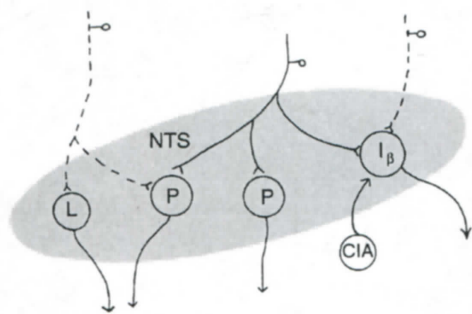


Central Nervous Control of Autonomic Function

*Edited by
David Jordan*



Part of the book series
The Autonomic Nervous System
Series Editor: *Geoffrey Burnstock*

Central Nervous Control of Autonomic Function

Edited by **David Jordan**

This, the eleventh volume in the **Autonomic Nervous System** book series, surveys our current understanding of central nervous control of autonomic function. Each chapter gives an overview of the nervous control of autonomic outflow to a particular organ or system, whilst maintaining an integrated approach to describe the simultaneous control of several outflows in response to different physiological situations. Providing an up-to-date account of experimental investigations, the book describes a neurophysiological, neuropharmacological and neuroanatomical approach to the problems involved. In addition to animal work, reference to any relevant studies in humans is also provided.

Providing an excellent background text for those teaching in the field, this volume will also serve as an important reference work for anyone active in research related to the Autonomic Nervous System.

About the Editor

David Jordan graduated in Biological Sciences from the University of Birmingham in 1974, where he also obtained a PhD in Physiology in 1977. After a period of post-doctoral research in Birmingham he moved to the Physiology Department of the Royal Free Hospital School of Medicine, University of London in 1980, where he now occupies the posts of Reader, and Deputy Head of the Department. In 1988 he was awarded the Julius H. Comroe Research Fellowship at the Cardiovascular Research Institute, University of California, San Francisco. His main research interests encompass physiological and pharmacological studies on the central nervous control of the heart, circulation and airways, and the central integration between the respiratory and cardiovascular control mechanisms.

Part of the book series

THE AUTONOMIC NERVOUS SYSTEM

Series Editor: **Geoffrey Burnstock**

Geoffrey Burnstock is Head of the Department of Anatomy and Developmental Biology at University College London. His early postdoctoral research work was carried out in Oxford, UK and Illinois, USA. In 1959, he moved to the University of Melbourne, Australia, where he was Professor of Zoology and Chairman of the department from 1964 to 1975. He returned to the UK in 1975 to take up his present post, and four years later founded the Centre for Neuroscience, of which he is Convener. He is a Fellow of the Australian Academy of Science and a Fellow of the Royal Society. He was awarded an honorary MRCP in 1987.

Each volume in **The Autonomic Nervous System** book series will deal with a different area of autonomic control in health and disease. Major advances have been made since the early 1960s that make it necessary to revise our thinking about the mechanisms of autonomic transmission and have significant implications for our understanding of diseases involving the autonomic nervous system and their treatment. The volumes include:

- autonomic neuroeffector mechanisms
- development, regeneration and plasticity of the ANS
- comparative physiology and evolution of the ANS
- autonomic-endocrine interactions
- disorders of the ANS
- central control of the ANS
- in-depth analyses of the nervous control of different visceral and cardiovascular organs, including heart, blood vessels, bladder, gut, eye, skin and lung

The series will allow a detailed study of specialist areas, each written and edited by leading figures in the field, in a way which would be impossible in a single book.

CENTRAL NERVOUS CONTROL OF AUTONOMIC FUNCTION

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Preface to the Series — Historical and Conceptual Perspective of The Autonomic Nervous System Book Series

The pioneering studies of Gaskell (1886), Bayliss and Starling (1899), and Langley and Anderson (*see* Langley, 1921) formed the basis of the earlier and, to a large extent, current concepts of the structure and function of the autonomic nervous system; the major division of the autonomic nervous system into sympathetic, parasympathetic and enteric subdivisions still holds. The pharmacology of autonomic neuroeffector transmission was dominated by the brilliant studies of Elliott (1905), Loewi (1921), von Euler and Gaddum (1931), and Dale (1935), and for over 50 years the idea of antagonistic parasympathetic cholinergic and sympathetic adrenergic control of most organs in visceral and cardiovascular systems formed the working basis of all studies. However, major advances have been made since the early 1960s that make it necessary to revise our thinking about the mechanisms of autonomic transmission, and that have significant implications for our understanding of diseases involving the autonomic nervous system and their treatment. These advances include:

- (1) Recognition that the autonomic neuromuscular junction is not a 'synapse' in the usual sense of the term where there is a fixed junction with both pre- and postjunctional specialization, but rather that transmitter is released from mobile varicosities in extensive terminal branching fibres at variable distances from effector cells or bundles of smooth muscle cells which are in electrical contact with each other and which have a diffuse distribution of receptors (*see* Hillarp, 1959; Burnstock, 1986a).
- (2) The discovery of non-adrenergic, non-cholinergic nerves and the later recognition of a multiplicity of neurotransmitter substances in autonomic nerves, including monoamines, purines, amino acids, a variety of different peptides and nitric oxide (Burnstock *et al.*, 1964; Burnstock, 1986b; Rand, 1992; Milner and Burnstock, 1995; Lincoln *et al.*, 1995; Zhang and Snyder, 1995).
- (3) The concept of neuromodulation, where locally released agents can alter neurotransmission either by prejunctional modulation of the amount of transmitter released or by postjunctional modulation of the time-course or intensity of action of the transmitter (Marrazzi, 1939; Brown and Gillespie, 1957; Vizi, 1979; Fuder and Muscholl, 1995).

- (4) The concept of cotransmission that proposes that most, if not all, nerves release more than one transmitter (Burnstock, 1976; Hökfelt, Fuxe and Pernow, 1986; Burnstock, 1990a; Burnstock and Ralevic, 1996) and the important follow-up of this concept, termed 'chemical coding', in which the combinations of neurotransmitters contained in individual neurones are established, and whose projections and central connections are identified (Furness and Costa, 1987).
- (5) Recognition of the importance of 'sensory-motor' nerve regulation of activity in many organs, including gut, lungs, heart and ganglia, as well as in many blood vessels (Maggi, 1991; Burnstock, 1993), although the concept of antidromic impulses in sensory nerve collaterals forming part of 'axon reflex' vasodilatation of skin vessels was described many years ago (Lewis, 1927).
- (6) Recognition that many intrinsic ganglia (e.g., those in the heart, airways and bladder) contain integrative circuits that are capable of sustaining and modulating sophisticated local activities (Saffrey *et al.*, 1992; Ardell, 1994). Although the ability of the enteric nervous system to sustain local reflex activity independent of the central nervous system has been recognized for many years (Kosterlitz, 1968), it has been generally assumed that the intrinsic ganglia in peripheral organs consist of parasympathetic neurones that provided simple nicotinic relay stations.
- (7) The major subclasses of receptors to acetylcholine and noradrenaline have been recognized for many years (Dale, 1914; Ahlquist, 1948), but in recent years it has become evident that there is an astonishing variety of receptor subtypes for autonomic transmitters (Rubanyi and Polokoff, 1994). Their molecular properties and transduction mechanisms are being characterized. These advances offer the possibility of more selective drug therapy.
- (8) Recognition of the plasticity of the autonomic nervous system, not only in the changes that occur during development and aging, but also in the changes in expression of transmitter and receptors that occur in fully mature adults under the influence of hormones and growth factors following trauma and surgery, and in a variety of disease situations (Burnstock, 1990b; Saffrey and Burnstock, 1994).
- (9) Advances in the understanding of 'vasomotor' centres in the central nervous system. For example, the traditional concept of control being exerted by discrete centres such as the vasomotor centre (Bayliss, 1923) has been supplanted by the belief that control involves the action of longitudinally arranged parallel pathways involving the forebrain, brain stem and spinal cord (Loewy and Spyer, 1990; Jänig and Häbler, 1995).

In addition to these major new concepts concerning autonomic function, the discovery by Furchgott that substances released from endothelial cells play an important role in addition to autonomic nerves, in local control of blood flow, has made a significant impact on our analysis and understanding of cardiovascular function (Furchgott and Zawadzki, 1980; Burnstock and Ralevic, 1994). The later identification of nitric oxide as the major endothelium-derived relaxing factor (Palmer *et al.*, 1988; *see* Moncada *et al.*, 1991) (confirming the independent suggestion by Ignarro and by Furchgott) and endothelin as an endothelium-derived constricting factor (Yanagisawa *et al.*, 1988; *see* Rubanyi and Polokoff, 1994) have also had a major impact in this area.

In broad terms, these new concepts shift the earlier emphasis on central control mechanisms towards greater consideration of the sophisticated local peripheral control mechanisms.

Although these new concepts should have a profound influence on our considerations of the autonomic control of cardiovascular, urogenital, gastrointestinal and reproductive systems and other organs like the skin and eye in both normal and disease situations, few of the current textbooks take them into account. This is largely because revision of our understanding of all these different specialised areas in one volume by one author is a near impossibility. Thus, this Book Series of 14 volumes is designed to try to overcome this dilemma by dealing in depth with each major area in separate volumes and by calling upon the knowledge and expertise of leading figures in the field. Volume 1, deals with the basic mechanisms of *Autonomic Neuroeffector Mechanisms* which sets the stage for later volumes devoted to autonomic nervous control of particular organ systems, including *Heart, Blood Vessels, Respiratory System, Urogenital Organs, Gastrointestinal Tract, Eye and Skin*. Another group of volumes will deal with *Central Nervous Control of Autonomic Function, Autonomic Ganglia, Autonomic – Endocrine Interactions, Development, Regeneration and Plasticity and Comparative Physiology and Evolution of the Autonomic Nervous System*.

