Principles of Exercise Neuroscience

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Edited by

Dawson J. Kidgell and Alan J. Pearce

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PREFACE

DAWSON J. KIDGELL, PHD AND ALAN J. PEARCE, PHD

Over the last 30 years, there has been a significant rise in research and teaching interest that has examined the neuromuscular responses to different types of exercise interventions. Two fields of research, neuroscience and exercise science, have merged to provide evidence for how the nervous system responds to exercise. An important component of exercise science, but one area that is less recognised, although used ubiquitously through other topics within exercise science, is the study of *motor control*. Motor control is primarily concerned with the neurophysiological mechanisms that contribute to human movement. Motor control is at the very heart of exercise and sport science. Motor control drives how we program appropriate exercise in health, injury and disease. Motor control is what underpins this book we call *Principles of Exercise Neuroscience.*

This textbook introduces the key concepts that emphasise human motor control and its application to exercise science and rehabilitation. The topics covered integrate research, theory and the clinical applications of *Exercise Neuroscience* that will support students, researchers and clinicians to understand how the nervous system responds, or adapts to physical activity, training, rehabilitation and disease. *Exercise Neuroscience* uses a mix of neuromuscular physiology, electrophysiology and muscle physiology to provide a synthesis of current knowledge and research in the field of exercise neuroscience that specifically examines the effects of exercise training, injury and rehabilitation on the human nervous system.

It is never easy writing a textbook like this from scratch. Indeed, this textbook came about from the initial teaching notes to assist tertiary students with some difficult learning concepts within the motor control subjects taught at our respective universities. As time progressed, the lecture notes developed into full chapters that eventually evolved into this textbook. Further, through our international collaborative network, we were able to draw upon international experts who were very happy to contribute and provide their extensive knowledge and experience to develop our initial chapters into state of the art reviews. Our guest authors are leaders in their respective areas of enquiry and provide the latest research findings in three key areas: principles of motor control; neuroscience of exercise performance; and clinical exercise neuroscience (injury and neuro-rehabilitation). We sincerely thank each of them for their time and efforts in helping us complete this book.

This is the first text devoted solely to the emerging topic of *Exercise Neuroscience*. It aims to assist readers in identifying current research findings and provide new avenues to explore the benefits of exercise on the human nervous system. We thoroughly enjoyed writing this and we hope that you find this text useful for your learning and professional development.

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June, 2020

Acknowledgements

A text such as *Principles of Exercise Neuroscience* is not the effort of just two authors. This text brings together the contributions of many research scientists who have examined the changes that occur in the human nervous system. We would like to especially thank Dr Eric Frazer for his assistance in providing suggestions for revisions to this book, in particular his attention to detail and endless editing. We would also like to acknowledge the contributions of all the authors, in particular Professor Glyn Howatson, who has established and leads a remarkable program of Applied Neuromuscular Research at Northumbria University; many former PhD students from this laboratory have contributed to this text.

CHAPTER 1

THE NEXUS BETWEEN NEUROSCIENCE AND THE SCIENCE OF EXERCISE

ALAN J. PEARCE, PHD

1. Background

The past thirty years have seen a significant rise in the disciplines of neuroscience and exercise science. However, within the last ten years we have seen these two disciplines become intersected. While neuroscience has been an area of research for over a century, it is only in the last 20-30 years that neuroscience has transformed from an interdisciplinary speciality under the umbrella of neurology, psychiatry and psychology, to a stand-alone discipline, and is now the fifth largest field of study in the sciences (Rosvall and Bergstrom, 2010). Particularly in the last decade, with advancements in technologies such as neuroimaging and electrophysiology, neuroscience has captured the imagination of the wider community. In particular, the concept of neuroplasticity, where evidence has demonstrated that the brain has the ability to reorganise and readapt over the lifespan, has ignited a huge interest across many unrelated fields. This has, of course, been both positive, with advances in our understanding of the brain and nervous system, but also negative where we are seeing the rise in what some call “neurobabble”, the phenomenon whereby neuroscientific explanations of cognitive and motor behaviour are more persuasive simply because they sound more technical and authoritative (Varazzani, 2017). Despite this, continued advances in neuroscience research will improve the lives of everyday people, as well as contributing to improved athletic performance.

