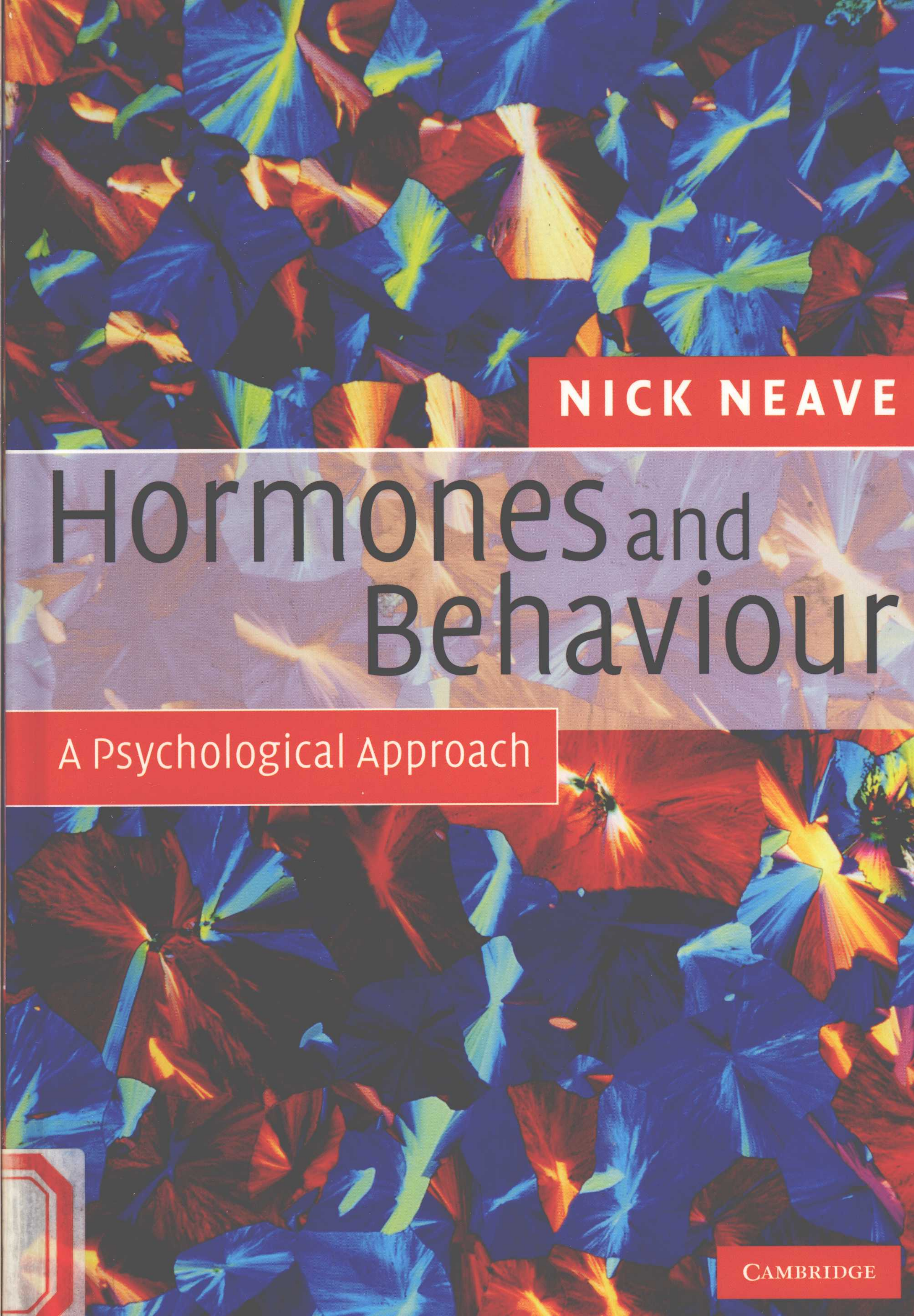

NICK NEAVE

Hormones and Behaviour

A Psychological Approach

CAMBRIDGE

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Hormones and Behaviour

Recent advances in non-invasive sampling techniques have led to an increase in the study of hormones and behaviour. Behaviour is complex but can be explained to a large degree by interactions between various psychological and physiological components, such as the interplay between hormonal and psychological systems. This new textbook from Nick Neave offers a detailed introduction to the fascinating science of behavioural endocrinology from a psychological perspective, examining the relationships between hormones and behaviour in both humans and animals. Neave explains the endocrine system and the ways in which hormones can influence brain structure and function, and presents a series of examples to demonstrate how hormones can influence specific behaviours, including sexual determination and differentiation, neurological differentiation, parental behaviours, aggressive behaviours and cognition. This is an accessible introductory textbook which will appeal to second and third year social science undergraduate students in psychology and biomedicine.

