPL, comprising the ventrobasal complex (VPL/M), are cytoarchitecturally distinct and receive tactile input from the face and head via the trigeminal system and from the trunk and limbs via the dorsal column nuclei, respectively. Together they receive a somatotopic representation of the head and body. In the brush-tailed possum and the tammar, VPM contains dorsoventrally aligned cellular aggregations corresponding to the mystacial vibrissae. The posterior nuclear group (Po) in the brush-tailed possum has been shown to receive input from the dorsal column nuclei and the spinal cord and presumably from the trigeminal system, given its cortical connections. Both VPL/M and Po in turn project to somatosensory cortex.

Up to five somatosensory cortical areas have been described in Australian marsupial species. S1 and S2 contain a complete or near complete representation of the body surface, while a parietal ventral area (PV) and two areas rostral and caudal to S1 (R and C, respectively) have been delineated in some species. In the brush-tailed possum there is a distinct barrel field in S1 in both Nissl- and SDH-stained material, with those areas mapping the face and forepaw especially clear. Such barrels of high cell density only appear to be present in the Phalangeridae. Although no barrels are present in the tammar wallaby, there are whisker-related patches of SDH and CO activity, but they are much less clear

than in the possum. Somatosensory cortex has reciprocal connections with VPM, VPL and Po, and S1 has intracortical connections with both higher-order somatosensory and other cortical regions.

The major difference between eutherians and metatherians is that metatherians are born in an immature state with a large part of development taking place postnatally, and in many species it is protracted. The tammar is the species for which most is known on somatosensory development and, in particular, the trigeminal system. At birth, vibrissal follicles are already innervated, but the follicles and receptors supplying them do not resemble the adult structure until postnatal day (P) 119. The period separating these events is much longer than in the rat (3 weeks). Similarly, development of pelage hairs and their innervation takes around 200 days. Maturation of all levels of the pathway is prolonged. At birth, trigeminal afferents are distributed throughout the rostrocaudal extent of the trigeminal complex in the brainstem, but whisker-related patterns do not begin to appear until P40. In the thalamus, trigeminothalamic afferents reach VPM by P15 and electrically evoked synaptic responses are present from this time, but it is not until P52 that whisker-related patterns begin appearing and excitatory responses become dominated by non-NMDA-mediated responses. Thalamic afferents reach the cortex by P15, well ahead of descending connections to the thalamus, which first appear at P60. Whisker-related patterns characterised by the clustering of afferents in layer 4Cx, the beginning of CO patches in the newly formed layer 4Cx, and of cells and their dendrites in layers 5Cx and 6Cx that project to the thalamus, all appear around the same time, at P72–76. A fast non-NMDA-mediated thalamocortical response dominates at this time, coincident with the onset of *in vivo* responses to whisker stimulation. The long delay between the arrival of afferents and pattern formation at each level suggests that maturation of target tissue, as well as signals from the periphery may play a role in pattern formation. This is supported by findings that an increase in the non-NMDA-mediated glutamatergic response, a measure of target maturation, correlates well with pattern formation in both thalamus and cortex.

Introduction

The somatosensory system encompasses those pathways that convey information from peripheral somatosensory receptors to the cerebral cortex. Sections in this chapter describe what is known of peripheral receptors and their innervation, ascending spinal pathways and medullary relay nuclei, somatosensory thalamus and somatosensory

cortex. Finally the development of these structures and the use of the whisker pathway to study pattern development in the nervous system are described.

Peripheral receptors and their innervation

The representation of the body surface in both the spinal cord and the brain reflects the distribution and density of the peripheral receptors. These can be divided broadly into three groups on the basis of function: mechanoreceptors, which are commonly encapsulated, and nociceptors and thermoreceptors, which are free nerve endings. They are primarily present in skin, muscles or joints.

Cutaneous receptors

For Australian marsupials, most information is available for the trigeminal system and mainly for the innervation of hairy skin of the face, including the mystacial vibrissae or sinus hairs, which are aligned in rows on the snout of the animal. Scant information is available for other structures innervated by the trigeminal nerve, but is included at the end of this section. The trigeminal nerve innervates the facial skin, oral and nasal mucosa, and structures such as the vibrissae, tongue and teeth. The mystacial vibrissae, upper lip and the post-orbital skin are innervated by its maxillary branch and contain a variety of encapsulated receptors and free nerve endings.

The structure of vibrissal follicles in the brush-tailed possum (Hollis and Lyne, 1974) and the tammar (Figure 10.1a) (Marotte *et al.*, 1992), is similar to that of eutherians (Rice *et al.*, 1986) although, like the rhesus monkey (Van Horn, 1970), they also lack a ringwulst. A thickening of the mesenchymal sheath, seen in both the possum and the tammar, does not appear to be simply a homologue of the ringwulst, because, unlike the ringwulst, it is densely innervated. Afferent innervation of the follicles has been described in a number of diprotodont (brush-tailed possum (Hollis and Lyne, 1974; Loo and Halata, 1991); tammar (Loo and Halata, 1991; Marotte *et al.*, 1992)) and polyprotodont (long-nosed bandicoot *Perameles nasuta*; kowari *Dasyuroides byrnei* (Loo and Halata, 1991)) Australian marsupial species. Broadly speaking, vibrissal innervation is similar in these species, in the polyprotodont North American opossum, *Didelphus virginiana* (Loo and Halata, 1991) and in eutherians (Rice *et al.*, 1986). Receptors include Merkel endings, which give slowly adapting type I responses in glabrous and hairy skin and probably subserve the same function in the vibrissae, lanceolate (Figure 10.1b) and lamellated endings and free nerve endings (Figure 10.1b). The functions