In parallel, exercise science has also emerged from the discipline of physical education. Since the early 1990s, when the first exercise science courses were beginning to be established in Australia, the growth in exercise science has been so rapid that physical education can now be regarded as one of the areas under the broader discipline of exercise science (along with exercise physiology, strength and conditioning, biomechanics, nutrition, functional anatomy, skill acquisition and psychosocial determinants of health). Indeed, many exercise science graduates will continue their learning, pursuing postgraduate studies in education and developing courses in sport and exercise science in secondary schools.

It should be no surprise then that the maturing disciplines of exercise science and neuroscience have overlapped. Significant interest and growth in research and application have occurred in the role of exercise on brain health, neural function and neuroplasticity. Conversely, greater understanding of clinical neurological disease has impacted on advancing exercise programming, with studies testing the efficacy of various exercise interventions on brain and neural integrity. Taken together, the understanding of human motor control occurs through exploring and investigating neural and neuromuscular function.

1.1 The neuroscience of human movement.

It is important to note that neuroscience has many different areas of research and study. Notwithstanding animal models of neuroscience, just focusing on the neuroscience of human nervous systems can traverse a wide continuum of study areas (Figure 1.1).

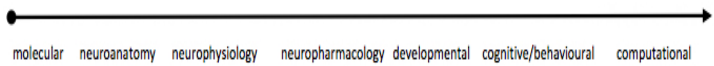

Figure 1.1. Continuum of general areas of study within neuroscience

It is not uncommon that neuroscientists from different research areas will not necessarily understand each other’s work. For example, there are those who investigate the neuroscience of a single cell under physiological or pharmacological interventions. Conversely, there are others who are interested in neuroimaging of the healthy or diseased brain. In between, we have various levels of neuroscientific inquiry that can overlap but are specific sub-disciplines in their own right. Further, like exercise neuroscience or neurophysiology, various other combined disciplines exist such as neuroanatomy, neurochemistry, neuropsychology and the like (see Table 1.1 for a list with definitions).

Table 1.1. List of combined areas of study within neuroscience.

Neuroanatomy	Study of anatomy of neurons and neural structures
Neurochemistry	Study of the compounds that generate physiological functioning in and between neurons
Neuroendocrinology	Study of the interaction between the endocrine and nervous systems
Neurodermatology	Study of the neural structures within the skin contributing to not only neural health but also sensory reception.
Neurogenetics	Study of the role of genetics in the development and function of the nervous system
Neuroimmunology	Study of the interaction between the immune and nervous systems
Neurooncology	Study of cancers of the brain and nervous system
Neuroopthamology	Study of the interaction between the visual system and nervous system
Neurotology	Study of the neural contribution to vestibular function
Neurophysiology	Study of the functioning of the nervous system
Neuropsychology	Study of the nervous systems influence in a person's cognition and behaviour

Of course, as this book will be focusing on aspects of exercise science and human movement, the aim will be to synthesize and translate the growing research output specific to human motor control. The result is that this text narrows itself to the neural basis of human movement. Pathways, structures, neurophysiological principles and application of these principles are discussed but always in the context of human function and movement.

The scientific study of the neuroscience of movement is termed motor behaviour. Motor behaviour is an umbrella term that encompasses a range of sub-disciplines that overlap:

Motor control – the study of the underlying neurophysiological mechanisms that contribute to movement;

Motor learning and skill acquisition – understanding the optimal environments to practice and refine specific, purposeful movements progressing the individual towards an accomplished level of expertise; and

Motor development – the study of movement across the lifespan; how children develop and learn fundamental motor skills, through to understanding the mechanisms by which older adults decline in motor control.