Nick Neave is a Reader in Psychology at Northumbria University.

Preface

In 1996 there was a timid knock at my office door. It was one of our final year undergraduates seeking a tutorial with me to discuss an idea for her dissertation, an empirical piece of research conducted independently by our students under the guidance of a supervisor. The student in question was Meyrav Menaged and (as per instructions) she had come along armed with several research papers that had given her some possible ideas for this important project. The papers were rather outdated, and concerned the possible differences in circulating hormone levels between heterosexuals and homosexuals. I read the papers with interest and not a little scepticism; her proposal sounded worthy of pursuit, but my main reservation was the lack of psychology (she was after all studying a psychology degree). I asked her to reconsider her plan and include something of psychological merit. She seemed fine with that suggestion and off she went. Several days later she returned with a pile of other papers, some addressing cognitive differences between heterosexuals and homosexuals, and others reporting links between circulating testosterone and certain kinds of spatial ability – a project was born. She would focus on cognitive differences taking into account sexual orientation and circulating hormone levels (testosterone).

The first bit was easy for me: I had taught a module on sex differences and was well acquainted with the literature, different theories, 'best' kinds of tasks to use, etc. The latter issue was more of a problem: how the hell were we going to measure testosterone? I had visions of us attempting to extract gallons of blood from some poor unsuspecting undergraduate with little idea of what to do with it afterwards. At that time our University, and my colleagues within our Division had neither the expertise nor the facilities to enable us to do this. I made a few inquiries and came across the name of David Weightman, an endocrinologist in the Medical School of our more prestigious and better-off rival (Newcastle University) across the road. With fingers firmly crossed behind my back I promised my Head of Division (and holder of the purse strings) that we would be sure to get a research paper out of this enterprise and, much as we hated to be seen to be providing funds for our rival, decided to go ahead. I made an appointment to see David and nervously gave him my spiel; while he knew little about psychology, or the supposed cognitive differences between heterosexuals and homosexuals, he knew a hell of a lot about endocrinology, and must have been impressed by our proposal, because he agreed to come on board and provide his expertise. The fact that we would be paying his group around £12 per sample of saliva, from which they assured us they could gain an accurate record of circulating (free) testosterone, was perhaps by the by.

We (or should I say Mey) went ahead and tested a smallish group of male and female homosexuals and heterosexuals on two spatial and two verbal tasks, and impressively managed to persuade them all to drool into a small plastic pot. Mey gathered the results, conducted the statistical analyses, and hey presto we had a story to tell. She got to complete her project, and I (with some assistance from Dave) set to work putting together and submitting my first paper in behavioural endocrinology. After a rather lengthy wait (I think it was the journal rather than the quality of the paper) it was revised, accepted and published, and I had found a new and exciting research avenue. Since those days my understanding of this field has multiplied enormously. I now have two excellent PhD students (Helen Brookes and Sarah Evans), both of whom are routinely extracting saliva from (almost) willing volunteers, and our technician Anthea Milne buys-in testosterone kits and assesses levels of this hormone in our purpose-built Biophysical Analysis Unit. The cost per sample has plummeted (which pleases the purse-strings holder enormously) and now our undergraduate and postgraduate students are able to conduct behavioural endocrinological research (typically on testosterone or cortisol) on an almost routine basis. We have even begun selling our expertise to other institutions. My principal research interests focus on the possible relationships between testosterone and various physical/psychological/behavioural characteristics, and over the last few years I have been able to share my burgeoning knowledge and deliver an option entitled 'Hormones and behaviour' to our final year undergraduates.

My key problem in delivering this option has been the lack of an appropriate textbook. There are two texts addressing behavioural endocrinology on the market – Nelson's *Introduction to Behavioral Endocrinology* and Becker *et al.*'s *Behavioral Endocrinology*. Both in their own way are excellent, but both from the point of view of social science students are not so good, focussing as they do on 'hard' endocrinology, and using examples principally drawn from non-human animals. Over the course of the last few years I have written a set of lecture notes that have addressed behavioural endocrinology from a more psychological point of view, addressing topics and drawing examples that are more pertinent to social scientists, hopefully without diluting the high level of science inherent in such an endeavour. This book, then, is those lecture notes, greatly expanded and offering hopefully a slightly different insight into behavioural endocrinology from what has previously been available.