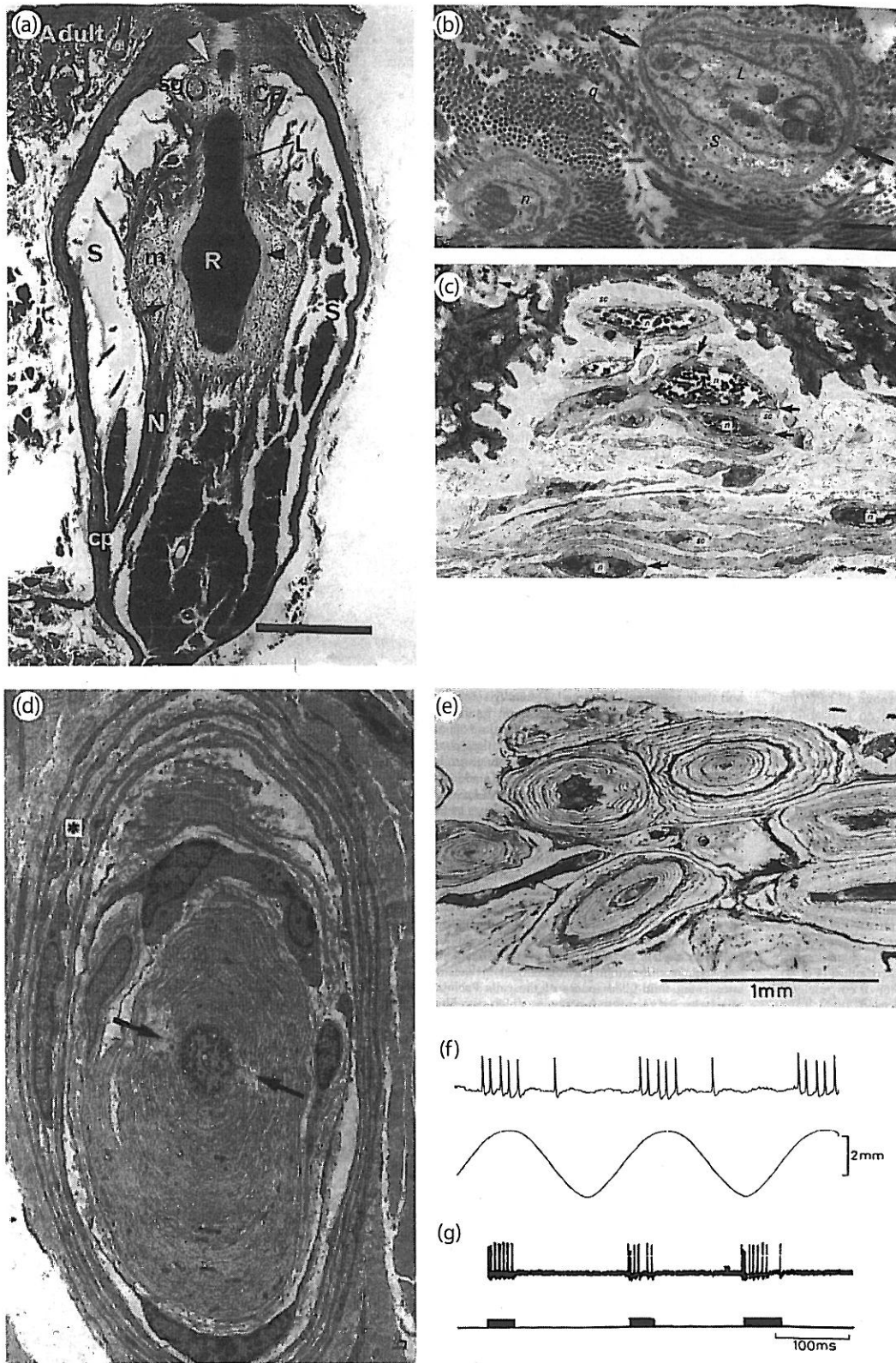


Figure 10.1 (a) Longitudinal section through an adult vibrissal follicle in the tammar wallaby (*Macropus eugenii*) stained by the Bodian method. Within the capsule (cp) the blood sinus is prominent (S). Branches of the deep vibrissal nerve (N) enter the mesenchymal thickening (m), giving rise to coarse branches (arrow) and fine branches (black arrowhead) adjacent to the root sheath (R) as well as lanceolate and lamellated (L) endings in the narrow waist region. The hair shaft in the root sheath is out of the plane of section. The inner conical body (ICB) has axons arranged circularly (white arrowhead) at the level of the sebaceous glands (sg); Scale bar = 0.5 mm. From Waite *et al.* (1994), Figure 1, with permission, copyright 1994 Wiley-Liss, Inc. (b) Electron micrograph of small lanceolate terminal (L) and free nerve ending (n) in the mesenchymal thickening of a vibrissal follicle of the tammar wallaby (*Macropus eugenii*). The terminal abuts

of the latter are not known, but lanceolate receptors are thought to be responsible for rapidly adapting responses (Iggo, 1974), and may detect acceleration of vibrissal deflection (Rice *et al.*, 1986). Free nerve endings are generally considered to mediate high threshold responses, but in the rat very few vibrissal responses are high threshold (Jacquin *et al.*, 1986) and their protected position in the wallaby follicle may indicate that they are low-threshold mechanoreceptors (Marotte *et al.*, 1992). Ruffini-like endings have been described in the rhesus monkey follicles (Halata and Munger, 1980), but were not observed in the marsupial species examined (Loo and Halata, 1991; Marotte *et al.*, 1992).

