



The motor system in neuroscience: a history and analysis of conceptual developments

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Abstract

Neuroscientific reflection on the integrative action of the nervous system was dominated by consideration of the motor system from the time of Aristotle in the 4th century B.C. to that of Sherrington, his contemporaries and proteges in the first-half of the 20th century. We describe the significant discoveries concerning the action of the spinal cord and cortex in motor phenomena during this period. This provides a vivid account of how great neuroscientists, over a period of more than 2000 years, have endeavoured to clarify notions concerning the integrative action of the nervous system in the context of the prevailing philosophical traditions of their times. We examine these traditions as well as the conceptual schemes offered by neuroscientists, especially in relation to the workings of the cortex. It is shown that neuroscientists cleave to this day to a tradition that goes back to Descartes, and that this is the case even for those who explicitly claim to reject such a tradition. The review concludes with what we take to be an appropriate basis for rejecting the Cartesian paradigm that we hope will assist neuroscientists in understanding the integrative action of the nervous system. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Aristotle's conception of the *psuche*

This essay is concerned with the history of our understanding of the integrative action of the nervous system. The essay begins with an account of Aristotle's conception of *psuche*, a notion quite foreign to contemporary neuroscientists but of great importance in the early history of their subject.

Aristotle is the first great biologist whose treatises and observational data survive. His philosophical world picture shaped European thought until, and in certain respects beyond, the scientific revolution of the 17th century. So although his knowledge of the nervous system was almost non-existent, his fundamental conceptions of animate life are indispensable to the understanding of the reasoning of the early scientists, such as Galen and Nemesius (see [Sections 2.1–2.3](#)), who probed the nature of the nervous system and its role in determining the cognitive, cogitative, affective and volitional powers of man. Moreover, as we shall see, his conception of the nature of man, of the relation between organs and function, between the body and the distinctive capacities that constitute what he called 'the *psuche*' was profound. The Aristotelian conception of the *psuche* and the Cartesian conception of the mind, which displaced it in the 17th century constitute in certain respects two fundamentally different ways of thinking about human nature, which have informed neuroscientific reflection on the integrated action of the nervous system throughout the ages.

Aristotle ascribed to each living organism a *psuche*. The *psuche* was conceived to be the form of a natural body that has life potentially.¹ It was also characterised as the first actuality of a natural body that has organs (DA 412^b5–6). Aristotle's technical terminology needs elucidation.

In its common meaning, 'psuche' signified 'breath' or 'life breath' (which one 'expires' at the moment of death or in a faint), as did the later Latin term *anima*, by which it was translated. It is linked with the idea of wind and of vital power. It was a pre-Aristotelian philosophical innovation to detach *psuche* from such associations. It was an Aristotelian innovation to link it firmly to all organisms as the principle of life that informs each living being. Although 'psuche' is

commonly translated as 'soul', it is important to realise that, as used by Aristotle, 'psuche' has none of the religious and ethical connotations of our term 'soul'. *Psuche* is 'the principle of animal life' (DA 402^a7–8), and indeed of vegetal life too. For plants, no less than animals, have a *psuche*. It would be equally misleading to translate 'psuche' as 'mind', since the mind and mental powers are not associated, as *psuche* is, with growth, nutrition or reproduction that characterise all forms of living things. Nor is *psuche* essentially linked with consciousness as is the Cartesian conception of the mind. The term 'psuche', which, in conformity with tradition, we shall in the sequel translate as 'soul', is a *biological concept*—not a religious or ethical one. It will be important to keep this in mind not only in regard to Aristotle, but also in respect of neuroscientific debates in the 17th and 18th century on the existence of a 'spinal soul' (see [Sections 4.1–4.3](#)).

Aristotle introduced the distinction between form and matter to provide the theoretic apparatus necessary for describing persistence through change. Natural substances, irrespective of whether they are space-occupying things of a given kind (such as a rock, a tree, a horse, an axe or a man) or whether they are partitioned quantities of stuff of a certain kind (of water, bronze, wine or cheese, which may occur as a drop, a nugget, a bottle or a slice) undergo change. The change may be 'accidental' or 'substantial' (essential). 'accidental change' is a change to the non-essential properties (accidents) of a given substance. It is the acquisition of a new attribute or loss of an existing attribute—as when a tree grows taller, an axe becomes blunter, a man becomes fatter, and as when a pool of water becomes warm, or a certain quantity of gold melts. Accidental change is compatible with the continued identity of the substance. Substantial change occurs when a substance changes its essential properties, as when wine turns to vinegar, or milk to cheese, and equally, when a living creature dies. Substantial change is incompatible with the continued existence of the substance in question—if the wine changes to vinegar, then there is no more wine, and if a horse dies, it ceases to exist and only its remains, a dead body, are left behind. Aristotle introduced the notion of *matter* as a technical term to pick out that which has a capacity for substantial change, and *form* to pick out that which makes a certain matter into the kind of substance it is. Accordingly there are both *accidental forms* (for

¹ Aristotle, *De Anima* 412^a20; subsequent references in the text to this treatise will be flagged 'DA'.

example the accidental forms of the different colours which a thing may acquire or lose, while remaining the very same thing), and *substantial forms* (e.g. of wine or vinegar, of a plant or of a man). When a substance undergoes accidental change, it retains its substantial form through change.

It is important to realise that although individual things of any given kind are said to be both form and matter, form and matter are not *parts* of a thing. Matter cannot exist without form—its form may change, accidentally or essentially, but it must have some form or other. Equally, form cannot exist without matter—for the form of X-ness to exist is just for there to be some substance that is X. It may well be argued that this conceptual apparatus is well suited to discuss stuffs and their transformation (e.g. milk to cheese), and perhaps also (with adjustment) to things and their constitutive stuffs (e.g. a sword and the steel from which it is made), as well as (with different adjustments) things and their constitutive parts (e.g. a house and the bricks of which it is made). It is questionable whether it is very well suited to be extended to the description of things and their capacities.² Be that as it may, Aristotle did so extend it in characterising the soul as the form of the living body, and in simultaneously conceiving of the soul as the first actuality of the living body.

The actualities (*entelechiai*) of a substance are those things which it is or is doing at a given time. Among its actualities are (rather confusingly) its powers (i.e. the active and passive potentialities which it actually possesses). Such powers may be possessed without being exercised at a given time—the sighted do not become blind when they sleep, and English speakers do not cease to know English when they are silent. The unexercised dispositional power (*hexis*) of an animal Aristotle refers to as a first actuality (e.g. being sighted, knowing English), by contrast with the exercise of a dispositional power (the actual activity of, for example, watching something or speaking English), which he refers to as a second actuality (*energeia*). When the soul is said to be the actuality of the body, it is so only as first actuality. For a living creature has a soul, i.e. possesses its distinctive defining powers, when it is asleep no less than when it is waking.

So, the phrase ‘to have a soul’ does not signify a relation, as does ‘to have a car’. Furthermore, the soul does not stand to the body as the brain does, for it is not a part of the body. How then should these things be conceived? Aristotle gives a pair of analogies. The matter of an axe is the wood and iron of which it is made. Its form is its capacity to chop. The axe’s first actuality is its power to chop wood, which it possesses in as much as its constituent matter has been appropriately fashioned into blade and handle. Its power to chop cannot exist independently of the matter (wood and iron) or the parts (handle and blade) of which it consists. (But, of course, an axe is an inanimate artefact, and inanimate things have no soul.) Similarly, Aristotle suggests, we can compare the relationship between an animal and its soul with the relation between an eye and the power of sight. If the eye were an

animal, as it were, then its soul would be sight (DA 412^b18); although, of course, the eye is not an animal, but a part of an animal—and accordingly, while it has a function, it has no soul.

The soul consists of the essential, defining functions of a living thing with organs.³ The essential functions of a living being can be exercised only because of its possession of organs, which confer upon it the potentiality of exercising the functions of life appropriate to the kind of living being it is. It is by the use of its organs that its second actualities are exhibited.

Aristotle distinguished a hierarchy of three kinds of souls in nature. The *nutritive soul* is the fundamental principle of biological life as such. ‘It is the most primitive and widely distributed power of soul, being indeed that one in virtue of which all are said to have life’ (DA 415^a23–6). It consists of the powers of growth, nutrition and reproduction. Plants possess only a nutritive soul. Their various organs (roots, leaves, stamen, etc.) enable them to exercise the essential functions of vegetal life. Animals have not only the nutritive powers, but also powers of perception, desire and locomotion. They are accordingly said to possess a *sensitive soul*. The possession of a sensitive soul presupposes possession of the powers of a nutritive soul, but not vice versa. Mankind, however, is unique in nature in possessing not only the powers of a nutritive and sensitive soul, but also the powers of a rational soul. These are thought (reasoning) and will (rational volition).

The *psyche*, therefore, is not an ‘inner agent’—the subject of experience and the originator of action, animating the body but independent of it. It is not a substance or part of a substance. It is, Aristotle insists, ‘not a body but something of a body’ (DA 414^a20–21). In general, the form of a thing is not a kind of entity. It is not made of anything, and for a form to exist just is for a thing thus *in-formed* to exist. So too, the *psyche*, which is the form of the living creature, is neither material, like the body or brain, nor immaterial, like a ghost. Body and soul ‘make up’ an animal, not as chassis and engine make up a car, but ‘just as the pupil and sight make up an eye, so in this case the soul and body make up an animal’ (DA 413^a1–2).⁴ To have a soul is not to possess something or to be related to something, it is to be, as it were, *en-souled* (*empsychos*).

Precisely because Aristotle did not conceive of the soul as a separate entity from the body, but rather as the powers of the living being, he did not make the mistake of attributing to the soul the exercise of the distinctive powers of the creature whose soul it is. Indeed, he noted that ‘to say that the soul is angry is as if one were to say that the soul weaves or builds. For it is surely better not to say that the

³ We disregard here Aristotle’s formulation ‘of a natural body that has life potentially’ (DA 412^a20).

⁴ It should be noted that Aristotle held that a sightless eye is no more an eye than a painted eye, just as a corpse is no more an animal than a statue.

² For a discussion of this point, see Ackrill (1979).

soul pities, learns or thinks, but that the man does these with his soul' (DA 408^b12–15).⁵ This observation marks a crucial divide between the Aristotelian conception and the later Cartesian one, in as much as Descartes ascribed all psychological functions to the mind (see Section 2.6). It also marks a crucial divide between Aristotelian thought and contemporary conceptions, in as much as current neuroscientists (and others) ascribe a multitude of psychological (especially cognitive and volitional) functions to the brain (see Section 8). To do so is in effect to ascribe to a part of an animal attributes which it makes sense to ascribe only to the animal as a whole.

Aristotle's conception was altogether different from that of his teacher Plato, who did indeed conceive of the soul as a separate entity from the body. Within the framework of Platonic, and much later, of Cartesian, dualism, the pressing, and indeed insoluble, problem is to give a coherent account of the relation between these two entities, and also to explain the essential unity of a human being. These questions cannot arise within the Aristotelian biological framework of thought. Indeed, he sapiently explains, 'we can dismiss as unnecessary the question whether the soul and the body are one: it is as though we were to ask whether the wax and its shape are one, or generally the matter of a thing and that of which it is the matter' (DA 412^b6–7). In short, to speak of the soul or *psyche* of a creature is to speak of that creature's essential powers. A thing of a given kind will retain its soul as long as it can continue to exercise its characteristic functions. To destroy its powers to engage in its essential activities is to destroy the thing itself.⁶

1.1. Aristotle's conception of the *sensus communis*

In his account of perception, Aristotle distinguished the five senses (sense faculties) and sense organs that correspond to (four of) them. Of course, the different sensory powers are all powers of a single unified being, the animal, with a single unified perceptual power. The senses are, Aristotle wrote, 'inseparable, yet separate in account', i.e. a different account is needed of the operations and mechanisms of each, but they are all constitutive elements of a unified perceptual power, and the sense organs are all parts of a connected apparatus that he thought to be centred on the heart. The animal actually perceives only when the impulses initiated by impact on a sense organ or any part of the body sensitive to touch are transmitted by the blood to the central sensorium in the heart. Aristotle in effect allocates to the

heart the unifying functions which we allocate to the brain.⁷

He characterised this locus of our perceptual capacities as a 'controlling sensory organ'⁸—wrongly so, for we do not perceive with the 'sensorium' (no matter whether it be the heart or the brain) in the sense in which we see with our eyes and hear with our ears, and it is not a sense organ in the sense in which the eyes and ears are.