The first four chapters lay out the science of behavioural endocrinology, chapter 1 providing a basic grounding in neurobiology, essential for any student who has not come from a biological/physiological background (as many social science students have not). Chapter 2 then provides essential coverage of the endocrine system and the key hormones that will be addressed further in this text. Chapter 3 explains what is meant by the term 'behavioural endocrinology' and provides some theoretical and conceptual background before describing the principal ways in which hormone–behaviour relationships can be established. Chapter 4 addresses the neurological effects of hormones. The following three chapters then consider the more psychological/behavioural effects of hormones, chapters 5 and 6 covering typical and atypical sexual determination and differentiation, chapter 7 focussing on neurological differentiation. Thus far the main emphasis in the chapters has been to consider predominantly unidirectional relationships, i.e. the effects of hormones on physiology/behaviour. The final three chapters then begin to bring in more bidirectional relationships and include assessments of the effects of behaviour on neuroendocrine systems. Chapter 8 discusses these more complex hormone/behaviour interactions by assessing reproductive/sexual behaviours, chapter 9 addresses attachment and parental behaviours, and chapter 10 looks at aggressive/competitive behaviours. Last but not least, the final chapter will perhaps be of most interest to psychologists as it considers the possible effects of hormones on cognitive processing. Because of the page limit, and my own particular research experience, this final chapter has had to be limited to the effects of the sex steroids. There is a glaring omission in that I have not been able to consider the glucocorticoids or the thyroid hormones, and should a second edition of this text be possible, then I shall correct this imbalance.

Acknowledgements

I would like first to express my thanks to those colleagues, PhD students and undergraduate/postgraduate students who have assisted me with various hormones–behaviour research projects over a decade. These are (in alphabetical order): Helen Brookes, Darren Cole, Angela Donaghy, Kirby Eccles, Saskia Ellis, Sarah Evans, Audrey Giles, Colin Hamilton, Sara Heary, Sara Herdman, Paul Hunter, Sarah Laing, Katharine Laughton, John Manning, Meyrav Menaged, Anthea Milne, Brooke Milton, Mary Soulsby, Frances Thorne, Delia Wakelin, Gemma Watson, David Weightman and Sandy Wolfson.

Particular thanks are due to Bernhard Fink from Göttingen, my long-term collaborator, who has ensured that my research interests remain varied and forever evolving.

Contents

Diagrams

1 Background to psychobiology

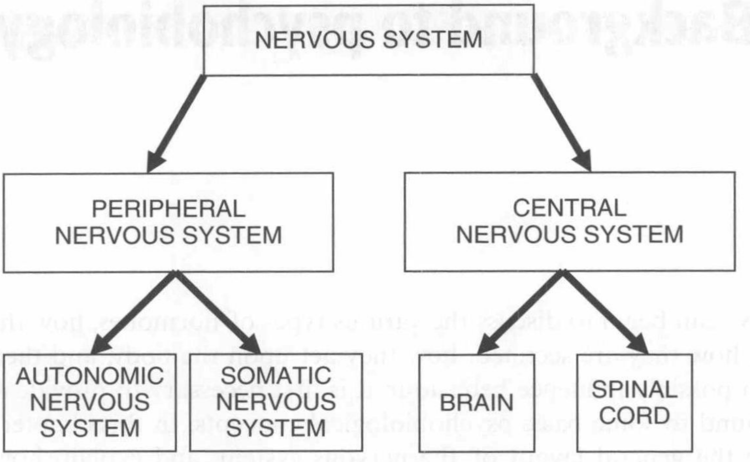
Before we can begin to discuss the various types of hormones, how they are formed, how they are secreted, how they act upon the body, and then how they can possibly influence behaviour, it is first necessary to provide a brief background to some basic psychobiological concepts. In this chapter I will describe the general layout of the nervous system, and explain how cells within the body (and especially within the central nervous system) communicate with one another.