1.2 What is 'motor control'? How does motor control relate within the larger discipline of exercise science?

As teachers in motor control for over 15 years, this is usually the first question that pops up from students. This is because motor control, as a term, is rather indistinct. Indeed, as the term 'motor control' is becoming used more widely, it has also been used and taken on slightly different meanings to different professionals within the exercise and sport science domain. For example, biomechanists discuss motor control in terms of physics being applied on, or from within, the body during proficient performance of a movement. Sport psychologists reference motor control in terms of actions having an emotional or cognitive basis, for example, the use of motor imagery to assist with rehabilitation of function or to improve on sports skills. Physiotherapists discuss motor control in the rehabilitation setting, with patients focusing on reducing "abnormal" movement and increasing movement patterns that are less likely to cause injury (or re-injury). Exercise physiologists may discuss the reduction in motor control performance when an individual experiences fatigue. Strength and conditioning and personal trainers need to consider motor control issues when prescribing correct technique and resistance, to optimise strength improvements and reduce likelihood of injury.

However, the core of motor control centres on the neuroscience that underpins neuromuscular movement of the human body. It goes without saying that people's lives are filled with *movement* (Latash, 2008). As undergraduates studying exercise science and related fields, human movement is the core focus: using movement to improve strength and muscle mass; using movement to improve skills; using movement to help people lose weight; and using movement to assist people back to functional daily activities.

Undergraduate study in exercise science will have motor control embedded within course content across a number of subjects, or as a 'stand-alone' course. As exercise neuroscientists, we may have a bias here (who doesn't!) but it is quite easy to illustrate how elements of motor control permeate throughout the curriculum of the major or core subjects areas taught in exercise science courses (Table 1.2).

Table 1.2. Interrelationship between motor control and other areas within the discipline of exercise science.

Study area	Relationship to motor control	Example
Anatomy (neuroanatomy)	Study of the structure and function of the brain and nervous system.	Damage to primary motor cortex leading to motor dysfunction.
Biomechanics/movement analysis	Study of efficient voluntary movement.	Relationship of sequential limb movement for a specific motor task.
Exercise/sport physiology	Study of biochemistry and physiological systems adapting to exercise and sport.	The role of the brain in fatiguing exercise.
Psychology of exercise and sport	Study of psychological influences in determining exercise behaviour, as well as psychological traits required in high performance sport.	Mood disorder influencing loss in motivation to exercise. Motor imagery to improve movement efficiency in sport.
Nutrition	Study of nutrients in food, how the body uses nutrients, and the relationship between diet, health, and disease.	Gut/brain interaction, how food intake can affect movement (interrelationship with exercise physiology).
Strength and conditioning	Study of methods to induce resistance for training adaptations.	Neural adaptations with strength or resistance training modalities.

So, where does this lead us in terms of establishing what motor control actually is? The common denominator in all these areas is the interaction of the brain and muscle to provide *meaningful* (Latash, 2008) goal-directed movement (Enoka and Stuart, 2005). Therefore, it can be argued that motor control has a basis in neuroscience. Motor control is concerned with the neurophysiological processes that allow movements to become more efficient (which may also include improvement in skills, movement efficiency, and strength). Similarly, motor control investigates how movements can be retrained after an injury. These scenarios now have a well-described term, *neuroplasticity* (Doidge, 2007), which will be discussed later and throughout the text.

1.3 Motor learning and skill acquisition: similarities and contrasts to motor control.

Historically, physical education courses have focussed on the understanding of the learning and teaching of motor skills (or motor learning). For example, understanding the development of fundamental motor skills (FMS) such as running, jumping, and throwing are important when teaching children these lifelong skills. These fundamental skills are the foundation for more advanced motor skills, particularly specific skills for sporting excellence. Teaching motor skills effectively is ingrained within the cognitive/psychological domain, whereby the teacher is creating an optimal learning environment. However, with the increased interest in the study of motor development (see section 1.4), exploration of FMS now sits within the development and changes of skills and motor actions across the lifespan, providing motor learning and skill acquisition the opportunity to have its own definition, succinct from motor control and motor development.