Aristotle emphasised that although we have different sense faculties, and although some objects of sense (the so-called *proper sensibles*) are uniquely discovered by a given sense faculty (e.g. colour by sight, sound by hearing), others, the so-called *common sensibles*, are discerned by more than one sense (e.g. motion, shape, size, number, unity). The latter fact is one among a number of not wholly perspicuous reasons for postulating a 'primary faculty of perception' or 'primary capacity for sense', which he occasionally refers to as the 'common sense'⁹ (and which later writers right down to the 18th century refer to as the '*sensus communis*').

The *sensus communis* is required, it seems, to explain how we can perceive common sensibles by perceiving proper sensibles (we could not see shape if we could not also see colour), and perceive them as unified attributes. For although we perceive shape, for example, both by sight and by touch, sight and touch are severally ways of detecting one and the same attribute, viz. shape (for we do not perceive, as it were, two distinct attributes, visual shape and tactile shape). Moreover, although, when we perceive, say, a rose, we perceive different proper sensibles with our different sense organs and their corresponding faculties, we perceive them as unified qualities of a single object.¹⁰ This, according to Aristotle, is a further reason for assuming a 'single sense faculty' and a 'master organ'—the heart. (Arguably what we have here is a fore-shadowing of contemporary neuroscientists' preoccupation with the so-called binding problem, but without their Cartesian and Lockean confusion of supposing that the sensorium must produce an internal image or representa-

⁵ Note that when Aristotle says that we do these things *with* our soul, this is *not* like doing something with our hands or eyes, but rather like doing something with our talents and abilities.

⁶ We disregard here the complexities, and incoherences, that arise with regard to Aristotle's distinction between the active and passive intellect and the intimation that the active intellect may be capable of existing without a body (DA 429^a18–29, 430^a18–25). These passages were crucial for the later scholastic synthesis of Aristotelian philosophy of mind with Christian doctrine concerning the immortality of the soul.

⁷ For his reasoning, see *De Partibus Animalium* 647^a22–34. In this respect, he differed from the Hippocratic tradition. The Hippocratic lecture on epilepsy noted that 'it ought to be generally known that the source of our pleasure, merriment, laughter and amusement, as of our grief, pain, anxiety and tears, is none other than the brain. It is especially the organ which enables us to think, see and hear, and to distinguish the ugly and the beautiful, the bad and the good, pleasant and unpleasant. ... It is the brain too which is the seat of madness and delirium, of the fears and frights which assail us, often by night, but sometimes even by day; it is there where lies the cause of insomnia and sleepwalking ...' (Lloyd (Ed.), *The Sacred Disease*, Section 17; *Hippocratic Writings*. Penguin Books, Harmondsworth, 1978). The Hippocratic insight is wonderful, the physiological reasoning is, however, no less erroneous than Aristotle's reasoning in support of his different hypothesis.

⁸ Aristotle, *De Somno* 455^a21. This is the Barnes translation; an alternative translation is 'for there exists a single sense faculty, and the master organ is single.'

⁹ His term is *aisthesis koine*, which occurs only in *De Anima* 425^a27, *De Memoria* 450^a10, and *De Partibus Animalium* 686^a27.

¹⁰ Aristotle, *De Sensu* 449^a5–11.

tion.¹¹) Other reasons for which a *sensus communis* is held to be needed are as follows.

- (i) We do not see that we are seeing or hear that we are hearing. Nevertheless, Aristotle held, we do perceive that we are seeing or hearing—and that is one of the functions of the common sense.¹² (Some contemporary neuroscientists and neuropsychologists engaged in the investigation of ‘blind-sight’ assign to some part of the brain the function of a self-monitoring device to fulfil the same function.¹³) However, the reasoning is faulty, since we do not *perceive* that we see or hear; rather, when we see or hear, we can *say* that we do so—but not because we in any sense perceive that we do. This form of self-awareness needs elucidation, but arguably not by this route.
- (ii) By means of the sense of sight, we discriminate white from red, and by means of taste we distinguish sweet from sour. But, Aristotle curiously observes, we also discriminate white from sweet and red from sour—and that neither by sight nor by taste.¹⁴ So, he infers, there must be some master faculty of perception which is employed to fulfil this function (DA 426^b).
- (iii) Since sleep affects all the sense faculties (i.e. we do not see, hear, taste, smell or feel while asleep), waking and sleeping must be affections of one single unifying sense faculty and controlling sense organ.¹⁵

Finally, Aristotle also allocated to the *sensus communis* the functions of (a) apprehension of time, (b) image-formation by the imagination or *fantasia*, (c) memory (which, in his view, presupposes both (a) and (b)), and (d) dreaming.¹⁶ Functions (b)–(d) are all which presuppose antecedent perception, but do not require any current use of a perceptual organ. They are, as it were, processes involving ‘decaying sense’ (or, as we might put it, ‘brain-traces’ or ‘engrams’).

In these early reflections on the human faculties, on the conceptual structure necessary to describe them and their exercise, and arguments on the need for a *sensus communis*, we can see the beginnings of systematic scientific thought on the integrative action of the nervous system.

¹¹ See, for example, Crick (1995, p. 22), Damasio (1999) and Kandel and Wurtz (2000, p. 492). For criticism of the ‘binding problem’ thus conceived, see Bennett and Hacker (2001).

¹² Aristotle, De Somno 455^a15–20.

¹³ For example, Weiskrantz (1980, 1986).

¹⁴ The argument is curious in as much as it is unclear in what sense he thinks we *discriminate* white from sweet. To be sure, we possess the faculties to see white things and distinguish them from other coloured things, and to taste sweet things and distinguish them from things with other tastes, and we (language users) also possess the concepts of white (and other colours) and sweet (and other gustatory qualities). But we do not *discriminate* white things from sweet things and we do not need any further organ to differentiate white from sweet (for what would it be to confuse them?).

¹⁵ Aristotle, De Somno 455^a.

¹⁶ Aristotle, De Memoria 450^a9–14.

Two further points before we leave Aristotle are as follows.

1. Like Empedocles, Aristotle believed that there were four sublunary elements, earth, water, air and fire. To this list he added a further supra-lunary element, ‘the first element’ or ‘the first body’, subsequently called ‘the aether’, from which heavenly bodies are constituted. The sublunary elements naturally move rectilinearly (upwards or downwards). The motion of the first element or aether differs: it is (a) eternal, and (b) circular. There is some suggestion that Aristotle may have given some sublunary role to the first element in his biology. In *De Generatione Animalium*, he wrote: ‘now it is true that the faculty of all kinds of soul seems to have a connection with a matter different from and more divine than the so-called elements . . . All have in their semen that which causes it to be productive; I mean what is called vital heat. This is not fire nor any such force, but it is the breath (*pneuma*) included in the semen and the foam-like, and the natural principle in the breath, being analogous to the element of the stars’ (736^b29–737^a1). It is difficult to know what to make of this (let alone of how it is meant to be applied to the soul of plants). Cicero, writing some centuries later on the basis of lost works of Aristotle’s, claimed that ‘he thinks that there is a certain fifth nature, of which mind is made; for thinking, foreseeing, learning, teaching, making a discovery, holding so much in memory—all these and more, loving, hating, feeling pain and joy—such things as these, he believes, do not belong to any one of the four elements. He introduces a fifth kind, without a name, and thus calls the mind itself ‘*entelecheia*’, using a new name—as it were, a certain continual, eternal motion.’¹⁷ Aristotle appears, therefore, to have associated the capacities which constitute the soul with a ‘divine’ element that is incorruptible, which is a kind of vital heat or breath (*pneuma*) present in semen and responsible for generation. The heart converted *pneuma* to *vital pneuma* which was then conducted in blood vessels to muscles in order to affect their contraction.
2. It is worth noting, and relevant to the conception of the ‘spinal soul’ that preoccupied neuroscientists in the 18th century (see Section 4), that Aristotle observed that ‘certain insects go on living when divided into segments.’ This shows, he argued, that ‘each of the segments has a soul in it identical in species, though not numerically; for both of the segments for a time possess the power of sensation and local movement. That this does not last is not surprising, for they no longer possess the organs necessary for self-maintenance’ (DA 411^a17ff). The reasoning is that since the two halves of the insect continue to display sensitivity and capacity for motion, each half

¹⁷ Cicero, Tusculan Disputations 1.10.22, quoted by Furley (1999). Cicero’s ‘entelecheia’ is the same as the *entelecheia* mentioned earlier. Note that Cicero must surely be mistaken in ascribing to Aristotle the view that the soul is *made* of anything.

must have its own sensitive (and motor) soul. It is important (and relevant to the 18th century debate on the spinal soul) that Aristotle did *not* think that the whole insect consists of a single ‘mastersoul’, as it were, and apart from that, two additional souls in each half of its body. Rather, the whole insect has a certain range of capacities, and if it is cut in half, the two halves will then have a certain more limited range of capacities.

2. The ventricular doctrine: from Galen to Descartes

2.1. *Galen: motor and sensory centres*

Aristotle’s ideas had to be modified with the discovery by Galen (130–200) and his students in the 2nd and 3rd centuries A.D. that nerves arising from the brain and spinal cord are necessary for the initiation of muscle contraction. They changed the Aristotelian account so that the *vital pneuma* was delivered by blood vessels to the brain where it was converted to *psychic pneuma*, the composition of which was unclear, whence it was conducted along nerves to be transmitted to muscles. Thus, ‘the nerves which in consequence enjoy the role of conduits, carry to the muscles the forces that they draw from the brain as from a source’ (Galen, 1854a, ‘The Movement of Muscles I’, p. 323). This allowed the muscles to contract, probably as a consequence of their ballooning as they filled with the *psychic pneuma* (for a review of this period see Bennett, 1999).

Galen developed from this the notion of motor nerves derived from the spinal cord. Thus, ‘dissection has shown us that the motor nerves for all the voluntarily moved parts of the animal below the neck take their origin from the spinal cord. You have been told frequently this part is called spinal cord, but often simply dorsal cord. You have also seen that the nerves that move the thorax take their origin from the cervical cord, and, moreover, you have been told that transverse incisions that sever the cord completely deprive all parts of the body below this level of sensation and movement, since the cord receives the faculties of sensation and voluntary movement from the brain. You have also seen during dissection that transverse incisions of the cord that reach only its centre (hemisection) do not paralyse all the lower parts but only the parts situated directly below the incision; the right when the right is cut, and the left when the left is cut. It is, thus, clear that when the faculties of the brain are prevented from reaching the origin of the cord (upper cervical), all structures below, but excluding the face, will be deprived of movement and sensation.’ ‘If one cuts the spinal cord along the median line from above downwards, there is no resultant paralysis of the intercostal nerves nor of those of the right or the left side, even in the lumbar region or in the legs’ (Galen, 1854b, ‘The Sites of Diseases III’). He went on to say that: “similarly, when you have read the book ‘On the Causes of Respiration’, and the book ‘On the Voice’, you understand what degree of damage falls upon the respi-

ration, and upon the voice, at the transaction of each single vertebra . . . If now you know from their anatomy where the nerves of these muscles arise, then you also know for certain when any single one of these muscles will be paralysed” (Galen, 1962, ‘Anatomical Procedures’, pp. 22–26).