Neuroanatomical directions

Neuroanatomists have devised a three-dimensional system of directional coordinates in order to navigate around the complex machinery of the brain. Instead of terms like 'front' and 'back' or 'top' and 'bottom', which are all relative, they instead employ the following terms that are always taken from the orientation of the spinal cord. There are three main axes: anterior–posterior, dorsal–ventral and medial–lateral. Thus, in most vertebrates that walk on four legs, the front (towards the nose) is called the 'anterior' while the back (towards the tail) is called the 'posterior', though when referring to the brain the terms 'rostral' (towards the front) and 'caudal' (towards the tail) are often used. Towards the surface of the back is referred to as 'dorsal' (think of a shark's dorsal fin) while the aspect towards the chest/stomach is referred to as 'ventral'. Towards the sides is 'lateral' while towards the middle is 'medial'. In addition, something lying above another part is called 'superior', while something lying below another part is called 'inferior'. 'Ipsilateral' refers to structures on the same side of the body or brain, while 'contralateral' refers to structures on the opposite side of the brain or body. This is slightly complicated in humans because we walk on two legs and so the position of our head and brain is altered relative to our spinal cord (Pinel, 2006).

Organisation of the nervous system

The nervous system is divided into two broad components: the central nervous system (CNS) and the peripheral nervous system (PNS). The CNS consists of the brain and the spinal cord, while the PNS consists of

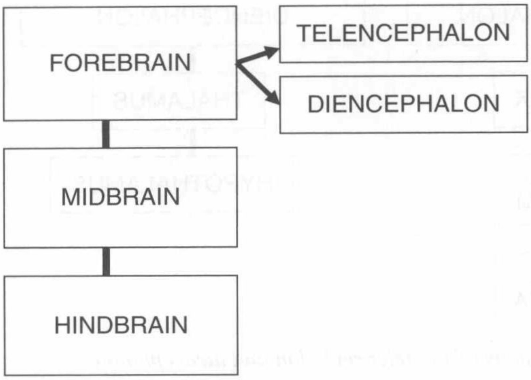


1.1 *Organisation of the nervous system*

the cranial nerves, the spinal nerves, and the peripheral ganglia (ganglion refers to a cluster of nerve cells). A basic way to differentiate these two separate but closely interlocking systems is to think of the CNS as being encased in bone (the skull and the spinal vertebrae), while the elements of the PNS are not. The PNS is further subdivided into the autonomic nervous system (ANS) and the somatic nervous system (SNS) – see diagram 1.1. The ANS acts as the regulator for the internal environment of the body, serving to relay sensory and motor information between the CNS and the internal organs. Thus, neurons (nerve cells) conduct sensory information from the internal organs to the CNS, and transmit motor commands from the CNS back to the internal organs. The SNS serves as the interface between the PNS and the outside world: its nerve cells conduct sensory information from the periphery (the skin, the joints and muscles, the senses, etc.) back into the CNS, while other neurons perform the opposite function by transmitting motor information from the CNS to the skeletal muscles.

Organisation of the brain

At first glance the human brain appears rather uniform in appearance, a globular lump of grey/white tissue overlaid with blood vessels and formed into a series of bumps and troughs. In fact the brain possesses clear divisions derived from the development of the early neural tube from which the brain forms during gestation (Cowan, 1979). Initially the tissue that will develop into the brain consists of a fluid-filled tube out of which three swellings become prominent; these swellings develop into the forebrain, the midbrain and the hindbrain. Later on in development the forebrain and hindbrain further divide into two parts, and thus the fully formed brain is



1.2 *Organisation of the brain*

recognised as having five major divisions: telencephalon[1] and diencephalon (which together constitute the forebrain), the midbrain (or mesencephalon) and the hindbrain, see diagram 1.2.

The forebrain

The telencephalon and diencephalon are subdivided further – see diagram 1.3.

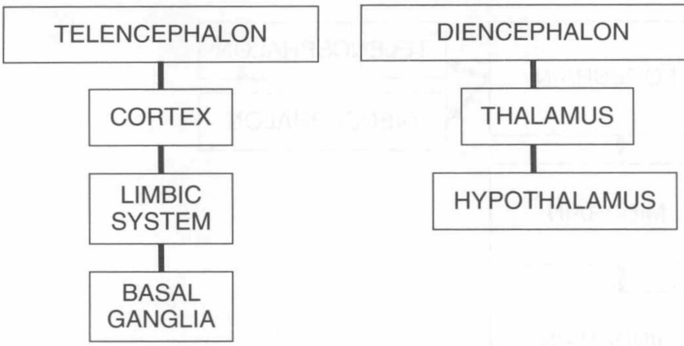
The telencephalon

The telencephalon comprises three key elements.

