Contents

Abbreviations ................................................................. xxv

1 Introduction to Nerve Cells and Nervous Systems ....................... 1
  The Nervous System and Control .................................... 1
  The Nervous System and Communication .............................. 2
  Nerve Cells ...................................................................... 2
    The Generalised Neuron ................................................. 3
    The Anatomy of Neurons ................................................ 6
  The Neuroglia .................................................................... 9
  The General Plan of Nervous Systems .................................. 10
  Regulation of the External Environment of Neurons ................. 12
  Summary ......................................................................... 14

2 The Cell Membrane: Ionic Permeability and Electrotonic Properties .... 15
  The Structure of Cell Membranes ....................................... 15
  Non-gated Channels and the Resting Membrane Potential .......... 16
    Resting Potential of an Ideal Cell ................................. 17
    Electrotonic Properties of Nerve Cells ......................... 22
  Summary ......................................................................... 25

3 The Action Potential and the Nerve Impulse .............................. 27
  Electrically Excitable Cells .............................................. 27
  Ionic Basis of Action Potentials in Nerve Fibres .................... 27
    Voltage-Clamp Experiments ............................................ 30
    The Initial Inward Current Is Due To Movement of Na+ .......... 32
    The Later Outward Current Is Due To Movement of K+ .......... 32
    The Inward and Outward Currents Can Be Separated by Drugs ... 32
    The Separate Na+ and K+ Conductances Can Be Determined .... 34
    Na+ Inactivation Is a Distinct Process ............................ 34
  Action Potential Shape and Propagation Can Be Predicted on a
    Theoretical Basis ......................................................... 35
  Changes in Internal Ion Concentrations Due to the Action Potential .. 35
  Summary of the Action Potential ....................................... 36
  The Nerve Impulse ......................................................... 36
    Local Circuits ............................................................ 37
    Effect of Axon Diameter on Conduction Velocity ................. 37
    Myelination and Saltatory Conduction ............................. 38
    Voltage-Gated Channels and Impulse Propagation ............... 39
The Length of Axon Involved in a Nerve Impulse ........................................ 39
Extracellular Field Potentials ................................................................. 40
Extracellular Recording from a Single Axon .......................................... 40
Extracellular Recording from a Nerve Bundle – The Compound Action
Potential .................................................................................................. 40
Classification of Nerve Fibres ................................................................. 42
Summary ................................................................................................... 43

4 Voltage-Gated Ion Channels in Excitable Membranes .......................... 45
Voltage-Gated Na\(^+\) Channels ................................................................. 45
The Voltage-Gated Na\(^+\) Channel Responsible for \(I_{\text{Na,t}}\) the Transient
Rapidly Activating and Inactivating Na\(^+\) Current .................................. 45
A Voltage-Gated Na\(^+\) Channel Responsible for a Persistent
Na\(^+\) Current \((I_{\text{Na,p}})\) ................................................................. 50
Voltage-Gated K\(^+\) Channels .............................................................. 50
The Voltage-Gated K\(^+\) Channel Responsible for the Delayed Rectifying
Current \((I_{\text{k}})\) ........................................................................ 51
Voltage-Gated K\(^+\) Channels Responsible for the A Current \((I_{\text{a}})\) ............... 51
Voltage-Gated K\(^+\) Channel Responsible for the M Current \((I_{\text{m}})\) ............... 51
Voltage-Gated Ca\(^{2+}\) Channels ............................................................. 51
Summary ................................................................................................. 53

5 General Properties of Intercellular Communication in the Nervous System .... 55
Electrical Synaptic Transmission ............................................................ 55
Excitatory Electrical Transmission .......................................................... 56
Inhibitory Electrical Transmission .......................................................... 58
Chemical Synaptic Transmission .............................................................. 58
General Outline of Chemical Synaptic Transmission ............................... 60
Summary ................................................................................................. 61

6 The Presynaptic Neuron I: Release of Neurotransmitter ......................... 63
Role of Ca\(^{2+}\) in Transmitter Release ..................................................... 63
Release of Transmitter in Packets or Quanta ......................................... 65
Quantal Content ...................................................................................... 67
Molecular Mechanisms Involved in Transmitter Release ....................... 70
Vesicle Manufacture ............................................................................... 70
Transmitter Release: Vesicle Docking, Fusion and Exocytosis ............... 71
Vesicle Endocytosis and Recycling .......................................................... 72
Role of Ca\(^{2+}\) in Molecular Mechanisms of Release ............................... 72
Changes in Synaptic Efficacy Due to Presynaptic Mechanisms ............... 73
Presynaptic Inhibition ............................................................................. 73
Summary ................................................................................................. 73