Figure 1.2 addresses not only similarities, but also differences, between the sub-disciplines of motor control and motor learning. Motor learning, it can be suggested, is aimed at how people learn and acquire expertise at motor skills. What are the environments that best optimise learning? For example, should athletes practice the same movement action in an unchanging setting repeatedly in a series of blocks to reinforce motor pathways? Or, should athletes randomise the environment with the intention of learning a particular skill but retaining the motor memory? Is it better for individuals to learn implicitly through discovery, or have an external source (such as a teacher or instructor) providing feedback on how their attempt was executed? In reality, motor learning and skill acquisition are part of memory formation and, therefore, it can be argued that this sits within the domain of cognitive psychology. Motor learning is creating motor memory, similar to other forms of learning (e.g., content knowledge) that leads to memory retention.

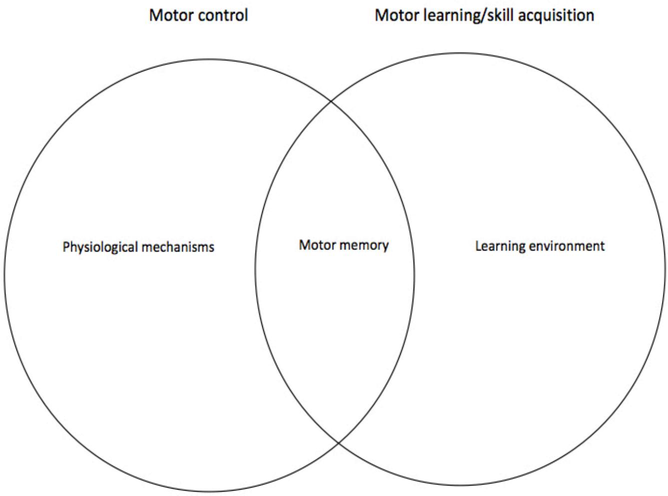

Figure 1.2. Differences and overlap between motor control and motor learning/skill acquisition.

Motor development focuses on the stages and underlying processes that allow children to gain motor skills. Traditionally, within the domain of developmental psychology, the study of motor development has taken a 'back seat' compared to other developmental science areas such as cognitive, social, language, personality, perceptual and emotional development (Adolf and Robinson, 2015). However, there has been a resurgence of interest in studying motor development due to its advantage in direct observation and translation to the psychological sciences. Moreover, with increased understanding of neuroplasticity, the study of motor development allows for the understanding of neurophysiological processes, providing a foundation for how adults learn new motor skills and retain motor memory.

Whilst motor development is primarily focussed in children and adolescents, it is also important to understand changes as people age, and the consequences of these. Our society is ageing, with significant increases in the number of people who will be aged 65 and older in the coming decades. Understanding the neuromuscular and motor control changes with ageing is important for current students, particularly in thinking of career opportunities upon graduating. As part of the Allied Health sector, exercise science students have a unique set of skills allowing application of their neuroscience knowledge to, for example, exercise programming for older people, or biomechanics to understand how to prevent falls. These will be key areas in the near future to which exercise science can make a unique contribution (if not already).

1.4 The challenge of translating neuroscience to exercise science

So, why does neuroscience cause such difficulty to the majority of exercise science students? The simple reason is because the neuromuscular system is complex. It has a number of levels contributing to meaningful movement that work at the conscious and subconscious levels, spinal and supraspinal levels, and between sensory interactions with the motor response. Further, it also may not necessarily have anything to do with exercise. Motor control is as concerned with how an individual can create a pincer grip to control a pen during writing, as it is concerned with how a person can increase strength without muscle hypertrophy, or how the central nervous system controls movement as it also responds to fatiguing exercise. It is also concerned about how control can be lost, through degeneration, or how control is lost after a brain injury and, in some cases, how it can be regained.