Cerebral cortex

The most notable features of the telencephalon are the two large and roughly symmetrical hemispheres which are in fact separate functional systems interconnected by major fibre pathways called the cerebral commissures. The principal commissure is the corpus callosum (which literally means 'hard body') and this wrist-thick bundle of fibres connects the corresponding regions of cortex, so that for example a specific area of temporal cortex in the left hemisphere is connected to the corresponding region in the right hemisphere. Both hemispheres are covered by a thin layer of tissue called cortex (in Latin this translates as 'bark of a tree'), which is not smooth but deeply convoluted, thus allowing for greatly increased material without an increase in overall brain volume. A deep cleft in the cortex is referred to as a fissure, and a shallow one is called a sulcus (the plural being sulci); each ridge is called a gyrus (plural being gyri). Some two thirds of the

[1] The suffix -encephalon is derived from the Greek and means 'in the head'.



1.3 *Subdivisions of the telencephalon and diencephalon*

surface of the cortex is hidden in these grooves, making the total surface area of an average brain around 2360 cm^2, with the thickness of the cortex being about 3 mm (Carlson, 2004). Because neurons predominate in the cortex, the cortex has a characteristic hue and is thus referred to as 'grey matter'. Beneath the surface of the cortex run millions of axons that connect the various regions together; as they are covered by a white-coloured protective tissue called myelin this gives rise to the name 'white matter'. The most prominent features of the cortex are the two lateral fissures (the deep grooves which run along each side of the brain), the central sulcus (which runs from the top centre of the brain to join up with the lateral fissures), and the longitudinal fissure (the major gap between the two hemispheres running from front to back). These conveniently clear anatomical divisions are used to help define the different lobes of the brain, and thus the hemispheres are divided into four lobes: frontal, temporal, parietal and occipital.

Functions of the different lobes

While the cortex acts as an integrated whole to coordinate behaviour, evidence from anatomical/histological examinations, animal experiments, human cases of localised brain damage, electrical recording and stimulation experiments, and neuroimaging studies, has shown that specific areas of the cortex are responsible for certain aspects of processing. Cytoarchitectonic (cellular architecture) maps have been developed of these subregions based upon differences in cell density, cell shape, size and connectivity. A commonly used map is that produced by the neuroanatomist Korbinian Brodmann in 1909. He used tissue stains to visualise different cell types in different brain regions and described fifty-two distinct regions that are now referred to as 'Brodmann's areas'. While these areas have experienced some modification and further subdivision, experimental and imaging techniques have broadly confirmed their existence and thus we possess specialised brain regions for touch, perception, movement, and even distinct cognitive processes

(Gazzaniga *et al.*, 1998; Kolb and Whishaw, 2001). A basic summary of the key functions of each lobe is provided below:

Frontal lobes

These extend from the central sulcus to cover the anterior portion of the brain. They contain primary motor cortex (area 4), premotor cortex (area 6), Broca's area (area 44) and the prefrontal cortex. Each area receives input from the thalamic nuclei, limbic system and hypothalamus, and connections from the other lobes, making it a 'control centre'. A key region of frontal cortex is referred to as 'prefrontal cortex', which forms around a third of the entire cortical mantle, and constitutes a larger proportion of the brain in humans than in other species. A major role of prefrontal cortex concerns working memory – the ability to retain pieces of information for short periods of time. Prefrontal cortex is also involved in higher-order cognitive behaviours such as planning, organisation, the monitoring of recent events, the probable outcome of actions and the emotional value of such actions.

Temporal lobes

The temporal lobe comprises all the tissue below the lateral (Sylvian) fissure running backwards to the parietal and occipital cortices. This region is also described by gyri that form it – the superior temporal gyrus, the middle temporal gyrus and the inferior temporal gyrus. The temporal lobe is richly connected to the other lobes, the sensory systems, the limbic system and the basal ganglia, which means that the temporal lobe does not subserve a single unitary function; it seems to have three key functions. First, areas 22, 41 and 42 are concerned with auditory and visual perception, specifically with focussing attention on relevant information and with the perception of speech (left hemisphere), music and faces (right hemisphere). Secondly, the classic case of patient 'H.M.' reported by Scoville and Milner (1957) showed that the hippocampus was critical for the formation of new memories. Finally, the amygdala adjoins the hippocampus and is concerned with emotional control (see later section on the limbic system).

Parietal lobes

These lie between the occipital lobe and the central sulcus. Just behind the central sulcus lies the postcentral gyrus (Brodmann's areas 1–3) which houses primary somatosensory cortex, the region of cortex housing the sensory representation of the body. The right hemisphere contains information about the left side of the body and vice versa. Parietal cortex thus integrates sensory and motor information and so spatial navigation and perception are thought to be key functions of this region of the brain. A common feature of damage to the right parietal lobe is 'sensory neglect' – the tendency to ignore the contralateral side of the body and features of the outside world.

