PROGRESS IN BRAIN RESEARCH

VOLUME 76

VESTIBULOSPINAL CONTROL OF POSTURE AND LOCOMOTION

EDITED BY

O. POMPEIANO

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Preface

The attraction of the vestibular system to several generations of scientists has been its apparent neuronal simplicity, despite the fact that a quite complicated set of postural and motor deficits are observed when a peripheral lesion to this system occurs. For decades the function of the three neuronal vestibulo-ocular reflex arc has been investigated in detail as a prelude to understanding the mechanisms underlying the postural and motor abnormalities which occur when the receptors of, or nerve to, the peripheral vestibular system no longer function normally. The major challenge to the experimental skills of scientists, however, has been to understand the spinal motor regulation provided by vestibulospinal pathways, since these pathways are, to some extent, far more complex than those of the vestibulo-ocular reflex. This challenge acts as an intellectual stimulus for scientists working on different aspects of sensory neurophysiology, because at the level of spinal motoneurons labyrinthine, visual and muscle proprioceptive inputs interact. Thus it appears necessary to examine not just how labyrinthine signals enter the motor system and act at segmental and suprasegmental levels to ensure appropriate adjustments of the motoneuronal output. Rather, proprioceptive inputs from the limb and neck musculature and visual inputs must be taken into account as well.

The last ten years have seen a great development in this interdisciplinary field. In particular, detailed experiments from different groups of researchers have investigated the mechanisms by which labyrinthine signals intervene in the static and dynamic control of spinal motor activities. The spinal networks and supraspinal structures involved in the vestibular control of posture and movement have also been investigated, including the neurophysiological and neurochemical mechanisms involved in the gain regulation of vestibulospinal reflexes. Finally, the role that neck and visual inputs exert in the regulation of vestibulospinal reflexes has been studied in detail.

Work on vestibulospinal reflexes has also been extended to man's equilibrating reactions. The most significant aspect of this development is understanding how segmental and supraspinal mechanisms are used in the vestibular control of human posture and movement and how they are reflexly regulated. Interpretation of data from human experiments requires a detailed knowledge of animal studies and also suggests specific control experiments in animals. An in-depth treatment of the mechanisms underlying vestibulospinal reflexes in animals and humans is an important prerequisite to understanding the phenomena of vestibular deficits and adaptation required under abnormal (microgravity) or pathological conditions.

In 1985 a group of experts in the field discussed these scientific developments and decided to review in a comprehensive way with invited speakers the new information available. This review was organized as a satellite meeting to the Bárány Society meeting in Bologna during June 1987. The meeting was held in the Congress Hall of the Royal Carlton Hotel where the main Bárány Society meeting was also held. We are most grateful to the President of the Bárány Society Prof. J. Stahle, and the current vice-President

Prof. E. Pirodda, for having accepted our plans and putting at our disposal most of the facilities prepared for the main Bárány Society meeting.

The subject matter in this book, which contains the review articles provided by each selected lecturer, has been divided into 7 main sections. The first three sections present basic neuroanatomical neurophysiological aspects of vestibulospinal reflexes and document the neck afferent and visual influences on these reflexes. Following sections deal with the control of locomotion, posture (predominantly human posture), and eye-head-trunk coordination by vestibulospinal signals. The final section provides current knowledge on the processes underlying compensation of vestibulospinal deficits. For those wishing an overview of the matter an overall review preceding each main section has been added, so that the reader is informed as to which questions are still controversial and require further investigation for an ultimate answer. We hope in this way to provide a basis for those wishing a connected account of the field of vestibulospinal reflexes.

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October 1987

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SECTION I

Vestibular Nuclei: Projection Pathways, Neurotransmitters and Synaptology

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O. Pompeiano and J.H.J. Allum (Eds.)
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Overview