Intervibrissal pelage hairs in a number of marsupial species (Loo and Halata, 1991) are reported to be innervated by lanceolate and free nerve endings, although in the tammar they are rarely innervated (Marotte *et al.*, 1992). Loo and Halata (1991) also reported that facial guard hairs contain Merkel, lanceolate, pilo-Ruffini and free nerve endings, while in the tammar pilo-Ruffini endings are not seen (Marotte *et al.*, 1992).

Glabrous skin from the snout region in the Northern brown bandicoot (*Isodon macrourus*) is richly innervated, having epidermal pegs with the suite of nerve endings typical of Eimer's organ: intra-epidermal nerve terminals, Merkel cells and corpuscular end-organs (Figure 10.1c), as well as free nerve endings in the dermis (Loo and Halata, 1985). The corpuscular endings have similarities to Meissner's corpuscles of the North American opossum and eutheria, such as the mole, dwarf pig and tree shrew, but differ in that they lack a capsule and the nerve terminal sometimes makes contact with the basal layer of the epidermis. Both the bandicoot and the opossum are nocturnal and the study noted that such innervation is indicative of the snout in these animals being a highly specialised organ for touch (Loo and Halata, 1985).

Intraoral receptors

Lamellated Pacinian corpuscles 'of the simple type' have been recognised in the apical region of the tongue of the tree kangaroo (*Dendrolagus ursinus*) (Kubota *et al.*, 1963), a native of New Guinea and Indonesia. Although two Australian species of kangaroo were also examined in the same study, there was no mention of the presence of corpuscles in these species. Information on the sensory innervation of the teeth is lacking for Australian marsupials, but in the South American opossum *Monodelphis domestica* three types of endings were observed: Ruffini and lamellated corpuscles, suggested to be part of the masticatory feedback system, and free nerve endings, which may act as thermo- or nociceptors (Schulze *et al.*, 1993).

Muscle and joint receptors

Muscle spindles in various limb muscles have been studied in detail for the brush-tailed possum (Jones, 1966a, 1966b) and resemble those of other mammals, including man, in both their structure and afferent and efferent innervation. Their distribution in forepaw lumbricals is not consistently related to the number of extrafusal fibres, confirming the view that it is the function of the muscle that drives the spindle content, not its size (Jones, 1966b). Golgi tendon organs, described as 'typical' were also noted near the musculotendinous junctions (Jones, 1966a).

In joint capsules of the kowari (Strasman *et al.*, 1987), three types of receptors are seen in the fibrous layer: Ruffini corpuscles, lamellated corpuscles (Figure 10.1d) and free nerve endings. The latter two types have also been noted in the joints of the upper cervical column in *Monodelphis domestica* (Strasman *et al.*, 1999). Lamellated corpuscles, similar to the Pacinian corpuscles of eutherian mammals, have also been described in the interosseous region

Caption for Figure 10.1 (Cont.)

the glassy membrane (g) while the free nerve ending lies within it. The lanceolate terminal is flanked by Schwann-cell processes (S), but is exposed to the basal lamina at each end (arrows); Bar indicates 0.5 μ m. From Marotte *et al.* (1992), Figure 5a, with the permission of the Journal of Anatomy, Anatomical Society of Great Britain and Ireland and Blackwell Publishing. (c) Electron micrograph of a simple coiled corpuscle in the papillary layer under the base of an epidermal peg in the glabrous skin of the snout of the short-nosed bandicoot (*Isodon macrourus*). Nerve terminals (n), Schwann-cell lamellae (sc) and terminal spikes (arrows) are present. An intra-epidermal nerve is indicated by an arrowhead. From Loo and Halata (1985), Figure 9, with the permission of Wiley-Blackwell. (d) Lamellated corpuscle in the joint capsule of the kowari (*Dasyuroides byrnie*), with a perineural capsule of four layers (*) and a symmetrical longitudinal cleft of the inner core (arrows); x 4000. From Strasman *et al.* (1987), Figure 5b, copyright Springer-Verlag 1987, with the kind permission of Springer Science and Business Media. (e) Transverse section through a cluster of lamellated corpuscles in the interosseous membrane of the tammar wallaby (*Macropus eugenii*); Masson's trichrome stain. From Gregory *et al.* (1986), Figure 5B, copyright Springer-Verlag 1986, with the kind permission of Springer Science and Business Media and the authors. (f) Upper trace. Responses of one vibration-sensitive unit recorded in the interosseous nerve of the pademelon (*Thylogale billardieri*) to vibration at 12 Hz, applied where maximally effective in the interosseous region. Lower trace shows the voltage applied to the vibrator, calibrated in terms of the proportional displacement generated. From Gregory *et al.* (1986), Figure 1A, copyright Springer-Verlag 1986, with the kind permission of Springer Science and Business Media and the authors. (g) Responses of a unit recorded in the interosseous nerve of the pademelon (*Thylogale billardieri*) to tapping lightly with the fingers on an upright mounted on the metal table supporting the animal. Lower trace shows the approximate timing of the taps. From Gregory *et al.* (1986), Figure 1B, Copyright Springer-Verlag 1986, with the kind permission of Springer Science and Business Media and the authors.

of the legs of macropod marsupials (Figure 10.1e) (Gregory *et al.*, 1986). The properties of mechanoreceptors recorded in the interosseous nerve, presumably representing the responses of these receptors, were investigated in the wallaby (*Thylogale billardieri*) (Figure 10.1f). Their functional properties are similar to eutherian Pacinian corpuscles, although less rapidly adapting, and it was speculated that they may detect ground-borne vibration (Gregory *et al.*, 1986).