As a consequence of his observations on injured chariot drivers, Galen also distinguished sensory from motor nerves. These different kinds of nerves were distinguished in terms of their relative ‘hardness’: motor nerves being ‘hard’ and sensory nerves ‘soft’. Thus, he comments that: ‘the hard are to be considered best adapted for motion and the most unsuited for sensation; on the contrary, the soft have good constitution for accuracy of sensation, but weakness for strength of motion’ (Galen, 1854c, ‘Use of Parts IX’, pp. 597–598). The hard motor nerves were uniquely associated with their origins in the spinal cord whereas the soft sensory nerves were uniquely associated with the brain. ‘Some are hard and some soft, and the origin of all the hard is from the spinal marrow. The lower extremity of the latter is the source of the hard, but the brain is the source of all the soft nerves; the middle of its anterior parts is asserted to be for the very soft’ (Galen, 1821a, ‘Commentaries on Hippocrates’, p. 257). It is clear that Galen saw the spinal cord or marrow of the cord as giving rise only to motor nerves with the brain alone as the source of pure sensory nerves. However, mixed motor and sensory nerves could occur, and naturally their origin was to be found at some intermediate position between the caudal part of the spinal cord which gave rise to the hardest nerves and the brain. ‘Those that are absolutely soft are not motor at all, and those less soft than these may be considered as approaching the mean; these are motor also, but they fall far short of the function of the hard nerves. Consider, therefore, that the source of all the hard nerves is the spinal cord, and its lower extremity is the source of the extremely hard ones; the source of all the soft nerves is the brain, and the parts between its anterior lobes are the source of the softest; this is the source of the substance of the intermediate nerves (mixed, motor and sensory) where both brain and spinal cord join’ (Galen, 1854c, ‘Use of Parts IX’, pp. 597–598).

Using the term ‘soul’ in an Aristotelian sense, Galen considered that there was a ‘motor soul’ and a ‘sensory soul’, which were not to be considered as two different entities but as two different functions or principles of activity. And further: ‘thus the sensitive soul has five distinct functions; seeing, smelling, tasting, hearing, and touching. The motor soul has one closely related instrument and one kind of movement, as has been demonstrated in the book, ‘On Movement of Muscles’, but it has various special instruments so that it may seem to have various forms. The remaining function of the soul, which arises from the principal faculty, is divided into imagination, reason, and memory’ (Galen, 1821b, ‘The Differentiation of Symptoms’, pp. 55–56). According to this notion, together with the relationship between the relative hardness/softness of nerves, the motor/sensory differentiation and the fact that the most hard nerves are found uniquely associated with the spinal cord (caudal), the notion of two

separate souls or principles of activity, one associated with the spinal cord and one with the brain is natural (although it is unlikely that Galen succumbed to this temptation). It was to have considerable vogue in the 18th century in order to explain the existence of a continuing function of spinal cord reflexes in decorticate animals (see [Section 4](#)).

2.2. *Galen: the functional localisation of the rational soul in the anterior ventricles*

This association of the pure sensory nerves with the brain, and the fact that these nerves were very soft carried with it important implications for brain function. ‘this (brain), then, is very similar in substance to the nerves, of which it was destined to be the origin except insofar as it is softer than they. I emphasise this, for it befits that which receives all sensations into itself, and also imagines all phantasies, and conceives all concepts and ideas. It is the most easily modified in all such functions and the most suitable for experiences, as a softer substance is always more easily modified than a harder. It is for this reason that the brain is softer than the nerves. Because of their need to be dual in nature, as was also said previously, the brain itself was likewise created dual, softer in front, and the rest, which the anatomists call the cerebellum, harder.’ ‘Since it was necessary that the front be softer, since it was destined to be the source of the soft nerves extended for sensations, and harder behind as the source of the hard nerves distributed to the entire body, and since contact of the soft with the hard would not be safe, therefore nature separated one from the other by placing between them the dura mater (tentorium cerebelli)’ ([Galen, 1854d](#), ‘Use of Parts VIII’, pp. 541–543). It is clear that Galen associated the whole brain and not just the ventricles with the mental capacities of humans. In ‘On the Usefulness of the Parts of the Body’ he states that: ‘in those commentaries I have given the demonstrations proving that the rational soul is lodged in the encephalon; that this is the part with which we reason; that a very large quantity of psychic pneuma is contained in it; and that this pneuma acquires its own special quality from elaboration in the encephalon’ ([Galen, 1968](#)) (note that ‘encephalon’ is a cognate of ‘enkephalos’ meaning literally ‘that which is in the head’). But Galen did not ascribe to the cortex a special function in mental life, for he observed that a donkey, not noted for its intelligence, had a highly convoluted brain. Consequently, he thought the cerebral convolutions could not be associated with intelligence.

It will be noted, most importantly, that unlike Aristotle, Galen regarded the encephalon as the principal organ of perception not the heart, but this did not distinguish between the relative roles of the cortex and the ventricles (see [Bennett, 1999](#)). Because of his observations on donkeys, Galen did not associate the higher mental powers like reasoning with the cortex. Instead, he identified the ventricles as their source: ‘it is, therefore, natural that when the anterior portion of the brain alone is affected, the movement of the tongue remains intact while all other parts of the face lose

their sensory functions and voluntary motions in one part, wither on the right or on the left. If the entire anterior part of the brain is injured, its upper ventricle (lateral ventricles) is necessarily also affected by sympathy, and the intellectual functions damaged’ ([Galen, 1859](#), ‘The Sites of Diseases’, p. 590). This clearly implies that intellectual functions are to be associated with the first ventricle.

Galen enjoyed absolute authority for more than a millennium. It is, therefore, no surprise that the association of the ventricles with such a higher mental function was elaborated in detail in the following centuries.

2.3. *Nemesius: the formal attribution of all mental functions to the ventricles*

It was Nemesius (about 390 A.D.) the Bishop of Emesa (now Homs) in Syria, who developed the doctrine of the ventricular localisation of all mental functions, rather than just the intellectual ones. Unlike Galen, he allocated perception and imagination to the two lateral ventricles (the anterior ventricles), placing intellectual abilities with the middle ventricle, reserving the posterior ventricles for memory. Hence, the idea that imagination/perception, reasoning and memory are to be found in the lateral, third and fourth ventricles, respectively ([Fig. 1](#)).

Nemesius claimed this localisation was based not on a whim but on solid evidence, for he states that: ‘now if we make this assertion, that the senses have their sources and roots in the front ventricles of the brain, that those of the faculty of intellect are in the middle part of the brain, and that those of the faculty of memory are in the hinder part of the brain, we are bound to offer demonstration that this is how these things work, lest we should appear to credit such an assertion without rational grounds. The most convincing proof is that derived from studying the activities of the various parts of the brain. If the front ventricles have suffered any kind of lesion, the senses are impaired but the faculty of intellect continues as before. It is when the middle of the brain is affected that the mind is deranged, but then the senses are left in possession of their natural function. If it is the cerebellum that is damaged, only loss of memory follows, while sensation and thought take no harm. But if the middle of the brain and the cerebellum share in the damage, in addition to the front ventricles, sensation, thought, and memory all founder together, with the result that the living subject is in danger of death’ ([Nemesius, 1955](#), pp. 341–342).

In relation to the anterior ventricles he states that ([Nemesius, 1955](#), p. 321): ‘now, as organs, the faculty of imagination¹⁸ has, first, the front lobes of the brain and the psychic spirit contained in them, then the nerves impregnated with psychic spirit that proceed from them, and, finally, the whole construction of the sense organs. These organs of sense are five in number, but perception is one, and is an

¹⁸ Presumably by the word ‘imagination’ here Nemesius means sensibility.

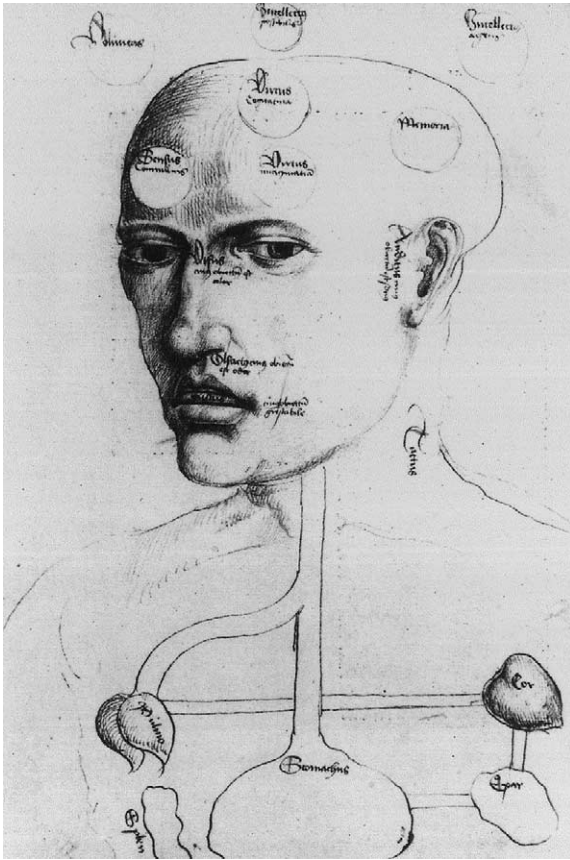


Fig. 1. From the 4th century A.D. until the 17th century the 'faculties of the mind' were taken as housed in the four ventricles of the brain. Shown is a 15th century illustration, with indistinct lettering, designed to illustrate the 1491 edition of Aristotle's *De Anima*. Four regions of the brain are labelled: *sensus communis*; *virtus cogitativa*; *virtus imaginativa* and *memoria* (Courtesy of the Incunabula Collection at the National Library of Medicine, Bethesda).

attribute of the soul. By means of the sense organs, and their power of feeling, the soul takes knowledge of what goes on in them.' Nemesius tried to explain why there are two anterior ventricles: 'for this reason he (the Creator) made there to be two ventricles in the front, only, of the brain, so that the sensory nerves running from each ventricle should constitute the sense organs in pairs.' In summary, 'now the faculties of the soul can be distinguished as imagination, intellect, and memory, respectively' (Nemesius, 1955, pp. 331–332). This localisation of the various mental functions in the ventricles became known as the ventricular doctrine.

It is worth noting that Nemesius conceived of the soul in very different terms from Aristotle and his followers. Nemesius was a Christian, more influenced by neo-Platonism than by Aristotelian philosophy (he was attracted by the doctrine of the pre-existence of the soul, and also by metempsychosis). He did not conceive of the soul as the form of the body, but as a separate, indestructible spiritual substance, linked with the body in a 'union without confusion' in which the identity of each substance is fully preserved. Conse-

quently, he did not attribute perception and cognition to the human being (i.e. to the whole animal) but rather to the soul. The attribution of psychological attributes to a subordinate part of a living creature deviates importantly from the Aristotelian conception. As we shall see, the tendency to explain how a living being perceives, thinks, feels emotions, etc. by reference to a subordinate part of that being's perceiving, thinking, feeling emotions, etc. runs like a canker through the history of neuroscience to this very day.

2.4. One thousand years of the ventricular doctrine

The ventricular doctrine for the localisation of psychological functions, established in the first centuries of the first millennium, was still accepted and being promulgated by scholars at the beginning of the second millennium. Thus, Avicenna (Abu 'Ali al-Hussain ibn' Abdullah ibn Sina), a great physician working in the years 980–1037 could write that: 'the *sensus communis* is located in the forepart of the front ventricle of the brain. It receives all the forms which are imprinted on the five senses and transmitted to it from them. Next is the faculty of representation located in the rear part of the front ventricle of the brain, which preserves what the *sensus communis* has received from the individual five senses even in the absence of the sensed object. Next is the faculty of 'sensitive imagination' in relation to the animal soul. This faculty is located in the middle ventricle of the brain. Then there is the estimative faculty located in the far end of the middle ventricle of the brain. Next there is the retentive and recollective faculty located in the rear ventricle of the brain' (Rahman, 1952, p. 31).