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This introductory section deals with connections of vestibular neurons: the inputs they receive from periphery and brainstem, the efferent projections they give rise to, the transmitters involved, and the related synaptic mechanisms. The experiments reviewed by Carpenter (Chapter 1) show how techniques such as transport of tritiated amino acids or horseradish peroxidase (HRP) have added to the earlier information on projections obtained with retrograde chromatolysis or degeneration studies. Knowledge of inputs to and outputs from the vestibular nuclei is now very comprehensive, but many specific questions remain unanswered even by the newer methods. For example, do commissural fibres interconnecting the bilateral vestibular nuclei issue from a specific population of neurons, or, more likely, are they collaterals of axons that project to other levels of the central nervous system? Questions such as these can be studied with the electrophysiological methods used by Dr. Fanardjian (Chapter 4) to map interconnections between the vestibular nuclei and other brainstem structures. They can also be answered by intra-axonal injection of HRP, the technique used by Dr. Shinoda (Chapter 2) to study the branching of vestibulospinal fibres. This work has confirmed that many of these fibres branch to different cord levels, and has revealed the apparent existence of synapses between lateral vestibulospinal fibres and forelimb motoneurons. As brought out in the discussion, however, there are neurons responding to natural stimulation in more dorsal spinal laminae, where vestibulospinal fibres do not seem to terminate. Is this because these neurons have dendrites that extend to regions where there are terminals, or because they are influenced by other descending systems? Finally, Dr. Raymond (Chapter 3) presents evidence that glutamate or aspartate is the transmitter liberated by vestibular afferent fibres. Important questions remain about the glutamate receptor types involved in various pathways, ipsilateral and commissural, impinging on vestibular neurons, and about denervation supersensitivity which may be used to identify receptor types: is it due to an increase in the number of receptors, or to an increase in binding characteristics?

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CHAPTER 1

Vestibular nuclei: afferent and efferent projections

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Vestibular ganglion cells innervating the utricle project upon neurons in the ventral LVN; cells innervating the saccule project upon ventral LVN, group *y* and lateral IVN, while ganglion cells innervating the cristae ampullaris of the SD project mainly upon MVN and SVN. Cerebellar afferents to the VN arise ipsilaterally from the anterior lobe vermis (LVN), the flocculus (SVN, MVN and *y*), the nodulus and uvula (MVN, IVN) and bilaterally from the fastigial nucleus (LVN, IVN). Commissural systems interconnect the MVN and peripheral SVN. The MVN, IVN and LVN receive modest projections from the dorsal regions of medullary and pontine RF. The SVN projects crossed and uncrossed fibres to TN and the OMC. The VST arises from the LVN and parts of other VN, provides collaterals to the LRN and projects preferentially upon cervical and lower lumbar segments by an elaborate collateral system. The MVN supplies the nuclei of the EOM and collaterals to cervical spinal segments. The IVN has diverse projections to the TN and the OMC, parts of the inferior olive, specific reticular nuclei, the cerebellum and the cervical spinal cord.

Introduction

Primary vestibular afferents constitute the major, but not the sole, input to the vestibular nuclei which in turn give rise to secondary vestibular fibres. Secondary vestibular projections play an important role in the maintenance of equilibrium, orientation in three-dimensional space and modification of muscle tone. This review concerns afferent projections to the vestibular nuclei and their projections within the neuraxis, except those to the thalamus.

Afferents to the vestibular nuclei

Inputs to the VN are derived from the VG, specific parts of the cerebellar cortex, the fastigial nuclei, a small number of brainstem nuclei and the spinal cord. Commissural connections interrelate the VN of the two sides and intrinsic connections exist among the VN of each side.

Primary vestibular fibres

Central projections of the VG terminate massively in the VN, in localized regions of the cerebellar cortex and in a few brainstem relay nuclei. Primary vestibular projections are ipsilateral and have aspartate/glutamate as their excitatory neurotrans-