Ascending spinal pathways and medullary relay nuclei

Spinothalamic tract

In eutherians, this pathway carries information on pain and temperature and also innocuous stimuli (Tracey, 2004b). Hemisection of the spinal cord in the possum revealed bilateral projections to the thalamus in the posterior nuclear group, (VPL) and the intralaminar system of nuclei (Rockel *et al.*, 1972). This is similar to that described for eutherians such as the rat (Tracey, 2004b) and more segregated than in the American opossum (Hazlett *et al.*, 1972).

Dorsal columns and nuclei

Cell bodies of peripheral mechanoreceptors in the dorsal root ganglia send their central processes to innervate dorsal column nuclei, including the gracile, cuneate and external cuneate nuclei (Tracey, 2004b). The medullary course and projection patterns of cervical dorsal root fibres have been described for the potoroo (Culberson and Albright, 1984) and in more detail for the brush-tailed possum (Culberson and Albright, 1984; Culberson, 1987), and are similar to eutherian species (Culberson and Albright, 1984). Fibres from most cervical roots separate into two as they travel rostrally into the cuneate and external cuneate nuclei. Fibres reaching the dorsal 'shell' region of the cuneate are topographically precise and mapping studies in the possum and other species (see Culberson, 1987 and below) show that this input is most extensive from cutaneous receptors in the distal extremity or forepaw. Thus distal dermatomes (C7-T1) provide a more extensive projection to the dorsal cuneate nucleus than proximal ones such as C2-C4, supplying the neck and shoulder. The ventrolateral and ventrocentral regions of the cuneate receive input from presumed low-threshold muscle afferents. The external cuneate nucleus also receives muscle afferents and in the possum this projection is large, from all cervical roots, and with a clear segmentotopic pattern, similar to that described for the

cat (Liu, 1956). Culberson (1987) noted that the extensive, well-developed cuneate system was not surprising, given the behavioural attributes of the possum, including dexterity in manipulating objects with the forepaws. However, he noted that the cells and the projections in the cuneate are not as precisely arranged as in those placental mammals with well-developed digital dexterity.

Information on the detailed somatotopic organisation of mechanosensory inputs to the cuneate/gracile nuclear complex is lacking for Australian marsupials, but has been reported for the North American opossum (*Didelphis marsupialis virginiana*; Hamilton and Johnson, 1973). Electrophysiological mapping showed that the somatotopy is similar to that in eutherians, although it was noted that the receptive fields were larger and had greater overlap compared to those seen in the racoon, for example. Consistent with the anatomical studies in the possum (above), the opossum cuneate receives a large projection from the hand, a smaller projection from the forearm and less from the upper arm and shoulder. The neck and pinnae were represented most laterally in the nucleus, whereas the gracile nucleus received inputs from the hindlimbs and feet.

In the brush-tailed possum, foci of SDH activity have been described in both the cuneate and gracile nuclei (Weller, 1983). This histochemistry is considered to reflect metabolic activity that is dependent on mitochondrial enzymic activity in dendrites and also in axon terminals (Wong-Riley, 1989), and has proved a useful marker for sensory-relay nuclei and their cortical terminations (Dawson and Killackey, 1987). Patches of high reactivity correlate with peripheral regions that have a high density of innervation (Goyal *et al.*, 1992).

Projections of the dorsal column nuclei in the brush-tailed possum have been shown to run contralaterally in the medial lemniscus to innervate Po and VPL in the thalamus (Clezy *et al.*, 1961; Rockel *et al.*, 1972), as in eutherians. These were reported to be relatively localised and discrete compared with the more widespread projections of the American opossum (Rockel *et al.*, 1972). Blumer (1963) noted in the quokka that the dorsal column projections also followed the usual mammalian plan.

Trigeminal brainstem sensory nuclei

The only systematic description of these nuclei, innervated by the central processes of trigeminal ganglion cells, is for the diprotodont Australian marsupial, the tammar (Waite *et al.*, 1994). The nuclear complex is similar cytoarchitecturally to other species (Olszewski, 1950; Torvik, 1956; Darian-Smith, 1973; Ma, 1991). The principalis nucleus (Pr5; atlas plates D23 to D25, W38 to W40), lying in the lateral pons between the trigeminal tract and the trigeminal

motor nucleus, is the most rostral nucleus of the complex. It has fairly closely packed, often clustered, medium-sized cells and obliquely oriented bundles of fibres. All the spinal nuclei (Sp5 nuclear complex) feature fibre bundles running rostrocaudally. Subnucleus oralis (Sp5O; atlas plates D26, D27, W41 and W42) begins rostral to the facial nucleus, overlapping with the caudal pole of principalis rostrocaudally, and extending to the caudal pole of the facial nucleus. It is smaller with a lower density of cells, as has been described for rodents (Bates and Killackey, 1985; Ma, 1991). Subnucleus interpolaris (Sp5I; atlas plates D28 to D32 and W43 to W46) is irregularly shaped with sparse cells, in contrast to the densely packed cells described in rodents (Bates and Killackey, 1985). With both Nissl and SDH staining it appears heterogeneous, partly due to numerous fibre bundles crossing the nucleus, as well as the vagus nerve, which passes through it obliquely, as in primates. Subnucleus caudalis (Sp5C; atlas plates D32, W47 to W51) consists of a marginal layer, substantia gelatinosa and magnocellular layers.