Ventricular localisation still held sway during the Quattrocento in Italy. Physicians like Antonio Guainerio (d1440) ascribed problems with memory in some patients as due to 'an excessive accumulation of phlegm in the posterior ventricle so that the 'organ of memory' was impaired' (Benton and Joynt, 1960). The doctrine was still being taught in the best teaching centres at the beginning of the 16th century, as is indicated by illustrations produced in the 1494 edition of Aristotle's *De Anima*. Leonardo da Vinci (1452–1519; Fig. 2A) went to great trouble to determine the first accurate description of the ventricles, given their presumed importance in the mental life of humans. In order to achieve this (circa 1506), he injected molten wax into the cavities in cattle. His drawings provide detail of a kind unmatched in accuracy, although they still ascribe the mental faculties to the different ventricles (Fig. 3A). In these drawings, Leonardo's only deviation from the doctrine laid down by Nemesius 1100 years earlier was to localise perception and sensation in the middle ventricle rather than the lateral ventricles, a change which Leonardo made on the ground that most sensory nerves converged on the midbrain rather than more anterior.

Andreas Vesalius (1514–1564; Fig. 2B) comments on the dominance of the ventricular doctrine when he was at the University of Louvain in 1503 (Fig. 1), thus, 'I have not



Fig. 2. The leading contributors to the understanding of brain function in the 15th–17th centuries. (A) Leonardo da Vinci (1472–1519). (B) Andreas Vesalius (1514–1564), a professor of anatomy at Padua, whose dissections and observations rekindled the study of anatomy during the Renaissance (Archives, Washington University Medical School, St. Louis, MO). (C) Rene Descartes (1596–1650) the philosophical theorist of the new science of the 17th century, who singled out the pineal gland as the locus of the interaction between mind and body. (D) Thomas Willis (1621–1675), author of *Cerebri anatome* (1664).

yet forgotten how when I was following the philosophical course in the Castle School, easily the leading and most distinguished school of the University of Louvain, in such commentaries on Aristotle's treatise, 'on the soul', as were read to us by our teacher, a theologian by profession and therefore, like the other instructors at the school, ready to introduce his own pious views into those of the philosophers, the brain was said to have three ventricles (this is not found in

Aristotle's treatise). The first of these was anterior, the second, middle, and the third, posterior, thus taking their names from their sites; they also had names according to function. Indeed, those men believed that the first or anterior, which was said to look towards the forehead, was called the ventricle of the *sensus communis* because the five senses, doors, colours, tastes, sounds, and tactile qualities are brought into this ventricle by the aid of the five nerves which subserve

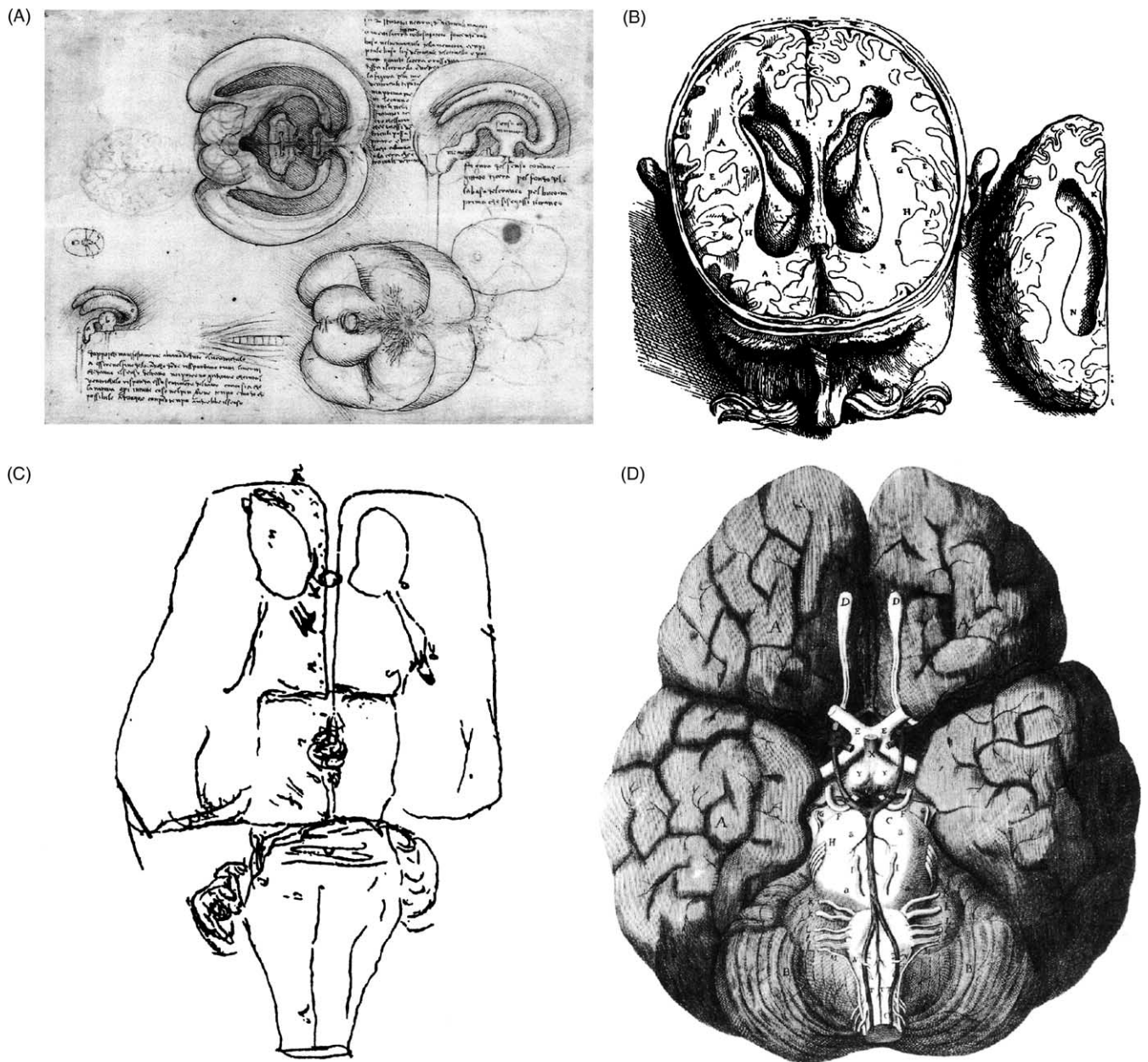


Fig. 3. Structure of the brain as determined in the 15th–17th centuries. (A) Leonardo da Vinci's determination of the correct structure of the ventricles. (B) A view of the brain from Vesalius *De humani corporis fabrica* (1543) showing the ventricles. (C) Descartes's incorrect drawing of the relationship between the pineal gland and the ventricles. (D) Thomas Willis's and the illustration of the base of the brain taken from his book *De cerebri anatome* (1664) and illustrated by Christopher Wren.

them. Therefore, the chief use of this ventricle was considered to be that of receiving the objects of the five senses, which we usually call the common senses, and transmitting them to the second ventricle, joined by a passage to the first so that the second might be able to imagine and reason, and cogitate about those objects, hence, cogitation or reasoning was assigned to the latter ventricle. The third ventricle (our fourth) was consecrated to memory, into which the second desired that all things sufficiently reasoned about those objects be sent and suitably deposited' (Vesalius, 1543, p. 623; Vesalius, 1542).

Vesalius gave detailed and accurate drawings of the human ventricles in 1543 and accompanied these in his *Fabrica* with descriptions of how psychic pneuma is generated in the ventricles and then distributed to the nerves in ways that are not much different to those suggested by Galen over 1300 years previously (Fig. 3B): 'I venture to ascribe no more to the ventricles than that they are cavities and spaces in which the inhaled air, added to the vital pneuma from the heart, is, by power of the peculiar substance of the brain, transformed into animal pneuma (previously referred to as 'psychic pneuma'). This is presently distributed through the

nerves to the organs of sensation and motion, so that these organs, with the help of this pneuma perform their functions' (Singer, 1952, p. 39). The brain prepares the very finely attenuated or animal psychic pneuma that it employs partly for the divine operations of the principal soul (in the brain) and partly for continuous distribution through the nerves, as through little fibres, to the instruments of sensation and movement. 'A considerable portion of psychic pneuma is distributed from this (fourth) ventricle into the dorsal marrow (spinal cord) and into the nerves arising from it. I believe that the pneuma is dispensed from the other (lateral and third) ventricles into the nerves taking origin near them, and so into the organs of sensation and movement. I have no desire to go into the question of whether that very refined pneuma is transmitted through passages in the nerves, like the vital pneuma through the arteries, whether it is transmitted along the sides of the nerve's body like light along a column, or whether the power of the brain extends to the parts merely by the continuity of the substance of the nerves' (Vesalius, 1543, p. 632).

Although Vesalius subscribed to the conception of ventricles as the origins of the psychic pneuma, following Galen, he was sceptical about the idea that psychological functions originate in the ventricles. His writings on this are important for they prepare the way for Thomas Willis who, a century later, was to provide the definite shift of attention away from the ventricles to the substance of the brain itself in the search for the physical basis of psychological functions. Vesalius noted that as the shape of the ventricles are much the same in a variety of mammals including humans, it is difficult to associate the psychological functions such as reasoning, that demarcate humans from the other mammals, to the ventricles. Thus, 'all our contemporaries, so far as I can understand them, deny to apes, dogs, horses, sheep, cattle, and other animals, the main powers of the 'rational soul'—not to speak of other (powers), and attribute to man alone the faculty of reasoning; and ascribe this faculty in equal degree to all men. And yet we clearly see in dissecting that men do not excel those animals by possessing any special cavity (in the brain). Not only is the number (of ventricles) the same, but also other things (in the brain) are similar, except only in size and in the complete consonance (of the parts) for virtue' (Singer, 1952, p. 40).

2.5. Fernel: the origins of 'neurophysiology'

The concepts of 'physiology' and of 'neurophysiology' originate at the time of Vesalius. Although some have credited Aristotle in his biological writings to have dealt with physiological subjects and have conceived of Galen's on the "Use of the Parts" as the earliest separate treatise dealing with human physiology, it is the 16th century physician and scholar Jean Fernel (1495–1558) who should be credited with the first formal treatment of physiology. *De naturali parte Medicinae* published by Fernel in Paris in 1542, contains the word 'physiology' for the first time. In it physio-

logy was first defined: 'physiology tells the causes of the actions of the body' (Fernel, 1542, *Physiol. li, praefatio*). Fernel distinguishes anatomy, which indicates only *where* processes take place, from physiology, which studies *what* the processes or functions of the various organs are. The book was renamed '*Physiology*' in the 1554 edition, and was soon regarded as the major treatise on the subject, a position it held for more than a century.

Fernel's empirical observations, as well as his general reflections, are accommodated within the framework of late medieval Aristotelian thought as modified by Christian thinkers (in particular Thomas Aquinas's great synthesis). Like Aristotle, Fernel holds that plants and animals have a soul (*anima*) or principle of life. Possession of a rational soul (i.e. a soul that includes the powers of the intellect and will) is distinctive of man. Unlike Aristotle, but like Aquinas, Fernel conceived of the rational soul of man as distinct from his nutritive and sensitive soul, as separable from the body, and as immortal.¹⁹ It is, to be sure, far from clear whether the Aristotelian conception of the *psyche* as the 'form' or 'first actuality' of the body, i.e. as an array of powers and capacities (second-order powers), can coherently be married with Christian doctrines concerning the immortality of the soul. But that had been precisely what Aquinas had endeavoured to do (and in the course of his endeavour, he had reified the intellect, treated form as separable from matter, and confused the incorporeality of powers (which are abstractions) with the alleged incorporeality of the soul, conceived as a *non-physical part* of a human being).²⁰ Other scholastic philosophers also contributed to the attempted synthesis of Christianity with Aristotelian philosophy. Fernel was heir to this (confused) tradition.

