Ultrastructure of sympathetic axons and their structural relationship with vascular smooth muscle

Susan E. Luff

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al. 1995). The axon plexus predominantly consists of sympathetic postganglionic axons, most of which are noradrenergic and have a vasoconstrictor function. Other axons that are found within the plexus around some vessels include cholinergic parasympathetic axons and sensory axons. The density of the non-sympathetic axons in the plexus varies considerably in different vessels, the cerebral vessels being particularly rich in parasympathetic and sensory nerves (Matsuyama et al. 1985). Most axons contain neuropeptides, and neuropeptide-Y (NPY) is commonly co-localised in sympathetic postganglionic axons. For a detailed account of the different types of axons and peptides contained in perivascular nerves in different vessels, see reviews by Owman (1988) and Morris and Gibbins (1992).

Most of the axons forming the plexus occur in bundles, and Schwann cells either surround individual axons or groups of axons within bundles (Fig. 2A, B). Around each axon bundle there is a basal lamina (small arrow, Fig. 2B; Devine and Simpson 1967; Burnstock 1972; Bevan et al. 1980; Luff et al. 1987; Gabella 1992) that is produced by the Schwann cell. This basal lamina consists of types IV and V collagens, laminin, entactin and heparan sulfate (Bunge et al. 1986). Within the adventitia two types of axon bundles can be identified: those which contain the more proximal non-varicose preterminal region of axons (Fig. 2A) and those which contain the more distal varicose or terminal region of axons (Fig. 2B). The main distinguishing features of preterminal axon bundles are: (1) the axon profiles have few if any vesicles and predominantly contain microtubules, (2) the axons are completely surrounded by Schwann cell forming mesaxons and (3) the bundles are usually encircled by collagen fibres and fibroblast processes (Fig. 2A). These bundles are located some distance away from the media: 2–10 μm from the smooth muscle cells (Luff et al. 1995) and some may even occur outside the adventitial layer running along the outside of the vessel (i.e. paravascular bundles). The number of axons contained in preterminal axon bundles range from a few to tens or, in the case of the paravascular bundles, even hundreds of axons. Axon bundles commonly follow vessels to reach more distal segments of the vascular tree (Bevan et al. 1980; Gabella 1992) and in some cases non-vascular effectors such as those in the kidney (Barajas and Müller 1973; Gorgas 1978; Luff et al. 1991) and the spleen (Ackerman et al. 1987).

Bundles of varicose axons are normally located closer (within 1 to 2 μm) to the medio-adventitial border (Fig. 2B). They typically contain some larger axon profiles packed with small synaptic vesicles that commonly have an incomplete Schwann cell sheath with regions of their plasmalemma exposed to the interstitial space. The size of these bundles varies considerably in different vessels, ranging from 2 to 25 axons (Devine and Simpson 1967; Luff et al. 1987; Luff et al. 1991; Klemm et al. 1993;