With the links between neuroscience and exercise becoming closer, it is important that exercise scientists have a competent understanding of the brain, and how it controls the neuromuscular pathways. Moreover, it is important that exercise scientists who may practice in related fields are able to constructively critique new developments in the area, and to confidently determine good neuroscience from *neurobabble*. With unprecedented access to news and information on a daily basis and the rise of pop-science, it is important that, as practitioners in the field, you will be able to advise your clients/patients what has been demonstrated using the scientific method, and what has not been supported (despite comprehensive spin). The contents in this book are based upon evidence-based research; however, each chapter aims to translate the findings allowing students to learn new concepts confidently.

1.5 How to get the best from this book

The topics in this book have come from our teaching of motor control to students over the last 15 years. While the topics can and do overlap, each chapter can be read independently and in any order. For some, all chapters will be of interest. For others, specific chapters will be helpful for personal and professional development. As the chapters are research based, our aim is to guide students through each chapter with the most robust concepts, but also some insights into future areas of enquiry. For some students, this text may serve as a pathway to a career as an exercise science research student, as much as it may inform students moving towards a practitioner career. Either way, we hope that students find this book engaging, but also challenging, in attaining future knowledge through scientific enquiry.

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CHAPTER 2

LEVELS OF MOTOR CONTROL

DAWSON J. KIDGELL, PHD
AND ALAN J. PEARCE, PHD

2. Background

Understanding motor control is through learning the macro and the micro arrangement of the nervous system. In this chapter, we will focus on the macro: structural, functional and hierarchical organisation of movement. In chapters four and five, we will discuss how motor control occurs through neuromodulation and neuroplastic changes. The study of neuroscience dictates that we need to learn the structural, functional and hierarchical anatomical arrangement of the nervous system in order for us to appreciate how individuals improve their movement, whether it be for sport, music, jobs requiring fine skills or, alternatively, how patients relearn and regain movement after an injury.

The chapter will start with the basics: the major structures identified in the central nervous system. Where appropriate, and in keeping with the objective of this textbook, we will focus examples and discussion on how the region contributes to movement and motor control. Bear in mind which cognitive functions, such as attention and decision-making, can and do influence motor output. From there, we will outline the functional arrangement of motor control. Here, we will focus on topographic arrangement of motor functions and, in later chapters, how their arrangement allows for adaptation and re-organisation. Finally, we will discuss the hierarchical levels of motor control where we will incorporate structural and functional understanding on how movement is planned and executed.

2.1 Structural arrangement of the brain contributing to movement

In simplistic terms, the brain can be divided into three parts: the *cerebrum, brain stem,* and the *cerebellum.* Each of these structures makes important contributions to the regulation of movement.

The cerebrum is the large 'dome' of the brain that is divided into right and left cerebral hemispheres. The most superficial layer of the cerebrum is the cerebral cortex, which is composed of tightly arranged neurons. The cortex performs three important motor functions: (1) the organization of complex movements; (2) the storage of learned experiences; and (3) the reception of sensory information. For the purpose of this chapter, we will limit our discussion to the role of the cortex in the organization of movement. However, to appreciate this, some information about the structure of the cerebral cortex is required.

2.1.1 Structure of the cerebral cortex

The cerebral cortex is well endowed with neurons, neuroglia, and blood vessels. The structural organisation of the three types of cells that populate the cortex, being pyramidal cells, stellate neurons and fusiform neurons, enables the classification of the cortex into three types: *allocortex*, *mesocortex* and the *neocortex*. The *allocortex* is the oldest region and is composed of only three layers and is located in the limbic system. The *mesocortex* is younger and is composed of three to six layers and is predominantly located in the insula and cingulate gyrus. The *neocortex* is the youngest region of the cortex and is composed of six layers that comprise the bulk of the cerebral cortex (Rothwell 1994). Whilst the cerebral cortex is structurally organised into layers, it also has organisation through functional connections. Most corticospinal output is mediated through pyramidal neurons and stellate (or granule) cells. The cellular organisation of pyramidal and stellate cells within the cortex gives it a characteristic layered or laminar appearance that can be identified as six distinct layers:

I. Molecular layer. A layer lying immediately inferior to the pia matter and containing very few cell bodies.

II. External granular layer. A layer of densely packed small cells including small pyramidal and stellate cells.

III. External pyramidal layer. A layer consisting of medium to large-sized pyramidal cells.

IV. Internal granular layer. This layer is predominantly composed of densely packed stellate and pyramidal cells.

V. Ganglionic layer. This layer contains large pyramidal cells (Betz cells).

VI. Multiform layer. This layer is relatively thin and mostly composed of densely packed, spindle-shaped cells, many with axons leaving the cortex.

Layer 1 contains mainly long horizontal dendrites and axons in deeper layers as well as thalamic afferents. The medium to large pyramidal cells in layers III and V contain long cortico-cortical connections. In addition, pyramidal cells in layer V also project to sub-cortical areas such as the basal ganglia, brain stem and to the spinal cord. Layers II and IV receive afferent inputs, with inputs from the thalamus generally terminating in layer IV. Layer VI contains small pyramidal cells which exhibit greater morphologic variability than the pyramidal cells located in other layers and have cortico-cortical and cortico-thalamic projections. Layers II through VI all contain stellate cells, some of which form excitatory connections onto pyramidal cells and some of which form inhibitory synapses.

2.1.2 The brain stem

The brainstem is located inside the base of the skull just superior to the spinal cord and is essentially an extension of the spinal cord. It is composed of a series of complicated neural tracts and nuclei (groups of neurons). The major structures of the brain stem include the *medulla, pons* and *midbrain*. In addition to these structures, a complex neuronal network known as the ***reticular formation*** resides in the brainstem. The brainstem performs motor and sensory functions for the face and head (i.e., cranial nerves) along with providing support to the body against gravity. For example, muscles of the spinal column and the extensor muscles of the legs maintain the body against gravity. These muscles are under the control of specific brainstem nuclei, in particular the ***pontine reticular*** nuclei, which excite activity in the antigravity muscles, and the ***medullary reticular*** nuclei, which inhibit the activity of antigravity muscles. Importantly, the ***medullary reticular*** nuclei receive collateral input from the corticospinal pathway, rubrospinal pathway, and other motor pathways. These systems can activate the inhibitory action of the ***medullary reticular*** nuclei and counterbalance the signals from the pons.

2.2 Transmission of cortical motor signals

The spinal cord is under the control of a number of neurons that descend from the primary motor cortex (M1). The largest of these are the corticospinal neurons that have their origins in layer V of the cerebral cortex and extend to form the bulk of the ***corticospinal or pyramidal tract*** (Porter 1985). Although corticospinal neurons are located within six cortical regions, the M1 has the largest concentration (Porter, 1985). Within the M1, these corticospinal neurons are functionally organised to project to motoneurons that control specific muscle groups (He et al. 1993), thus they are somatotopically organised. Corticospinal neurons that arise within the M1 descend through the internal capsule, brainstem, and medulla oblongata and continue to descend in the dorsolateral funiculi of the spinal cord (Alawieh et al. 2017). As the corticospinal neurons leave the M1 and descend to the medulla, they are organised somatotopically. At the medullary spinal junction, approximately 85-90% of the corticospinal neurons cross the midline to form the motor pyramidal decussation (Alawieh et al. 2017), where they continue as the dorsolateral funiculi of the spinal cord and converge onto motoneurons within the ventral horn of the spinal cord that innervate limb muscles (Alawieh et al. 2017). Anatomical mapping studies reveal that the connectivity of the corticospinal tract suggests that the remaining uncrossed ipsilateral corticospinal tract fibres descend primarily in the dorsolateral lateral or ventral funiculi of the spinal cord (Alawieh et al. 2017).