'Physiology', according to Fernel, is concerned with the processes that give rise to a healthy body and soul. He comments that 'in all animate beings, and most in man, the body has been created for the sake of the soul (*gratia animae*). It is for that soul not only a habitation (*diversorium*) but an adjusted instrument for use by its (the soul's) inherent powers (Fernel, 1542, v, c1). This was an Aristotelian doctrine. As we have noted, the relation of the soul to the body, according to Aristotle, is analogous to the relation of sight to the eye. The eye exists for the sake of sight (Aristotle's *De Anima* 412^b17–24), that is its point and purpose. So too, the body exists for the sake of the soul, i.e. for the sake of the powers and capacities of which the soul consists. Without these, and their actualisation in the behaviour of the living animal, there would be no point to the existence of the body

¹⁹ Aquinas, capitalizing on Aristotle's obscure remarks on the active intellect, argued that 'the intellectual principle which is called the mind or intellect has an operation through itself (per se) in which the body does not participate. Nothing however, can operate through itself (per se) unless it subsists through itself, for activity belongs to a being in act ... Consequently, the human soul, which is called the intellect or mind, is something incorporeal and subsisting.' *Summa Theologiae* I, 76, 1.

²⁰ For a discussion of Aquinas's philosophy of psychology, see Kenny (1993).

(Aristotle's *De Anima* 415^b15–21; *De Partibus animalium* 645^b19). To make the biological point more perspicuous to the modern reader, the explanation of the actions of the parts of an organism must be in terms of their contribution to the optimal functioning of the whole of which they are the parts.

Fernel conceived of perception as produced by the transmission of images from the sense organs to the common sensorium in the brain, where they are apprehended by the internal sense. Memory and imagination are two subordinate faculties of the sentient soul, and they enable the sentient animal to apprehend what is pleasant or unpleasant, beneficial or harmful. Appetite causes a movement towards a pleasing or beneficial object, or a movement away from a displeasing or harmful one. This is effected by the contraction of the brain forcing the animal spirits from the front ventricle into the fourth (rear) ventricle, and thence down the spinal chord and out along the nerves into the muscles.

All this was received doctrine. What is most important from the point of view of the present work is that Fernel observed that some of our acts occur without the action of the will or from intent or any other directive of the mind. These, he held, are exemplified by certain movements of the eyes and eyelids, of the head and hands during sleep, as well as the movements associated with breathing. According to Fernel, these muscular movements do not involve an act of will, and therefore can be regarded as reflexes. Fernel was emphatic that muscular movement can occur without the will initiating a voluntary act, i.e. there are motor acts in which thinking takes no part (Fernel, 1542, Vol. 9, p. 109a, Chapter 8 of the original edition). This insight marks the beginning of an investigation that was completed only with the work of Sherrington in the 20th century.

'Physiology' went through several editions and had an influence that extended for a century. However, it could not continue as the definitive text in physiology beyond the middle of the 17th century in as much as the Aristotelian concepts and conceptions on which it was based were no longer held to be viable. What, above all, made them obsolete was the rise of Keplerian physical astronomy and Galilean mechanistic physics. The spectacular success of the new physics led to the rapid demise of Aristotelian teleological science, i.e. to the replacement of teleological explanations of natural phenomena by mechanistic explanations. This was no less evident in the advances in the biological sciences than in those of the physical sciences. First, Harvey showed that the heart was a mechanical pump. Secondly, Descartes argued persuasively that the activities of the body, the subject matter of physiology, could be considered in purely mechanical terms.

2.6. Descartes: the beginning of the end of the ventricular doctrine

Descartes (1596–1650; Fig. 2C) marks a profound upheaval in European thought. Although aspects of his philosophy are still rooted in scholastic-Aristotelian thought, the

novelty of his philosophical reflections are the starting point of modern philosophy. Although much of his neuroscientific research proved wrong, it provided a crucial impetus and shift of direction for neuroscience. Descartes agreed with the Aristotelian scholastics that the intellect can operate independently of the body, that the soul or mind is incorporeal, that the soul or mind can exist independently of the body, and that it is immortal. However, he broke with them radically over the following four matters.

First, he held that the mind is the *whole* soul. The scholastics, by contrast, conceived of the mind (understood as the intellect) as merely a part of the soul (the immortal part that is separable from the body). The other parts of the soul, namely the nutritive and sensitive functions, are to be conceived, according to the scholastics, in Aristotelian fashion, as the form of the body. Descartes disagreed radically. Unlike Aristotle, he did not conceive of the soul as the principle of *life*, but as the principle of *thought* or *consciousness*. The functions of the Aristotelian nutritive soul (nutrition, growth, reproduction) and of the sensitive soul (perception physiologically conceived, and locomotion) are not essential functions of the Cartesian mind, but of the body. All the essential functions of animal life are to be conceived in purely mechanistic terms. This was to have profound effects for the further development of neurophysiology.

Secondly, Descartes redrew the boundaries of the mental. The essence of the Cartesian mind is not that of the scholastic-Aristotelian rational soul, i.e. intellect alone, but rather *thought* or *consciousness*. A person is essentially a *res cogitans*, a thinking thing—and Descartes extended the concepts of thought and thinking far beyond anything that Aristotle or the scholastics would have ascribed to the rational soul. The functions of the rational soul, according to the scholastics included the ratiocinative functions of the intellect and the deliberative—volitional functions of the will (rational desire), but excluded sensation and perception, imagination and animal appetite. By contrast, Descartes understood *thought* as including 'everything which we are aware of as happening within us, in so far as we have awareness of it.' Hence, *thinking* is to be identified here not merely with understanding, willing, imagining, but also with sensory awareness (Descartes, *Principles of Philosophy*, I-9). Thought, therefore, was, in a revolutionary step, defined in terms of consciousness, i.e. as that of which we are immediately aware within us. And consciousness was thereby assimilated to self-consciousness in as much as it was held to be impossible to think and have experiences (to feel pain, seem to perceive, feel passions, will, imagine, cogitate) without knowing or being aware that one does. The identification of the mental with consciousness remains with us to this day and casts a long shadow over neuroscientific reflection.

Thirdly, he held that the union of the mind with the body, though 'intimate', is a union of two distinct substances. Contrary to scholastic thought, according to which a human being is a unitary substance (an *ens per se*), Descartes intimated, that a human being is *not* an individual substance, but

a composite entity. The person (the *ego*), on the other hand, is an individual substance, and is identical with the mind. To be sure, *because* the human mind is united with the body, it has perceptions (psychologically understood). But perceptions are conceived of as modes of thought or consciousness, produced by the union of the mind with the body. Indeed, it is precisely by reference to the intimate union of mind and body that Descartes explained the non-mechanical perceptual qualities (i.e. colours, sounds, tastes, smells, warmth, etc.) as being produced in the mind in the form of ideas consequent upon psycho–physical interaction. Similarly, the mind, *because* it is united with the body, can bring about movements of the body through acts of will. Hence, neuroscience must investigate the forms of interaction between the mind and the brain that produce sensation, perception and imagination (which are ‘confused’ forms of thought), on the one hand, and voluntary movement on the other.

Fourthly, just as he conceived of the mind as having a single essential property, namely thought, so too he conceived of matter as having a single essential property, namely extension. He conceived of the principles of explanation in the physical and biological sciences alike as purely mechanical, save in the case of the neuropsychology of human beings, who are unique in nature in possessing a mind.

Descartes contributed substantially to advances in neurophysiology and visual theory (Descartes, *Discourses and Essays, Optics*, pp. 130–137). Although his theories proved to be largely wrong, they were essential steps on the path to a correct understanding. Moreover, his conviction that fundamental biological explanation at the neurophysiological level will be in terms of efficient causation has been triumphantly vindicated by the development of neurophysiology since the 17th century (Bennett, 1999).

Descartes replaced the conceptions of Aristotle and Galen, in which the psychic pneuma was generated in the ventricles, with the hypothesis that the ventricles are the site of generation of corpuscles or particles that directly participate in mechanical phenomena. These are the animal spirits that are conducted by nerves and transmitted to muscle cells and so effect action (for details on the development of this idea see Bennett, 1999). As to the origin of these corpuscles: ‘the parts of the blood which penetrate as far as the brain serve not only to nourish and sustain its substance, but also and primarily to produce in it a certain very fine wind (that is ‘composed of very small, fast-moving particles’), or rather a very lively and pure flame, which is called the *animal spirits*’ (Descartes, *Treatise on Man*, p. 129). This is an unfortunate name as it is not an apt descriptive term for components of a mechanical theory, for the word ‘spirit’ can be interpreted as a principle of life that animates the body or as the active principle of a substance extracted as a liquid. However, he is quite explicit that ‘animal spirits’ are material, namely, a certain very fine air or wind’ (Descartes, *Passions of the Soul*, I-7) and that what I am calling ‘spirits’ here are merely extremely small bodies which move very quickly, like the jets

of flame that come from a torch. They never stop in any place, and as some of them enter the brain’s cavities, others leave it through the pores in its substance. These pores conduct them into the nerves, and then to the muscles. In this way, the animal spirits move the body in all the various ways it can be moved (Descartes, *Passions of the Soul*, I-10). Descartes thus argued that the flow of these animal spirits from the ventricles (in the case of motor action) involved the opening of particular valves in the walls of the ventricles, with a consequent flow of spirits into the appropriate motor nerve and contraction of muscle. In the case of involuntary behaviour associated with, for example, a pinprick, this would lead to a tension on just those filaments which open the appropriate valves in the walls of the ventricles to release the animal spirits into the motor nerves that contract muscle for moving the limb away from the point of the indentation.

Descartes used the word ‘reflex’ only once in developing his conception of non-human animals as automata, although it is implied throughout his descriptions of animal behaviour and human non-volitional reactions. Although Descartes does not quote Fernel’s *Physiology* in his *Treatise on Man*, it is clear that his development of the doctrine of mindless motor acts in humans and animals has for its foundations the concept of the reflex first enunciated by Fernel (see Sherrington, 1951, p. 152). *Treatise on Man* argues that such motor acts require not only an excitatory process but also an inhibitory one, a speculation that was later to be experimentally confirmed by Sherrington and analysed at the cellular level by his student John C. Eccles. Descartes then argued that the excitatory and inhibitory processes, when acting together, allow animals and the bodies of human beings (when functioning independently of the intervention of the mind) to be described as automata.

These suggestions of Descartes’s about the mechanism of reflex or involuntary movement, involving as they do the animal spirits stored in the ventricles, raise the question of the mechanism of voluntary movement. Here, Descartes departed fundamentally from the ventricular doctrine. He denied that the ventricles are the seat of the sensitive and rational (including volitional) powers of human beings. He also denied that non-human animals have any sensitive powers *in the sense in which human beings do* in as much as they lack consciousness. And he held that the human mind or soul interacts with the body in the pineal gland, which he incorrectly placed inside the ventricle (Fig. 3C). In his words ‘we need to recognise also that although the soul is joined to the whole body, nevertheless there is a certain part of the body where it exercises its functions more particularly than in all the others. It is commonly held that this part is the brain, or perhaps the heart—the brain because the sense organs are related to it, and the heart because we feel the passions as if they were in it. But on carefully examining the matter I think I have clearly established that the part of the body in which the soul directly exercises its functions is not the heart at all, or the whole of the brain. It is rather the innermost