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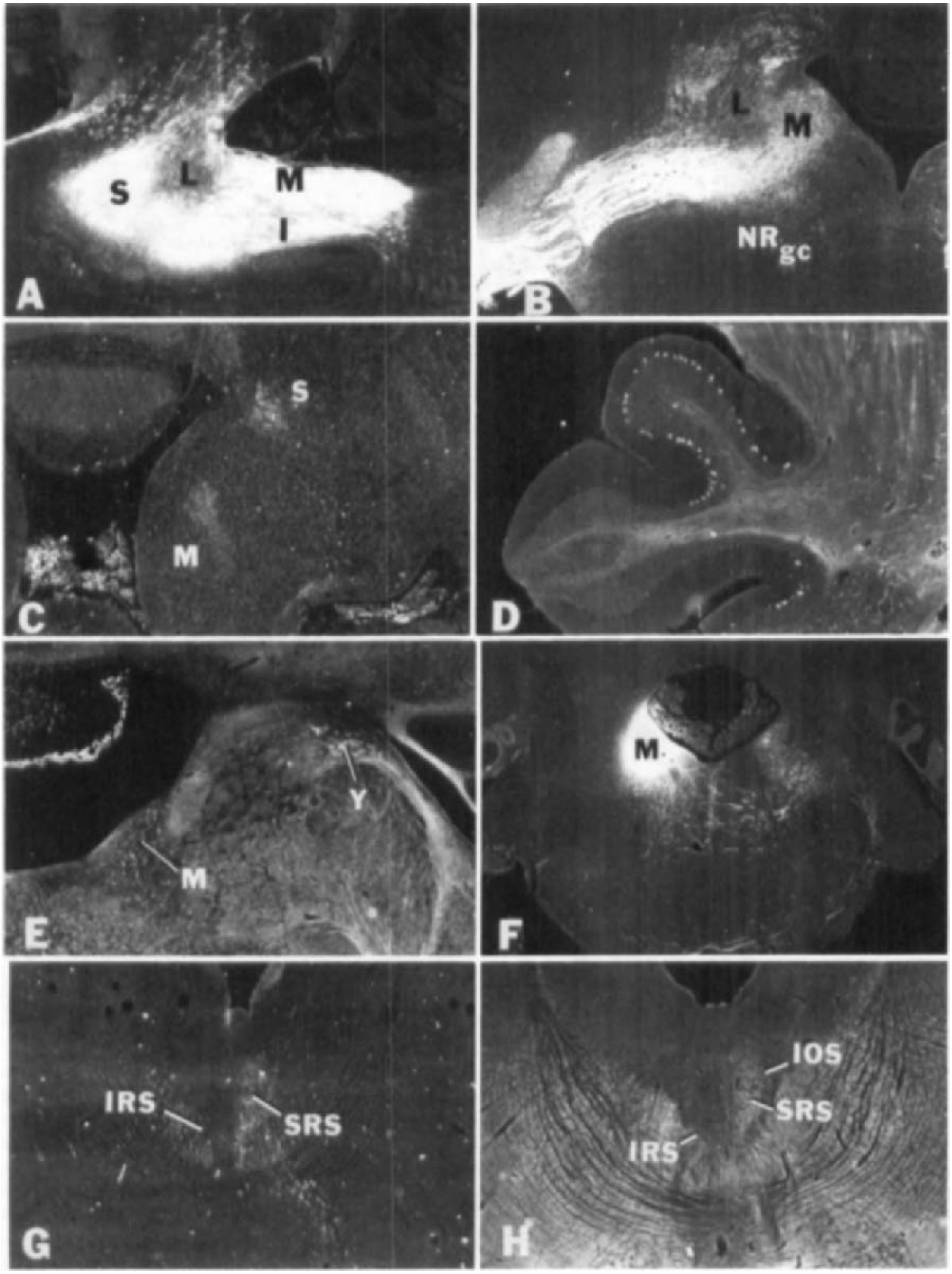
Abbreviations: ACN, accessory cuneate nucleus; ACN, anterior canal nerve; AIN, abducens internuclear neuron; AN, abducens nucleus; EOM, extra-ocular muscle; FN, fastigial nucleus; GABA, γ-aminobutyric acid; GAD, glutamic acid decarboxylase; HRP, horseradish peroxidase; INC, interstitial nucleus of Cajal; INVN, interstitial nucleus of the vestibular nerve; IOS, inferior oblique subdivision; (Ri)MLF, (rostral interstitial nucleus of the) medial longitudinal fasciculus; ND, nucleus of Darkschewitsch; NIC, nucleus intercalatus; NPP, nucleus prepositus hypoglossi; NR, nucleus of Roller; NRgc, nucleus reticular gigantocellularis; OMC, oculomotor nuclear complex; PC, Purkinje cell; PPRF, pontine paramedian recticular formation; RF, reticular formation; (I/S/M)RS, (inferior/superior/medial) rectus subdivision; SCP, superior cerebellar peduncle; SD, semicircular duct; TN, trochlear nucleus; VG, vestibular ganglion; (L/I/M/S) VN, (lateral/inferior/medial/superior) vestibular nucleus; VOC, vestibulo-ocular cervical; (L/M)VST, (lateral/medial) vestibulospinal tract.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