In the tammar, all the above sensory trigeminal nuclei have higher SDH and CO activity compared to surrounding structures, as seen in other species (Belford and Killackey, 1978, 1979a, 1979b; Nomura *et al.*, 1986; Noriega and Wall, 1991), with Pr5 showing the highest reactivity (Figure 10.2a). Particularly in rodents, patches of high reactivity reproducing the pattern of individual mystacial vibrissae on the snout, are present in Pr5, Sp5I and Sp5C (Bates and Killackey, 1985; Ma, 1991). In the tammar, patches are also seen in these nuclei, but only Pr5 (Figure 10.2a) and Sp5I display some regions where they are arranged in lines reminiscent of the rows of mystacial vibrissae. However, they are not clear enough to be identified with individual vibrissae. In the possum, SDH staining appears to more clearly reflect vibrissae-like patterns and these, as in rodents, are seen in all trigeminal subnuclei except Sp5O (Weller, 1983).

The major projection of Pr5 is contralaterally, to VPM of the thalamus, and at least in early stages of development there is no evidence of a projection to Po (Leamey *et al.*, 1996). In the rodent, Pr5 also projects to Po (Chiaia *et al.*, 1991), so this may be a genuine difference between the species or the projection to Po in the wallaby may form later in development. The connections of the spinal subnuclei have not been described in any Australian marsupial and there is scant information for other marsupials. In the South American opossum, Sp5C is reported to project to the inferior colliculus (Willard and Martin, 1983). In rodents, the thalamic projections of Sp5I and Sp5C include VPM, Po and ZI, like Pr5; Sp5O primarily innervates other brainstem nuclei, but also provides an input to Po and ZI. A number of other areas also receive input from the trigeminal brainstem nuclei and the reader is referred to Waite (2004) for an overview of connections in the rodent.

Somatosensory thalamus

The thalamus of the tammar is well differentiated and displays many features similar to the cat (Mayner, 1989c), while the brush-tailed possum (Rockel *et al.*, 1972; Haight and Neylon, 1978a) appears to have features that lie between that of the tammar and the polyprotodont eastern quoll (*Dasyurus viverrinus*) (Haight and Neylon, 1981a, 1981b). Nevertheless, these species show more resemblance to each other than they do to the North American opossum, which has poorly differentiated thalamic nuclei (Oswaldo-Cruz and Rocha-Miranda, 1967).

Ventrobasal complex

This comprises VPM, which receives somatosensory input from the face and head via the trigeminal system, and VPL, which receives inputs from the trunk and limbs via the dorsal column nuclei and spinothalamic tracts. VPM and VPL in turn project to S1 of the somatosensory cortex (Haight and Neylon, 1978a). In the three Australian species mentioned above, VPM and VPL are cytoarchitecturally distinct (Rockel *et al.*, 1972; Haight and Neylon, 1981a, 1981b; Mayner, 1989c; Leamey *et al.*, 1996). In coronal section, VPL, a crescent-shaped nucleus, lies mediodorsal to the external medullary lamina and VPM is a distinct nucleus of densely packed cells, dorsal and medial to it (Figure 10.2b). Haight and Neylon (1978a) also identified a third small region in the brush-tailed possum, the posteromedial ventroposterior nucleus (VPP), which, on the basis of cortical connections, they considered part of the ventrobasal complex (Haight and Neylon, 1978b); however, this was only visible in some brains. In an early study, Dennis and Kerr (1961) noted that the hindlimb is represented lateral to the forelimb in VPL in the brush-tailed possum. In the tammar, VPM and VPL together receive a somatotopic representation of the head and body with the head having a disproportionately large representation (Faulks and Mark, 1982). The overall organisation is similar to that in eutherians (Jones, 2007) and to the North (Pubols and Pubols, 1966) and South American opossum (*Didelphis marsupialis aurita*) (Souza *et al.*, 1971).