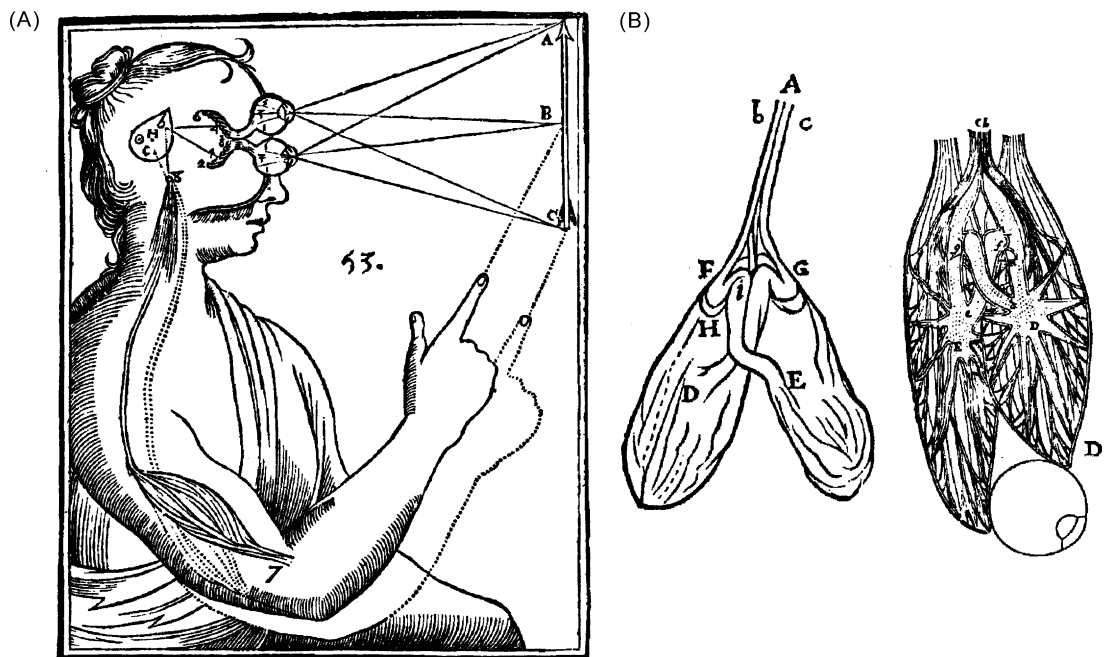


Fig. 4. Descartes's conception of the role of motor nerves in initiating muscle contraction. (A) A drawing from *De homine* (1662) by Descartes showing how light enters the eye and forms images on the retina. Hollow nerves from the retina project to the ventricles; the motion of the pineal gland (H) then releases the animal spirits into the motor nerves to produce motion. (B) Left shows Descartes's sketch of reciprocal muscles of the eye *De Homine*. Right is a redrawing showing closure of valves on relaxation, opening on contraction to allow animal spirits to flow in and swell the muscle (*L'Homme*, the French edition of 1677).

part of the brain, which is a certain very small gland situated in the middle of the brain's substance and suspended above the passage through which the spirits in the brain's anterior cavities communicate with those in the posterior cavities. The slightest movements on the part of this gland may alter very greatly the course of these spirits, and conversely any change, however, slight, taking place in the course of the spirits may do much to change the movements of the gland' (Descartes, *The Passions of the Soul*, I-31; Fig. 4A).

It is interesting to note the reasoning (or part of the reasoning) whereby Descartes concluded that the pineal gland is the locus of the *sensus communis* and of interaction between the body and the soul. It was because it is located *between* the two hemispheres of the brain and is not itself bifurcated. Consequently, he reasoned, it must be in the pineal gland that 'the two images coming from a single object through the two eyes, or the two impressions coming from a single object through the double organs of any other sense (e.g. hands or ears) can come together in a single image or impression before reaching the soul, so that they do not present it with two objects instead of one' (*Passions of the Soul*, CSM I, p. 340; AT XI, p. 353, our italics). These images or figures 'which are traced in the spirits on the surface of the gland' are 'the forms of images which the rational soul united to this machine (i.e. the body) will consider directly when it imagines some object or perceives it by the senses' (*Treatise on Man*, CSM I, p. 106; AT XI, p. 119).

It is worth noting that Descartes warned that although the image generated on the pineal gland does bear some resemblance to its cause (immediately, the retinal image, mediately, the object perceived) the resultant sensory perception is not caused by the resemblance. For, as he observed, that would require 'yet other eyes within our brain with which we could perceive it' (*Optics*, CSM I, p. 167; AT VI, p. 130). Rather, it is the movements composing the image on the pineal gland which, by acting directly on the soul, cause it to have the corresponding perception.

The warning was apt, but the caution insufficient. Descartes was, of course, wrong to identify the pineal gland as the locus of a *sensus communis*, and wrong to think that an image corresponding to the retinal image (and hence to what is seen) is reconstituted in the brain. These are factual errors, and it is worth noting that they still have analogues in current neuroscientific thought, in particular in the common characterisation of the so-called binding problem (Bennett and Hacker, 2001). Descartes was, of course, right to caution that whatever occurs in the brain that enables us to see whatever we see, our seeing cannot be explained by reference to *observation* of such brain events or configurations. For, as he rightly observed, that would require 'yet other eyes within our brain.' Nevertheless, he was confused, *conceptually* confused, to suggest (i) that images or impressions coming from double organs of sense must be united in the brain to form a single representation in order that the soul should not be presented with two objects instead

of one; (ii) that the soul ‘considers directly’ the forms or images in the brain when it perceives an object; and (iii) that it is the *soul*, rather than the living animal (human being) that perceives. The first error presupposes precisely what he had warned against, for only if the images or impressions are actually *perceived* by the soul would there be any reason to suppose that the ‘two images’ would result in double vision or double hearing. The second error is the incoherence of supposing that in the course of perceiving the soul or mind ‘considers’ anything whatsoever (no matter whether forms or images) *in the brain*. And the third is the error of supposing that it is the *soul* or *mind* rather than the living animal that perceives. We have already noted the much earlier occurrence of this confusion in Nemesius. The confusion is a form of a *mereological fallacy* (mereology being the logic of the relations between parts and wholes; see Bennett and Hacker, 2001). For it consists in ascribing to a part of a creature attributes which logically can be ascribed only to the creature as a whole. The particular form which this mereological fallacy took in Descartes consisted in ascribing to the soul attributes which can be ascribed only to the whole animal.

Descartes explained his theory as follows: ‘let us now take it that the soul has its principal seat in the small gland located in the middle of the brain. From there, it radiates through the rest of the body by means of the animal spirits, the nerves, and even the blood, which can take on the impressions of the spirits and carry them through the arteries to all the limbs. Let us recall what we said previously about the mechanism of the body. The nerve fibres are so distributed in all the parts of the body that when the objects of the senses produce various different movements in these parts, the fibres are occasioned to open the pores of the brain in various different ways (Fig. 4A). This, in turn, causes the animal spirits contained in these cavities to enter the muscles in various different ways (Fig. 4B). In this manner, the spirits can move the limbs in all the different ways they are capable of being moved. And all the other causes that can move the spirits in different ways are sufficient to direct them into different muscles. To this, we may now add that the small gland which is the principal seat of the soul is suspended within the cavities containing these spirits, so that it can be moved by them in as many different ways as there are perceptible differences in the objects. But it can also be moved in various different ways by the soul, whose nature is such that it receives as many different impressions—that is, it has as many different perceptions as there occur different movements in the gland. And conversely, the mechanism of our body is so constructed that simply by this gland’s being moved in any way by the soul or by any other cause, it drives the surrounding spirits towards the pores of the brain, which direct them through the nerves to the muscles; and in this way the gland makes the spirits move the limbs’ (Descartes, *The Passions of the Soul*, I-34).

By the middle of the 17th century, Descartes had replaced the ventricular doctrine localising psychological functions in the ventricles of the brain with his idiosyncratic interac-

tionist doctrine localising all psychological functions in the pineal gland, which he conceived to be the point of interaction between mind and brain. This is how he met the objection of Vesalius that it is difficult to reconcile the idea that the different ventricles are associated with different psychological attributes when the ventricles of humans are so similar to those of other mammals. Furthermore, he had replaced psychic *pneuma* by animal spirits as the medium through which the pineal gland produces its effects. This amounted to replacing the fluid derived from the *pneuma* described by Aristotle with mechanical corpuscles that possessed special properties. However, his contemporaries were soon to point out that the pineal gland was not inside the ventricles and furthermore, as other mammals possessed this gland, Descartes’s response to Vesalius was not adequate.

Nevertheless, Descartes had made the fundamental contribution of opening up all animal activity to mechanical analysis, i.e. to what became physiology and neuroscience. Furthermore, by associating the psychological capacities of humans with the pineal gland he had moved consideration of their physical dependence from the ventricles (filled now with particles of the animal spirits rather than with the psychic *pneuma* of Galen) to the matter of the brain, in his case the pineal gland. This shift of attention away from the ventricles to the substance of the brain was to reach its conclusion in the hands of a young man Thomas Willis who was 29 years when Descartes died.

3. The cortical doctrine: from Willis to du Petit

3.1. Thomas Willis: the origins of psychological functions in the cortex

As a consequence of his observations on patients with neurological problems, who subsequently died and so could be examined through post-mortem, the Professor of Medicine at Oxford, Thomas Willis (1621–1675; Fig. 2D) reached the conclusion that the psychological attributes of humans are functionally dependent on the cortex and not the ventricles (Fig. 3D). This he argued at length and with great force in his classical work, *De Anima Brutorum* (Willis, 1672) and in his ‘*Cerebri anatome, cui accessit Nervorum descriptio et usus*’ (Willis, 1664), the persuasive power of which was greatly assisted by the magnificent drawings made from Willis’s sketches by the young Christopher Wren. Willis gave the first cortical theory of the control of the musculature and of reflex control. This is of such importance in the history of the integrative action of the nervous system that it warrants a full description.

Willis consigned to man and to all other animals (which he called brutes) a system of particles found throughout their bodies which he called the Corporeal Soul. He comments: ‘I shall attempt to philosophise concerning the soul which is common to brutes and to man, and which seems to depend altogether on the body, to be born and die with it, to actuate

all its parts, to be extended through them and to be plainly of a material nature (i.e. the Corporeal Soul)' (Willis, 1683, p. 1). Willis emphasises the material nature of this 'soul' in his comments on its origin: 'this soul . . . arises together with the body out of matter rightly disposed . . . it cannot be perceived by our senses, but is only known by its effects and operations. If the body or this soul is hurt in such a way that the particles of the soul disappear from the concretion . . . the body being made soulless tends to corruption' (Willis, 1683, p. 6). He then specifies the role of this 'soul': 'as to the operations in general of the Corporeal Soul, we say that as soon as it exists it chiefly performs two functions: first, to frame the body as it were its domicile or little house, and then the body being wholly made, to render it apt and fitted to all the uses necessary both to the kind, and to the individual; for which uses it is furnished with many faculties or powers' (Willis, 1683, p. 7).

Having set up his scheme, Willis now defined in detail the role of the 'vital spirits' (or vital liquor) of the blood circulated in the heart and vessels and that of the 'animal spirits' (or animal liquor) of the brain and nerves, with the term 'spirits' being taken in the sense in which Descartes meant it, namely, as the distillation of a 'liquor'. First, the 'animal spirits' are derived from the 'vital spirits' for: 'the life and flame of the blood, the vital flame, is not visible and is not destructive like normal flames . . . so that it does not destroy the blood . . . but rather dissolves the blood in such a way that of the particles which arise, some are burnt while other are let go. Amongst these latter particles, the most subtle, which like beams of light sent from a flame, are distilled into the brain and cerebellum. These most subtle particles are called the 'animal spirits' (Willis, 1683, pp. 22–23). The Corporeal Soul inhabits both of these 'liquors', with that part in the 'vital liquor' 'being inkindled like flame, and the other being diffused through the 'animal liquor', seems as it were light, or the rays of light, flowing from the flame.' This is 'extracted and in manifold ways reflected and refracted by the brain and nerves, as it were by a mirror, and then diverted for the exercise of the animal's faculties' (Willis, 1683, pp. 22–23).

The role of the 'animal spirits' in integrating the activity of the cortex and the movement of muscle is then spelt out: 'we have shown that the 'animal spirits' are made in the cortex of the brain and cerebellum, from whence they descend and flow into the middle and marrowy parts where they are kept in sufficient amounts to be used for the various purposes of the 'soul'. 'animal spirits' flow from there to the oblong and spinal marrow, and thence into the nerves and nervous shoots, activating and expanding these. Finally, sufficient amounts of 'animal spirits' are distilled from the ends of the nerves implanted in the muscles, membranes and viscera, and so activate them, the organs of sense and motion' (Willis, 1683, p. 24).