7 The Presynaptic Neuron II: Neurotransmitters ....................................... 75
Definition and Identification of Transmitters .......................................... 75
Classification of Transmitters ................................................................ 76
Low-molecular-weight Transmitters ....................................................... 76
Neuroactive Peptides ............................................................................. 80
Adenosine triphosphate (ATP) ................................................................. 82
Unconventional Transmitters ................................................................. 82
Some General Principles About Transmitters ....................................... 85
Some Transmitters Appear To Be Either Excitatory or Inhibitory but
Not Both ............................................................................................... 85
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Some Transmitters May Have Either Excitatory or Inhibitory Actions</td>
<td>85</td>
</tr>
<tr>
<td>Many Neurons Contain Several Transmitters</td>
<td>85</td>
</tr>
<tr>
<td>A Single Neuron May Release More Than One Transmitter</td>
<td>85</td>
</tr>
<tr>
<td>Some Neuronal Systems Containing Particular Transmitters Have Very</td>
<td>85</td>
</tr>
<tr>
<td>Wide-ranging Actions in the Brain</td>
<td>85</td>
</tr>
<tr>
<td><strong>Summary</strong></td>
<td>85</td>
</tr>
<tr>
<td><strong>8</strong> The Postsynaptic Neuron I: Actions of Neurotransmitters</td>
<td>87</td>
</tr>
<tr>
<td>Postsynaptic Receptors</td>
<td>87</td>
</tr>
<tr>
<td>Ionotropic Receptors</td>
<td>87</td>
</tr>
<tr>
<td>Metabotropic Receptors</td>
<td>90</td>
</tr>
<tr>
<td>Consequences of Transmitter-Receptor Combination</td>
<td>90</td>
</tr>
<tr>
<td>Actions at Ionotropic Receptors</td>
<td>90</td>
</tr>
<tr>
<td>Actions at Metabotropic Receptors</td>
<td>96</td>
</tr>
<tr>
<td><strong>Summary</strong></td>
<td>99</td>
</tr>
<tr>
<td><strong>9</strong> The Postsynaptic Neuron II: The Neuron as an Integrative Device</td>
<td>101</td>
</tr>
<tr>
<td>Neuron Doctrine and the Law of Dynamic Polarisation</td>
<td>101</td>
</tr>
<tr>
<td>The Generalised Neuron Concept</td>
<td>101</td>
</tr>
<tr>
<td>The Generalised Neuron as a Model for the Mammalian Motoneuron</td>
<td>102</td>
</tr>
<tr>
<td>The Generalised Neuron as a Model for Other Neurons</td>
<td>107</td>
</tr>
<tr>
<td>Synapses on Axon Terminals – Axo-axonic Synapses</td>
<td>108</td>
</tr>
<tr>
<td>Impulses in Dendrites</td>
<td>109</td>
</tr>
<tr>
<td>Dendritic Spines</td>
<td>113</td>
</tr>
<tr>
<td>The Importance of Synaptic Location</td>
<td>114</td>
</tr>
<tr>
<td>Excitatory Synaptic Location on Motoneurons</td>
<td>114</td>
</tr>
<tr>
<td>Inhibitory Synapses</td>
<td>115</td>
</tr>
<tr>
<td>Consequences of Synaptic Location Specificity</td>
<td>116</td>
</tr>
<tr>
<td><strong>Summary</strong></td>
<td>116</td>
</tr>
<tr>
<td><strong>10</strong> Transmission Between Pairs of Identified Neurons</td>
<td>119</td>
</tr>
<tr>
<td>Transmission Between Ia Afferent Fibres from Muscle Spindles and</td>
<td>119</td>
</tr>
<tr>
<td>Spinal α-Motoneurons</td>
<td>119</td>
</tr>
<tr>
<td>Anatomy of the Ia–α-Motoneuron System</td>
<td>120</td>
</tr>
<tr>
<td>Ia Afferent Fibres</td>
<td>121</td>
</tr>
<tr>
<td>Ia Afferent Contacts upon Motoneurons</td>
<td>121</td>
</tr>
<tr>
<td>Actions of Ia Afferent Fibres on α-Motoneurons</td>
<td>121</td>
</tr>
<tr>
<td>Transmission Between Cutaneous Afferent Fibres and Neurons of</td>
<td>125</td>
</tr>
<tr>
<td>Somatosensory Pathways</td>
<td>125</td>
</tr>
<tr>
<td>Transmission Between Hair Follicle Afferent Fibres and Spinocervical</td>
<td>125</td>
</tr>
<tr>
<td>Tract Neurons</td>
<td>125</td>
</tr>
<tr>
<td>Transmission Between Cutaneous Afferent Fibres and Neurons of the</td>
<td>128</td>
</tr>
<tr>
<td>Dorsal Column Nuclei</td>
<td>128</td>
</tr>
<tr>
<td><strong>Summary</strong></td>
<td>128</td>
</tr>
<tr>
<td><strong>11</strong> Sense Organ Mechanisms</td>
<td>131</td>
</tr>
<tr>
<td>Sense Organ Specificity</td>
<td>131</td>
</tr>
<tr>
<td>Sensory Transduction Mechanisms</td>
<td>132</td>
</tr>
<tr>
<td>Mechanoreceptors</td>
<td>132</td>
</tr>
<tr>
<td>Vertebrate Photoreceptors</td>
<td>134</td>
</tr>
<tr>
<td>Adaptation of Sensory Signals</td>
<td>138</td>
</tr>
<tr>
<td>Stimulus Encoding</td>
<td>139</td>
</tr>
<tr>
<td>Dynamic and Static Components of the Response</td>
<td>140</td>
</tr>
</tbody>
</table>
## Contents