In parts of VPM in the brush-tailed possum (Weller, 1980) and the tammar (Figure 10.2b) (Leamey *et al.*, 1996), cells are arranged in dorsoventrally aligned bands separated by bundles of myelinated fibres, resembling the vibrissae-related barreloids in rodents (Van der Loos, 1976). VPM shows high CO activity compared to surrounding nuclei, with segmentation into bands of reactivity reflecting the arrangement seen with Nissl staining (Leamey *et al.*, 1996). In horizontal sections these are seen as circles of reactivity, surrounded by a thin region of low activity corresponding to the myelinated

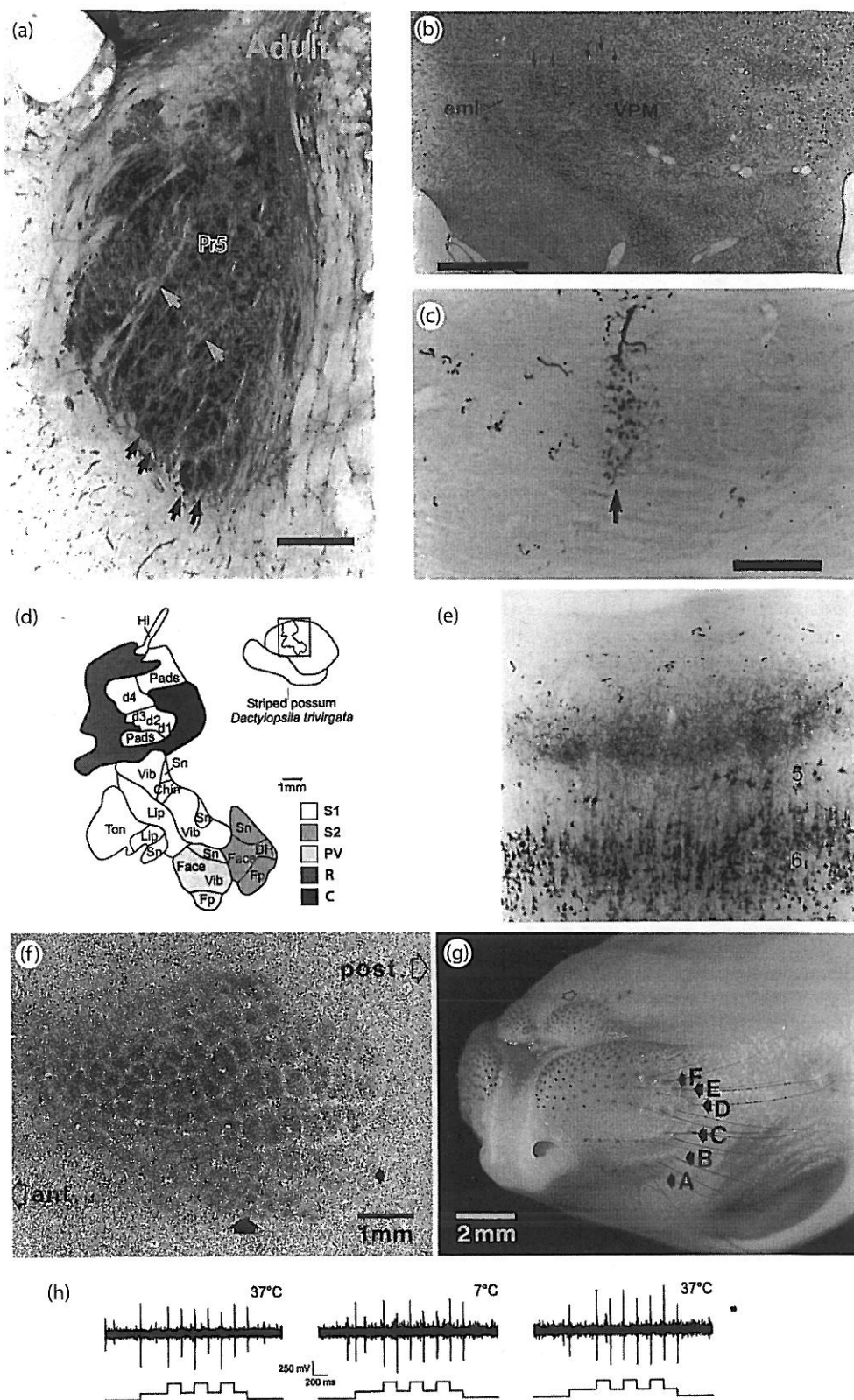


Figure 10.2 (a) Transverse section through nu. principalis (Pr5) in the tammar wallaby (*Macropus eugenii*) stained with succinic dehydrogenase. Dense patches of activity are seen aligned obliquely across the nu. (black arrows). Bundles of fibres (white arrows) also run obliquely across the nucleus; Bar = 0.5 mm. From Waite *et al.* (1994), Figure 7B, with permission, copyright 1994 Wiley-Liss, Inc. (b) Stained coronal section through the somatosensory thalamus of the tammar wallaby (*Macropus eugenii*) showing the normal histology of the ventroposteromedial nu. (VPM), which is characterised by intensely stained cells. Arrows point to the dorsoventrally aligned bands of cells in VPM; eml: external medullary lamina; bar = 2 mm. From Marotte *et al.* (1997), Figure 1b, with permission, copyright 1997 Wiley-Liss, Inc. (c) Unstained coronal section through VPM in the tammar wallaby (*Macropus eugenii*) showing the dorsoventrally aligned band of label

bundles surrounding the cell clusters (Leamey *et al.*, 1996). Anatomical and electrophysiological studies in rodents support the idea that inputs from individual facial vibrissae end on cell clusters in VPM and these in turn project to individual cortical barrels (Van der Loos, 1976; Petersen, 2003). It appears likely that a similar relationship exists in the brush-tailed possum and the tammar wallaby; electrophysiology has shown that vibrissae are represented in VPM of the tammar (Faulks and Mark, 1982) and that there is a strong correlation between vibrissae and the patches of CO or SDH activity seen in the somatosensory cortex of the tammar (Waite *et al.*, 1991) and possum (Weller, 1993). Further, a small injection of tracer in the physiologically identified area of whisker representation in somatosensory cortex of the tammar retrogradely labels a discrete band of dorsoventrally aligned cells in VPM which resembles the band seen in Nissl-stained sections (Figure 10.2c; Marotte *et al.*, 1997). Terminals within the band are also labelled, demonstrating the reciprocal connections between VPM and cortex.