The question next arises how this flow of the 'animal spirits' in and from the cortex of the brain to muscle is initiated. In order to answer this, Willis first describes how the

flow of 'animal spirits' occurs in the brain when an organ of perception is excited: 'first, the knowing faculty of the Corporeal Soul is fantasy or imagination, which is planted in the middle part of the brain, receives the sensible objects, first only impressed on the organs of sense, and thereby quick radiation of the 'animal spirits' delivered inwards, and so apprehends all the several corporeal things, according to their exterior appearances' (Willis, 1683, p. 38). Willis now links an animal perceiving something with a subsequent motor act: 'when a sensible impression is brought through the 'animal spirits', being affected by a continued series, from the organ to the common sensory, if it be light it is there terminated, and the perception of the external sense quickly vanishes, without any other affection. But if (which more often happens) the impulse of the object be stronger, the sense excited from thence, like the vehement waving of water in a whirlpool, both partly passes through the streaked bodies, and going forward to the callous body, it often raises up two other internal senses, to wit, the imagination and memory, either one or both of them; and also is partly reflected from them, and from thence, by a declining of the spirits, leaping into the nerves, local motions are made' (Willis, 1683, p. 59). This description places the cortex in a reflex arc from sensation to motor act, and it is clear that Willis thought that in all animals other than man, all motor acts are reflex, for he comments that: 'because brutes or men, whilst they as yet know not things, want spontaneous appetite. So long, therefore, they being destitute of the internal principle of motion, move themselves or members, only as they are excited from the impulse of the external object, and so sensation preceding motion, is in some manner the cause of it' (Willis, 1683, p. 59). The reflex nature of many motor acts is emphasised in his comments on the behaviour of some animals when they are cut in pieces: 'notwithstanding, frogs, eels and snakes, after their hearts are removed, live for some time, and leap about; this is due to the animal spirits being intermingled with the viscous matter, and not easily dissipated, retain for a while motion and sense, after their bodies are cut in pieces, and the several portions divided, and laid apart' (Willis, 1683, p. 17). This phenomenon in which animals continue to move after they have been cut into pieces, especially when the brain has been severed from the spinal cord, was to lead some neurophysiologists in later centuries to conceive of a 'spinal soul' (see Section 4).

But what of volitional acts that brutes do not perform but man does? Here, Willis turns to the idea of the Rational Soul, which is immortal: 'the prerogatives of the Rational Soul, and the difference from the other Corporeal, may be further noted, by comparing the acts of judgement and discourse or thought, which it puts forth more perfectly and often times demonstratively than this power in the brutes' (Willis, 1683, p. 39). Now in order to carry out a volitional act we must be aware of the object towards which the volitional act is directed: 'hence, it follows, that for the action of sensation, two things are required. First, that the sensible species be expressed, so as it may be impressed on the sensory; secondly,

that the idea of the same impression, be carried thence, by a like affection and motion, by the ‘animal spirits’ flowing in the intermediate passages, to the common sensory, for otherwise sensation is not performed, as it appears, when being intent on other things’ (Willis, 1683, p. 58).

Willis identifies the Rational Soul in the brain as doing the sensing, which he spells out in detail, partly recapitulating the description of the process of sensation already given: ‘therefore, in every sensation the ‘animal spirits’ are moved; and their motion being excited, in the utmost sensory, from the approach of the object, and harmonised according to its impression, turns inwards, and (as has been said) is conveyed to the first or common sensory; therefore, it is not to be thought, that the little bodies sent by the object, do penetrate deeply, and enter inward into the parts of the brain itself (as some have asserted); but it suffices that they be cast forth like darts from the sensible thing, and so effect the ‘spirits’ placed in the forefront; and then from thence most swiftly pass through, by their irradiation, the impressed motion. As to the parts, within which the ‘animal spirits’ dwell, they carry the impressed species of sensible things by, as it were, pipes and optical lenses, which are the fibres, nerves and the oblong marrow, and primarily the top of it, namely, the streaked bodies. The fibres being stretched forth in every sensory, like nets spread out, take the particles of the object, diffused and entering here and there, from which, while the ‘spirits’ implanted in those fibres, are affected, and are marked with the type of shadow of the object. Forthwith, the same character being expressed by a continuous series of ‘spirits’, passed forward, through the little pipes of the nerves, and the medullar trunk, into the streaked bodies, and is there represented as upon a white wall. But the Rational Soul, easily beholds the image of the thing there painted; or perhaps carried forward beyond into the callous body, the imagination and fantasy being excited’ (Willis, 1683, p. 59). The Rational Soul, Willis held, beholds this image in the corpus callosum: ‘but more particularly it is possible to conceive of a middle part of the brain, a kind of interior chamber of the soul equipped with dioptric lenses; in the innermost part of which images or representations of all sensible things, sent in through the passages of the nerves, like tubes or narrow openings, first pass through the corpora striata as through a lens; then they are revealed upon the corpus callosum as if on a white wall, and so induce perception and at the same time a certain imagination of the things sensed’ (Willis, 1672, pp. 43–44).

It is worth noting that Willis’s conception of the formation of an *internal representation* upon the corpus callosum is reminiscent of Descartes’s idea that an image of what is seen must be produced on the surface of the pineal gland, where it is ‘presented to the soul’; and Willis’s supposition that the Rational Soul ‘beholds the image of the thing there painted’ at least approximates the very error Descartes warned against (and then partly succumbed to), namely, of explaining how the human being can see an object by appealing to the soul’s seeing a representation of the object in the brain.

So, volitional acts are then initiated by the Rational Soul located in the corpus callosum after the ‘animal spirits’ had delivered ‘the images or representations of all sensible things’ from the common sensory: ‘nothing seems more probable than that these parts (corpora striata) are that common sensorium that receives and distinguishes all the appearances and impressions and transfers them in suitably ordered arrangement into the corpus callosum, represents them to the imagination presiding there, and transmits the force and instinct of those spontaneous movements begun in the brain into the nervous appendix for performance by the motor organs’ (Willis, 1672, pp. 43–44).

Willis then associated the functions of perception, memory and volition with the cerebral cortex. In particular, he associated these functions with the gyri of the cortex, so that animal spirits moved between the gyri. This explained why these gyri were so much more numerous in humans than in other animals, namely, because of the superior psychological attributes of human beings. As Willis explains: ‘but a no less important reason and necessity for the twistings in the brain arises from the distribution of the animal spirits. Since for the various acts of imagination and memory the animal spirits must be moved back and forth repeatedly within certain distinct limits and through the same tracts or pathways, therefore numerous folds and convolutions of the brain are required for these various arrangements of the animal spirits; that is, the appearances of perceptible things are stored in them, just as in various storerooms and warehouses, and at given times can be called forth from them. Hence, these folds or convolutions are far more numerous and larger in man than in any other animal because of the variety and number of acts of the higher faculties, but they are varied by a disordered almost haphazard arrangement so that the operations of the animal function might be free, changeable, and not limited to one.’ ‘The reason that in the more perfect animals the individual twistings are made of *two substances*, that is, *cortical and medullar*, seems to be that one part serves for the *production* of animal spirits, the other for their *distribution*. It seems most likely that the *animal spirits are created* wholly or in large part in the brain’s *cortical substance*, for this more immediately strains out and receives the subtle liquid from the blood; then imbuing it with a volatile salt, exalts it into pure and perfected spirits. Meanwhile the medullar substance of the brain seems throughout like that of the *medulla oblongata* and the *spinal marrow*, and it is well known that the medullar parts serve for the *operation and distribution* of the animal spirits but not at all for their *generation* . . .’ (Willis, 1664, pp. 65–68). Here, the ‘*medullar*’ substance is to be understood as the white matter and the ‘*cortical*’ substance as the grey matter.

Willis explicitly subscribes to the Cartesian idea of an immaterial soul or mind, that perceives and performs acts of will initiating motor action, and that interacts with the body. Like Descartes (and many others), Willis held that because the Rational Soul is immaterial, therefore it has

no parts. And because it has no parts, therefore it is indestructible. For all destruction is decomposition into parts. The important difference between Willis and Descartes is that Willis locates the point of contact and causal interaction between the mind or Rational Soul and the body in the cortex, namely, in the corpus callosum, and not like Descartes, in the pineal gland, incorrectly located in a ventricle. However, just as Descartes was left with the insoluble problem of explaining the interaction of the mind with the pineal gland, Willis was left with the problem of explaining the interaction between the immaterial Rational Soul and the material Corporeal Soul in the corpus callosum: ‘when, therefore, we have plainly detected in man, besides the Corporeal Soul, such as is common with the brutes, the prints of another superior, more spiritual one, we shall next seek out by what bond, and by what necessity, these twins are joined, and intimately together, in the frame of the body. Therefore, supposing that the Rational Soul, does come to the body that is first animated by another Corporeal Soul, we shall enquire, by what bond or knitting, since it is pure spirit, it can be united to it, for as much as it hath no parts, by which it might be gathered to, or cohere with this whole, or any of its parts’ (Willis, 1683, pp. 41–41). Willis attempts to avoid the necessity of identifying this ‘knitting’ with his comment: ‘but as the Rational Soul will stay and preside in the court of fantasy, there is no need that it should be shut out from thence, or bound by any bond; because destined to this by the most high Creator (Willis, 1683, p. 41). So, no explanation is provided as to how the bond is formed between the Rational Soul and the Corporeal Soul, which are placed in a state in which they can interact at birth by God: ‘that this immortal soul (the Rational Soul), for as much as it cannot be born, as soon as all things are rightly disposed for its reception, in the humane formation of the child in the womb, it is created immediately of God, and poured into it’ (Willis, 1683, p. 42).

The result of these researches and conjectures of Willis was to move attention completely away from the ventricles for the first time in over 1000 years and to centre both research and speculation on the cortex as the source of the psychological attributes of humans.

3.2. *The cortex 100 years after Willis*

The revolution due to Willis led in the next century to a focus on the relationship between the cortex and those nerve trunks that could be argued to have an especially intimate relationship with it. For 100 years after Willis there was no advance on the problem of functional localisation in the brain. At the end of the 18th century attempts were still being made to locate the sites of the sensus communis and mental processes in the brain. In 1784, Prochaska did not go much beyond Willis: ‘since, however, the Sensorium commune, by certain laws peculiar to itself and without the consciousness of the mind, reflects sensory impressions into motor, and

because we have declared the Sensorium commune to be comprised of the spinal marrow, medulla oblongata, and the whole origin of the nerves, it follows that, with the exception of the Sensorium commune, the cerebrum and cerebellum and their parts are the organs of the faculty of thought’ (Prochaska, 1784, pp. 141–143).

However, there was one remarkable contribution during this time by Domenico Mistichelli (1675–1715) and Francois Pourfour du Petit (1664–1741). They both described the decussation of the pyramids, that is the crossing over of nerves from left to right and right to left at the spino-medullary junction called the pyramid. In 1709, Mistichelli made this quite clear with his drawing of the decussation and his comments that (Fig. 5A): ‘what I have recently observed, that is, that the medulla oblongata externally is interwoven with fibres that have the closest resemblance to a woman’s plaited tresses. Hence, it occurs that many nerves that spread out on one side have their roots on the other; so for example, those that extend to the right arm, through such plaiting, can readily have their roots in the left fibres of the meninges. The same may be understood of those on the left proceeding from the right; and so one may go on describing many, if not all the other nerves, that have their origin immediately from the spinal cord’ (Mistichelli, 1709, pp. 282–283). However, du Petit went further than this in 1727, tracing the origins of the fibres that decussate back to the cortex: ‘all the cortical substance of the cerebral hemispheres supplies the medullar part which is itself but a mass of an infinite number of tubes, some of which constitute the corpus callosum while the others collect together to form the middle-fluted bodies. The inferior part of the cerebral peduncles (i.e. in his terminology, midbrain, pons, and medulla oblongata) which can be seen between the optic nerve (optic tract) and the pons, is a continuation of the middle fluted bodies. The medullar fibres of which it is composed pass through the pons separated from each other by the pontine fibres with which they are intertwined. They collect together again at the inferior part of the pons in order to form exclusively the pyramidal bodies.’

Thus, each pyramidal body divides at its inferior part into two large bundles of fibres. But more often there are three and sometimes four. Those on the right side pass to the left and those on the left pass to the right, binding themselves together (Pourfour du Petit, 1727; Fig. 5B). This remarkable work, in placing the origins of the pyramidal fibres in the cortex, was clearly elaborated further by du Petit’s identifying the fibres as motor in function. As a consequence of his observations as a military surgeon in identifying that contralateral motor paralysis followed a wound to the cerebral cortex, du Petit explained movement by the passage of animal spirits from the cortex, through the striatum and basal ganglia, and then across the pyramids to muscle. He gave the first explicit description of the motor cortex’s controlling movement through the pyramidal tract. This prescient work of du Petit has a remarkably modern ring about it.