Occipital lobe

Occipital cortex is primarily concerned with visual perception. It is located at the caudal end of the cortex and comprises primary visual cortex (area 17) and visual association (areas 18 and 19). Area 17 is also referred to as striate (striped) cortex or area V1, and is the main target for the thalamic nuclei that receive input from the visual pathways; this information is relayed to secondary visual cortex (area 18 or V2) and then on to additional areas (area 19, V3, V4 and V5). As in the other cortices, the left half of the visual field is relayed to the right hemisphere, though the map is considerably distorted as much of our visual processing concerns the analysis of information from the central visual field (fovea).

The Limbic system

An important group of forebrain structures were defined in the 1930s and their key role was assumed to reflect motivational and emotional processing (Papez, 1937). MacLean (1949) provided further modifications to what was then called 'Papez circuit', and we now refer to it as the limbic ('ring-shaped') system which includes the amygdala, hippocampus, cingulate cortex, fornix, mammillary bodies and septum. The amygdala (means 'almond-shaped') lie at the front end of each of the temporal lobes and are not single structures but in fact consist of around a dozen interconnected nuclei (Aggleton, 1993). Bilateral removal of the amygdala in monkeys leads to profound impairments in social and emotional behaviours, while bilateral amygdala damage in humans leads to similar deficits in emotional processing, with fear and anger being particularly affected (Broks *et al.*, 1998; Scott *et al.*, 1997). The hippocampus ('seahorse') is a bilateral structure located within the temporal lobes. Many studies involving both experimental animals, human cases of brain damage, and brain functioning in undamaged humans have clearly demonstrated that the hippocampus is crucial for what is called 'declarative memory', i.e. memory for explicit facts and episodes (Squire, 1992; Squire *et al.*, 1992).

Lying above the corpus callosum is a large region of cortex formed within the cingulate gyrus; it encircles part of the thalamus (and shares dense interconnections with the various thalamic nuclei) and is referred to as cingulate cortex. Evidence from experimental animal and human case studies demonstrates that damage to cingulate cortex leads to a profound disturbance in the experience and expression of emotion: generally the individual seems completely unresponsive to affective situations or stimuli (Damasio and Van Hoesen, 1983). The fornix ('arch') is a fibre pathway connecting the hippocampus to the mammillary ('breast-shaped') bodies which are part of the hypothalamus, and the septum.

The basal ganglia

The third element of the telencephalon is a collection of individual nuclei that together are involved in the control of voluntary movements. The principal structures of this system include the caudate ('tailed') nucleus and the putamen ('shell'), which are collectively referred to as the striatum ('striped structure'), and the globus pallidus ('pale globe').

The diencephalon

The diencephalon contains two key elements: the thalamus and the hypothalamus. The thalamus is not a single structure but is a two-lobed collection of separate but interconnected nuclei. Most of these nuclei receive input from the sensory systems, process it, and then transmit the information to the appropriate sensory processing areas in the neocortex. The thalamus thus seems to act as a kind of sensory relay centre and can thus influence almost the whole of the brain. Some of the thalamic nuclei may also play a key role in certain aspects of learning and memory. The hypothalamus lies underneath the thalamus at the base of the brain. It too is not a single structure but comprises twenty-two small nuclei, the fibre pathways that pass through it, and the pituitary gland attached to the hypothalamus via the pituitary stalk. This array of nuclei control the autonomic nervous system and the endocrine system. Almost all aspects of basic motivations and survival behaviours (such as fighting, escape, mating, feeding, etc.) are coordinated from here. I shall describe the form and functions of the hypothalamus and pituitary gland in more detail in the next chapter.

The midbrain

The mesencephalon consists of two major parts: the tectum ('roof') and the tegmentum ('covering'). The tectum contains two main structures, the superior colliculus and the inferior colliculus, which appear as four bumps ('colliculus' is Latin for 'mound') on the surface of the brain stem. The inferior colliculus forms part of the auditory system, and the superior colliculus forms part of the visual system, appearing to be important in visual reflexes and reactions to moving stimuli. The tegmentum lies beneath the tectum and it includes portions of the reticular formation, a set of more than ninety interconnected nuclei in the brain stem which play a role in sensory processing, attention, arousal, sleep, muscle tone, movement and reflexes. Two key structures of the tegmentum are the red nucleus and the substantia nigra ('black substance') which are important components of the motor system as they connect to parts of the basal ganglia.