VPL/M projects to the somatosensory cortex and the most detailed information on its cortical projections is known for the brush-tailed possum (Haight and Neylon, 1978b). Its field of projection is coincident with S1, as defined electrophysiologically (Haight and Weller, 1973). VPM and VPL project to S1 in a non-overlapping manner. VPL, which projects medially, apparently displays a stricter homotopy

than VPM, which projects laterally. VPP projects anteriorly and is surrounded by VPM projections caudally. VPL also has projections to S2 and it was assumed that this is also the case for VPM (Haight and Neylon, 1978b). The organisation of these projections is similar in the eastern quoll (Haight and Neylon, 1981b).

Posterior nuclear group

The nomenclature of this region in both eutherians and metatherians varies, depending on the authors, but Neylon and Haight (1983) noted that the pattern of inputs to the region is similar across species. In the brush-tailed possum (Neylon and Haight, 1983) and the eastern quoll (Haight and Neylon, 1981b) they identified a lateral and medial division of Po, as did Mayner (1989c) in the tammar. The former authors stated that the region designated as Po in their study was equivalent to the subdivision lateralis B in the study of the same species by Rockel *et al.* (1972) and corresponded fairly closely with medial Po of eutherian species.

In the brush-tailed possum, the major somatosensory projections to lateral Po found by Haight and Neylon (1981b) are from the dorsal column nuclei and the spinal cord (Rockel *et al.*, 1972). It might be expected, given its cortical connections (see below), that medial Po would receive an input from the trigeminal system. However, conclusive information is

Caption for Figure 10.2 (Cont.)

(arrow) resulting from a cortical deposit of horseradish peroxidase conjugated to wheat germ agglutinin (WGA-HRP); bar = 500 μ m. From Marotte *et al.* (1997), Figure 1c, with permission, copyright 1997 Wiley-Liss, Inc. (d) Functional organisation of the somatosensory cortex in the striped possum (*Dactylopsila trivirgata*). There is a complete and inverted representation of the contralateral body surface in S1 (white); individual body areas are given to show receptive field progression. Receptive field progressions are also given for S2 and the parietal ventral area (PV). Since receptive field progressions have not been studied as extensively in the rostral (R) and caudal (C) somatosensory fields, only the outermost borders are shown. d1-4 - digits 1-4; DH - dorsal head; Fp - forepaw; Hl - hindlimb; R - rostral; Sn - snout; Ton - tongue; Vib - vibrissae. Reprinted from Karlen and Krubitzer (2007), copyright 2007 with permission from Elsevier. Based on Huffmann *et al.* (1999a), copyright 1999, Wiley-Liss Inc. with the permission of Wiley. (e) Coronal section through the cortex of the tammar wallaby (*Macropus eugenii*) after an injection of WGA-HRP in VPM. Terminals in layer 4Cx are patchy. Retrogradely labelled cells are present primarily in layer 6Cx. From Mayner (1985), with the kind permission of L. Mayner. (f) and (g) Comparison of the arrangement of cortical barrels with the arrangement of mystacial vibrissal follicles in the brush-tailed possum (*Trichosurus vulpecula*). (f) The larger barrels are arranged in six roughly parallel, slightly curved, anteroposterior rows (ant - anterior; post - posterior). The ventral-most of these rows (small solid arrow) consists of only two or three barrels, which are more obvious in the next deeper section. Within a row the more anterior barrels are smaller than the posterior barrels and are not arranged in rows. Anterior to the short, ventral-most row of large barrels is a compact group of very small barrels (large solid arrow); thionin stain, 150 μ m thick. (g) This photograph illustrates the distribution and arrangement of the possum's mystacial vibrissae, especially the six rows of large vibrissae (solid arrows A-F), and submental vibrissae adjacent to the lower lip (above, open arrow). The head, shown upside down to aid comparison with the pattern of barrels, is that of a pouch young possum estimated to be 57 days old. The position of each vibrissae follicle on the skin is marked by its pigmentation. The arrangement of follicles and the arrangement of barrels are clearly homeomorphic. From Weller (1993), copyright 1993 Wiley-Liss Inc. Reprinted with permission of John Wiley & Sons, Inc. (h) Absence of effect of S1 inactivation on an S2 neuron in the somatosensory cortex of the brush-tailed possum (*Trichosurus vulpecula*). Impulse records are shown of the response of an S2 neuron to stimulation of its receptive field on the pad of the forepaw, proximal to digit 4, with low frequency (2.7 Hz, 225 μ m amplitude) rectangular pulses, superimposed for 1 s on a 1.5 s background step indentation (amplitude 200 μ m). The neuron responded to each of the ON- and OFF-phases of the rectangular pulses with bursts of 2-3 action potentials during both pre- and post-cooling controls and when S1 was inactivated by cooling to 7 °C. From Coleman *et al.* (1999), Figure 5A, used with permission, The American Physiological Society.

not available for the possum and as previously mentioned in the tammar, at least at early developmental stages, there is no projection evident from Pr5 (Leamey *et al.*, 1998). In the opossum, an equivalent region to Po of the possum receives input from the trigeminal system (Walsh and Ebner, 1973), as it also does in the rat (Chiaia *et al.*, 1991). In the brush-tailed possum (Neylon and Haight, 1983), the projections of Po to the somatosensory cortex are organised in a point-to-point manner and cover most of the head and body areas, but are not as homotypically precise as the projection from VPL/M. Lateral Po projects to the body region, whereas medial Po projects to the head region. Cells in Po retrogradely labelled by injections in the head region are continuous with the label in VPM. Po also projects to posterior parietal cortex. More limited data in the eastern quoll (Haight and Neylon, 1981a) indicate that the cortical projections in this species are similar to those in the possum.