Abnormal as well as normal mechanisms will be covered to a variable extent in all these volumes depending on the topic and the particular wishes of the Volume Editor, but one volume edited by Robertson and Biaggioni, 1995, has been specifically devoted to *Disorders of the Autonomic Nervous System* (see also Bannister and Mathias, 1992).

A general philosophy followed in the design of this book series has been to encourage individual expression by Volume Editors and Chapter Contributors in the presentation of the separate topics within the general framework of the series. This was demanded by the different ways that the various fields have developed historically and the differing styles of the individuals who have made the most impact in each area. Hopefully, this deliberate lack of uniformity will add to, rather than detract from, the appeal of these books.

G. Burnstock
Series Editor

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Preface

Other volumes in this series have considered the control of individual organs by their autonomic nervous innervations. However, the central nervous control of these individual organ outflows, and their integration into organised patterns of response has been somewhat neglected in the past. This is mainly due to the legacy of the experimental protocols employed in the last and earlier this century. Experiments involving brainstem transections, and the deficits they produced, led to the concept of 'brainstem centres' responsible for such functions as cardiac and vascular control, micturition and respiratory control. These were compounded by the much quoted study of Alexander (1946) wherein controlled brainstem transections were combined with localised electrical stimulation of the brainstem and afferent nerves. He suggested that the medulla contained two discrete 'centres' mediating pressor (sympathoexcitatory) and depressor (sympathoinhibitory) responses respectively. Each of these centres was proposed to have its own spinal output, capable of independent tonic activity, and reflexes evoking alterations in sympathetic activity acted by modifying activity in these brainstem centres. Although that study was concerned with vascular control, its implications were taken to embrace other areas of autonomic innervation so that cardiac, micturition and vomiting 'centres' were all proposed. Even today, some physiology textbooks still discuss autonomic control on the basis of the Alexander model even though numerous pieces of evidence have accumulated which make the model untenable (Hilton, 1975; Wurster, 1984; Jordan, 1995).

Our current understanding of the control of autonomic outflow has developed from concepts originating in the Sherringtonian model of motor control. With the advent of modern anatomical tracing methods, and the application of classical neurophysiological and neuropharmacological techniques, it is clear that we can now define a model of autonomic control based around discrete reflex controls of individual sympathetic and parasympathetic outflows upon which is superimposed a suprabulbar organisation which produces coordinated patterns of outflow, appropriate for any particular physiological situation (Jordan, 1995; Marshall, 1995b). The differential control of individual autonomic outflows is the basis of this organisation. The objective of this volume is to provide a coherent description of our current understanding of the ways in which the central nervous system is involved in generating, controlling and integrating autonomic discharges to individual target organs. Authors were asked to review the underlying central nervous substrate responsible for controlling autonomic outflow at particular levels, concentrating on contemporary studies but also putting the more historical data into a modern context.

To this end, the functional, anatomical and chemical heterogeneity of individual sympathetic and parasympathetic preganglionic neurones is discussed in Chapters 1, 3, 4 and 5. The basis of the spinal organisation underlying sympathetic activity is discussed in detail in Chapter 2, and the supraspinal pathways in Chapters 1, 5, 6 and 9. This underlying spinal, supraspinal and reflex control of individual autonomic outflows is integrated to produce appropriate physiological responses to any environmental situation. For example, in Chapter 7 Hansen and colleagues demonstrate clearly the remarkable regional and temporal differentiation in the mechanisms which control sympathetic activity during muscular exercise, whilst in Chapter 8 Paton discusses the possible roles of the cerebellum in organising the cardiovascular and respiratory responses during exercise and in the context of the alerting (defence) response. Electrodermal activity, which is often used as a marker of autonomic arousal in emotional situations such as during alerting, is controlled at multiple levels of the neuraxis, from the brainstem to cortex, as described in Chapter 9. At this level of organisation, autonomic outflow is not independent, but is matched to evoked behavioural (somatic) and endocrine activity appropriate for the perceived situation (Jordan, 1990; Marshall, 1995a). Such matching of autonomic and somatic activity is seen even at rest in respect of respiratory activity. The majority of autonomic nerves show some degree of respiratory activity in their ongoing discharge (Richter and Spyer, 1990). This interaction is in part responsible for the matching of cardiac and respiratory outputs seen under many different physiological conditions, and is particularly prevalent in the parasympathetic innervations of the heart and lungs as described in Chapters 3 and 4. Indeed, the interaction is so important that primary reflex effects are often masked or even overridden by concomitant changes in respiratory activity.

Whilst this book is not meant to be comprehensive, I hope that it provides the reader with an awareness of our current understanding of CNS control of autonomic outflow, and thus prepares the reader for the more detailed accounts of the autonomic innervations of particular targets in other volumes of this series.

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