15 The Nervous System and the Internal and External Environments –

### Homeostasis and Interactions ........................................ ........................................ 197
- The Neuroendocrine System ........................................ 197
- The Magnocellular Neurosecretory System ...................... 198
- The Parvocellular Neurosecretory System ....................... 200
- Circadian Rhythms .................................................. 201
  - The Photoreceptive System ..................................... 201
  - The Suprachiasmatic Nucleus .................................. 201
  - Output Systems from the Suprachiasmatic Nucleus ......... 201
- Behavioural State – Sleeping and Waking .................... 201
  - Sleeping and Waking ........................................... 201
- Motivational Behaviour ............................................ 205
  - Non-Specific Activation ....................................... 205
  - Homeostasis and Motivational Behaviour ................... 206
- Control of Nociception ............................................. 209
  - Segmental Control of Nociceptive Input .................... 209
  - Descending Control of Nociception ........................... 209
- Interactions with Other Organisms .............................. 210
  - Animal Communication ........................................ 210
  - Human Language ................................................ 212
- Summary .............................................................. 212

16 Formation, Maintenance and Plasticity of Synapses ........... 215
  - Development of the Nervous System ........................... 215
  - Determination of Nervous Tissue ............................... 215
  - Cell Differentiation .............................................. 217
  - Synapse Formation and the Maintenance of Connections .... 219
    - Formation of the Neuromuscular Junction ............... 219
    - Synapse Elimination ........................................ 221
    - Formation of Synaptic Connections in the Visual System 222
  - Matching of Neuronal Populations ............................ 223
    - Programmed Cell Death and Nerve Growth Factor ....... 224
  - Effects of Denervation in the Adult Central Nervous System 226
  - Abnormal Experience and the Formation of Synaptic Connections –
    - Critical Periods .............................................. 226
- Summary .............................................................. 229

17 Learning and Memory .................................................. 231
  - Forms of Learning and Memory ................................ 231
  - Cellular Mechanisms of Learning and Memory in Invertebrates 232
    - Non-associative Learning: Habituation and Sensitisation 232
    - Associative Learning in Invertebrates: Classical Conditioning 234
  - Cellular Mechanisms of Learning in Vertebrates ............ 234
    - Mechanisms Underlying Long-Term Potentiation in the Hippocampus 234
    - Long-Term Depression in the Cerebellum ................ 236
  - Learning and Memory in Humans .............................. 236
    - The Major Memory Systems ................................. 237
- Summary .............................................................. 237

References ................................................................. 239
Index ................................................................. 249
Nerve Cells and Nervous Systems
An Introduction to Neuroscience
Brown, A.G.
2001, XVI, 253 p. 134 illus., Softcover
ISBN: 978-3-540-76090-0