A small proportion of corticospinal tract fibres do not crossover at the pyramidal decussation at the medulla; rather, they project to ipsilateral spinal motoneurons, where they could alter the excitability of ipsilateral pathways (Porter and Lemon 1993, Carson 2005). In the clinical neurophysiology literature, it has been suggested that increased utilisation of the ipsilateral pathway may provide a viable method for re-establishing motor control of upper-limb muscles following lesions to the M1 (Alawieh et al. 2017, see Chapter 11 for more detail). There is now good evidence for a functional role of the corticospinal system in the control of the upper limb and changes in its functional organisation following different forms of exercise training (Frazer et al. 2018).

2.3 Motor functions of the cerebellum

For a long time, the cerebellum has been referred to as the *silent area* of the brain mainly because electrical stimulation of the cerebellum does not evoke any conscious sensation or movement. However, intriguingly, removal of the cerebellum causes highly abnormal human movement. Although it is difficult to study the function of the cerebellum in a conscious person, it is generally accepted that the cerebellum is vital for rapid motor actions which include cycling, running, playing the piano and talking. Because the cerebellum does not cause muscle contraction *per se*, its main function is to assist in the sequencing of motor actions and to monitor and correct movements whilst they are being executed. The ability to adjust motor sequences during movements enables the M1 and other parts of the brain to ensure that the intended movements are performed correctly.

The cerebellum continuously receives updated information about the intended/desired sequence of muscle activity from specific motor control centres of the cortex. It receives sensory information from peripheral receptors such as muscle spindles and Golgi tendon organs, thus allowing corrective adjustments to be sent to the motor system to increase or decrease the level of muscle activation of specific muscle groups. A critical function of the cerebellum is to assist the cerebral cortex to plan the next series of sequential movements in advance whilst the initial movement is still being performed. This essentially enables movements to transition smoothly from one movement to the next. The cerebellum also learns to correct movement, via special cerebellar nuclei (the deep cerebellar nuclei) that can adjust motor output. The cerebellum is able to perform these functions because of its anatomical and functional organisation.

2.3.1 Anatomical and functional organisation of the cerebellum

The cerebellum is divided into three lobes: 1) anterior lobe, 2) posterior lobe and 3) flocculonodular lobe and two deep cerebellar fissures. The cerebellar hemispheres are separated along the longitudinal axis by a narrow band called the *vermis*. The vermis plays an important role in controlling muscle activity of the axial body, shoulders and head. To either side of the vermis, are cerebellar hemispheres, whereby each hemisphere divides into an *intermediate* and *lateral zone*. The *intermediate zone* controls motion of distal portions of upper and lower limbs especially the hands and feet, whilst the *lateral zone* controls sequencing movements of muscles including timing and coordination of muscle activity. The vermis and intermediate zones contain a topographical representation of the body, similar to that observed in the sensory cortex, motor cortex, basal ganglia, red nucleus and the reticular formation. The topographical regions of the vermis and lateral zones receive afferent projections from all respective parts of the body, as well as from corresponding topographical motor areas from the cerebral cortex. The lateral zone of the cerebellar hemisphere is not topographically organized, rather, it receives input signals from the cerebral cortex that enable the cerebellum to assist the motor pathways to organise and plan movement.

2.3.2 Afferent and efferent pathways of the cerebellum

Several neural tracts from the cerebral cortex to the cerebellum regulate human movement. For example, the *corticopontocerebellar* pathway originates from motor and premotor areas of the cerebral cortex and somatosensory cortex and send their axons to mainly the lateral zone of the cerebellar hemisphere. In addition, neural tracts from the brainstem, such as the *olivocerebellar tract, vestibulocerebellar tract (vestibular apparatus),* and *reticulocerebellar tract,* terminate predominately in the vermis. The *dorsal spinocerebellar tract* transmits information mostly from muscle spindles but also from Golgi tendon organs, tactile, and joint receptors in the periphery to the cerebellum. Thus, it appraises the brain of the momentary status of muscle contraction, muscle tension and limb position and forces acting on the body surface. The other afferent pathway is the *ventral spinocerebellar tract* that is mainly excited by motor signals that arrive at the ventral horn of the spinal cord from the brain via the corticospinal tract and from the internal motor pattern generators of the spinal cord itself.