Somatosensory cortex

Up to five somatosensory areas have been described in Australian marsupial species examined so far (Figure 10.2d) (reviewed in Karlen and Krubitzer, 2007). At least two fields, S1 and S2, contain a complete or almost complete representation of the contralateral body surface. In addition, the parietal ventral area (PV) and two areas rostral (R) and caudal (C) to S1 have been delineated in some species (see below). The latter two areas may also be involved in motor and sensorimotor processing, respectively.

In the brush-tailed possum (Adey and Kerr, 1954; Elston and Manger, 1999; Haight and Weller, 1973; Huffman *et al.*, 1999a), the wallaby (*Thylogale eugenii*) (Lende, 1963), the wombat (Johnson *et al.*, 1973), and the striped possum (*Dactylopsila trivirgata*) (Figure 10.2d) and the northern quoll (*Dasyurus hallucatus*) (Huffman *et al.*, 1999a), electrophysiological mapping has shown that S1 contains an inverted map of the contralateral body surface. Most of the neurons in S1 respond to cutaneous stimulation, and Elston and Manger (1999) noted that they were non-habituating. The face and oral structures are represented laterally, progressing through the forelimbs, body and hindlimbs to the tail, which is represented medially. As in the thalamus, the head representation occupies a relatively large area, in particular the facial vibrissae. For example, in the northern quoll the representation of the snout, chin, cheek and lip vibrissae occupies 35–40% of S1. Other structures, such as digit or forepaw specialisations in some species, may also be disproportionately represented e.g. the fourth digit in the striped possum (Figure 10.2d) (Huffman *et al.*, 1999a; see Chapter 8 of this book, Figure 8.5). This organisation is

also typical of American marsupials (reviewed in Karlen and Krubitzer, 2006b) and eutherians and monotremes (reviewed in Krubitzer and Hunt, 2006).

S1 is distinguished cytoarchitectonically by a densely packed, darkly Nissl-staining layer 4Cx in the brush-tailed possum (Adey and Kerr, 1954; Elston and Manger, 1999) and tammar (Ashwell *et al.*, 2005a). In material sectioned parallel to the surface, it stains heavily for myelin, SDH and CO in the northern quoll, striped possum and fat-tailed dunnart (Huffman *et al.*, 1999a). In the brush-tailed possum there is a distinct barrel field in layer 4Cx in both Nissl- and SDH-stained material (Weller, 1972, 1993). In tangential sections, the barrels form a map of the body, with those of the face and forepaw especially clear. There are six rows of mystacial barrels (Figure 10.2f) that are homeomorphic to the six rows of large mystacial vibrissae (Figure 10.2g) and forepaw barrels that are homeomorphic to the glabrous palmar and apical digital pads. Recordings of receptive fields confirmed that the individual barrels represent specific cutaneous regions such as individual vibrissae. In coronal sections, the barrels are seen as regions of high cell density alternating with septa of low cell density where myelinated fibres are concentrated. They resemble the barrels seen in rats, in having cells throughout the barrel sides and centres, compared with those in mice, where the centres are relatively empty of cells (Woolsey and Loos, 1970; Welker and Woolsey, 1974). Weller (1972), in a large survey of Nissl-stained material in the marsupial families Didelphidae, Dasyuridae, Peramelidae, Phalangeridae, Vombatidae and Macropodidae, only found such barrels in the Phalangeridae. In the tammar, although no barrels are seen in Nissl stains, there are patches of SDH and CO activity associated with the whisker representation in the adult (Waite *et al.*, 1991), but they are more clearly seen in developing animals (Waite *et al.*, 1991; Marotte *et al.*, 1997; Mark *et al.*, 2002). These reflect patches of thalamic afferents from VPM terminating in layer 4Cx (Figure 10.2e) and corresponding clusters of cell bodies in layer 6Cx that project to the thalamus (Mayner, 1985). In the striped possum, similar barrel-like patches of CO activity have been described in the cortex, but whether barrels are apparent in Nissl-stained material was not mentioned (Huffman *et al.*, 1999a). It is not clear why neuronal aggregations are seen in phalangers, but not in the tammar (see Waite *et al.*, 1991), which are both diprotodonts, but they do not appear to be present in either Australian (Weller, 1972) or American polyprotodonts (Weller, 1972; Woolsey *et al.*, 1975; Beck *et al.*, 1996). Indeed, it is not clear why barrels or SDH/CO patches corresponding to the whiskers are seen in some species and not in others. Woolsey *et al.* (1975), in a large survey, observed that they were not associated with whisking behaviour, they were not obscured or absent even if the behaviour of the animal was