The main *efferent* pathways that exit the cerebellum include the *fastigioreticular* tract and the *cerebellothalamocortical* tract, along with the cerebellar nuclei. The *fastigioreticular* tract works in close association with the equilibrium apparatus and brainstem nuclei to control balance and works with the reticular formation of the brainstem to control postural stability. The *cerebellothalamocortical* tract is extremely complex and passes through many neuronal structures to finally terminate at the level of the motor cortex, whereby it coordinates the reciprocal contractions of agonist and antagonist muscles in the limbs; thus, it is involved in the turning ‘on’ and ‘off’ of muscle activity.

In addition to the efferent neural pathways located deep in the cerebellum, on each side are three deep cerebellar nuclei, the *dentate*, *interposed* and *fastigial nuclei*. The deep cerebellar nuclei all receive input signals from the cerebellar cortex and the deep sensory afferent tracts to the cerebellum. The primary source of motor output from the cerebellum is via the deep nuclear cells. Every time an input signal is sent to the cerebellum, the afferent signals go directly to the deep cerebellar nuclei and to the corresponding area of the cerebellar cortex overlying the deep nucleus. Once the input signal has been received by the deep nuclei, an inhibitory output signal from the deep nuclei is generated. Simplistically, all afferent signals to the cerebellum end in the deep nuclei as excitatory signals followed a few milliseconds later by inhibitory signals. These inhibitory signals from the deep nuclei exit the cerebellum via efferent pathways described above.

2.4 Motor functions of the spinal cord

The spinal cord is about 45 cm long and approximately 14 mm in width. It has a laminar structure (i.e., flows down from the brain without any abrupt changes). Transection of the spinal cord reveals a characteristic butterfly picture, consisting of gray matter (cell bodies of spinal neurons) and the remaining white matter (neural tracts that transmit information to and from the brain) constitutes the rest of the spinal cord (Figure 2.1).

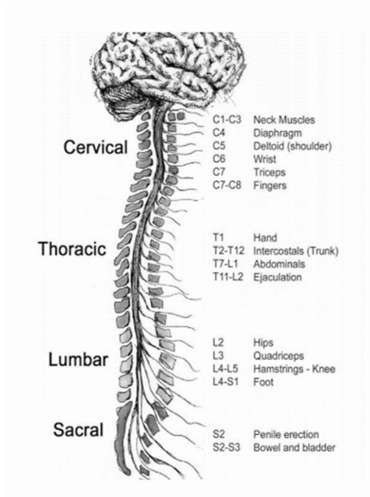

Figure 2.1. Gross anatomy of the human spinal cord.

The spinal cord is protected by the spinal vertebra and each vertebra has two pairs of horns. The dorsal horns (closer to the back) serve as an input pathway for sensory information from peripheral receptors. As you can see in Figure 2.2, the cell bodies of the receptors are located in spinal ganglia just outside of the spinal cord (i.e., the dorsal root ganglion). These cell bodies have T-shaped axons where their distal branches travel to sensory endings located in the periphery and their proximal branches enter the spinal cord via the dorsal horn. The axons of many different peripheral receptors (e.g., muscle spindles, golgi tendon organs) form a *dorsal root* and enter the spinal cord through the same dorsal horn. In contrast, the ventral horns are the major output pathway of neural signals to peripheral structures, in particular muscles (the axons of α-motor neurons) and the muscle spindles (the axons of gamma-motor neurons). The axons of these neurons form the *ventral roots*. Most of the neurons within the spinal cord are not motor neurons, rather they are *interneurons.* These neurons receive information from both afferent and efferent fibres and