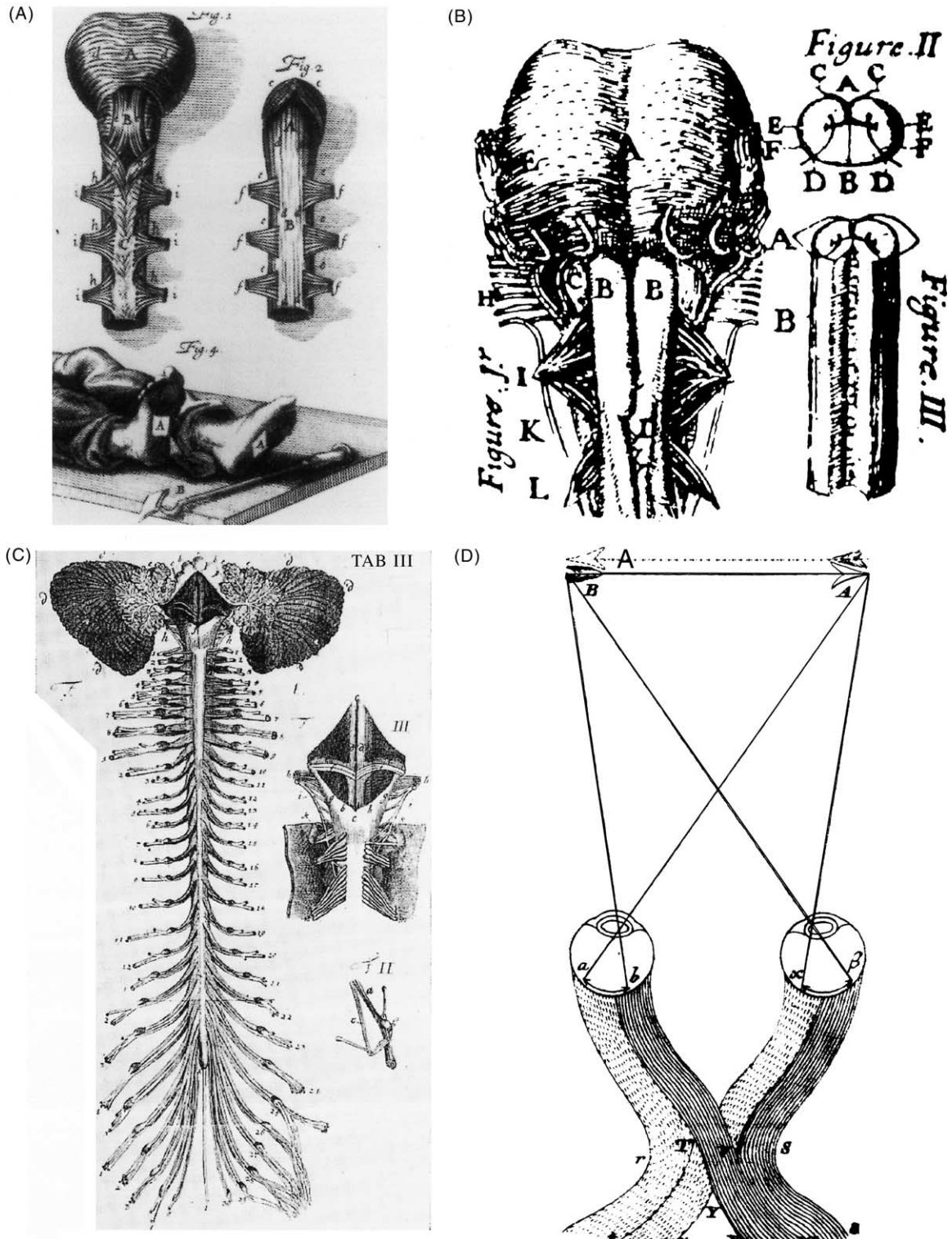


Fig. 5. Conceptions in the 18th century of the origins of motor and sensory nerves. (A) Domencio Mistichelli's figure of 1709 showing the decussation of the pyramids and the outward rotation of a paralyzed limb; (B) the crossing of the pyramids as described and experimentally demonstrated on injury to the brain in dogs by a pupil of Duverney. His drawings are from his *Lettres d'un médecin* (1727). From the copy in the Bibliothèque Nationale; (C) Prochaska's illustration of the spinal roots and their ganglia; (D) John Taylor's diagram of 1750 showing the partial crossing of the optic nerves at the chiasma.

4. The spinal soul, the spinal sensorium commune and the idea of a reflex

4.1. The spinal cord can operate independently of the encephalon

It had been noted since time immemorial that cutting off the head of a snake did not stop its movements in response to a touch for some days. However, a thorough study of the ability of the spinal cord to mediate the contraction of muscle and movement in the absence of the encephalon was not made until the investigations of Alexander Stuart (1637–1742). In his Croonian Lecture to the Royal Society of London in 1739, Stuart described experiments in which he first cut-off the head of a frog and then thrust a blunt instrument to bring pressure on the medulla, resulting in the movement of limbs and of the eyes thus (Fig. 6A): ‘this experiment is performed by suspending a live frog by the fore legs in a frame. When having cut-off the head from the first vertebrae of the neck with a pair of scissors, a small probe, the button at its extremity being first filed flat, is to be pushed very gently down upon the upper extremity of the medulla spinalis, in the first vertebrae of the neck; upon which the inferior limbs, which hung down loose, will be immediately contracted. The same probe pushed gently through the hole of the occiput of the scull on the medulla oblongata, will make the eyes move, and sometimes the mouth open’ (Stuart, 1739, p. 36). From these experiments, he concluded that compression had forced the animal spirits out of the spinal cord into the nerves to the muscles, thus: ‘this motion may be justly ascribed to a propulsion of a small

quantity of the contained fluid, through these slender canals into the muscles, in which they terminate. Hence, we may conclude that voluntary muscular motion in a living animal is begun in the same manner, by an impulse of the mind or will on the animal spirits through the nerves, into the muscles’ (Stuart, 1739; Fig. 6B). In this way, Stuart thought that he had provided experimental evidence for the flow of animal spirit from the spinal cord to the muscle as the agent which initiated contraction.

The problem of how animals can continue to function at some level in the absence of the encephalon was taken up next by Robert Whytt (1714–1766; Fig. 7A) in his works ‘Essays on the Vital and Involuntary Motions of Animals’ and ‘Observations on the Sensibility and Irritability of the Parts of Man and Other Animals’ written about 1751 in Edinburgh. He noted that: ‘if the motions of a tortoise after decollation, or the loss of its brain, cannot proceed from mere mechanism, but must be undoubtedly ascribed to the living principle which was the cause of its motions in a sound state; and, if the same is true of the actions performed by butterflies after the loss of their heads, it must follow, that the motions and other signs of life which are observed in the body and limbs of a frog for above 30 min after its head is cut-off, are to be attributed to the sentient principle, to which its motions and actions were owing when in an entire state; and if so, then the motions of this body, when divided into two parts, must also be referred to the same cause, since they are of a like kind, although of shorter duration. Shall we then deny that the motions of its separated heart and limbs, which are similar to these, and are increased and renewed by the application of the same causes,

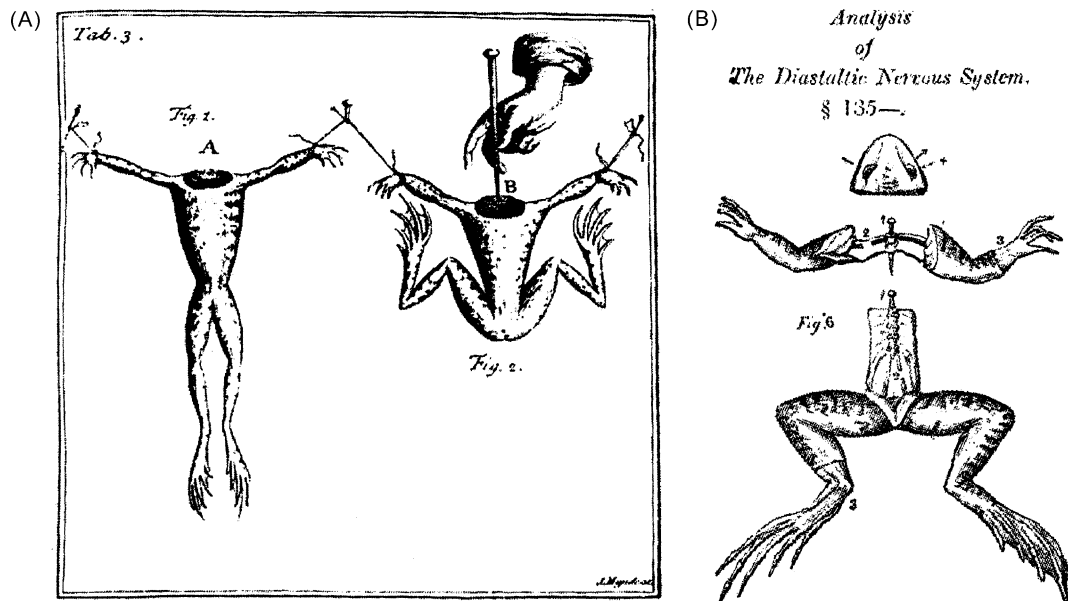


Fig. 6. Experiments in the 18th century showing that the isolated spinal cord mediates reflex actions. (A) Alexander Stuart's experiment confirming the observations of Stephen Hales that a decapitated frog convulses on being pithed and then becomes immobile (from Stuart, Croonian Lectures, p. 1738; Woodward, London, p. 1739). (B) One of his experiments to demonstrate the three parts of the reflex arc; the arc was broken by either of the following procedures: (a) skinning the extremity (at 3; the 'esodic' nerves); (b) sectioning of the Öbrachial or the lumbar or femoral nerve leading to the point.



Fig. 7. Pioneers in our understanding of the functions of the spinal cord in the 18th and 19th centuries. (A) Robert Whytt (1714–1766) (from the portrait in the Royal College of Physicians, Edinburgh, by courtesy of Mr. G.R. Pendrill). (B) Francois Magendie (1783–1855) (courtesy of the College de France). (C) Sir Charles Bell (1774–1842) (Archives, Washington University Medical School, St. Louis, MO). (D) Marshall Hall (1790–1857).

proceed from the sentient principle still acting in these parts' (Whytt, 1751, p. 115). Whytt then was not able to accept the mechanical principle that both Descartes and Willis had no trouble in considering, namely that of the reflex which does not require the intervention of a soul to initiate it. This is made clear in Whytt's comments that: 'the motions performed by us in consequence of irritation, are owing to the original constitution of our frame, whence the soul or *sentient principle*, immediately, and *without any previous ratiocination*, endeavours by all means, and in the most effectual manner, to avoid or get rid of every disagreeable sensation conveyed to it by whatever hurts or annoys the body' (Whytt, 1751, p. 113). He anticipated Sherrington on the stretch reflex: 'whatever stretches the fibres of any muscle so far as to extend them beyond their usual length, excites them into contraction about in the same manner as if they had been irritated by any sharp instrument, or acrid liquor.' However, Whytt was unable to grasp the essential mechanical nature of a reflex. He comments further that: 'not to perplex ourselves with metaphysical difficulties, we shall recite

"a few experiments and observations, from which we are led, by analogy, to conclude that the motions of the separated parts of animals are owing to the soul or sentient principle still continuing to act in them." A frog lives, and moves its members, for 30 min after its head is cut-off; nay, when the body of a frog is divided into two, both the anterior and posterior extremities preserve life and a power of motion for a considerable time.' If the soul were confined to the brain, as many have believed, whence is it that a pigeon not only lives for several hours after being deprived of its brain, but also flies from one place to another? 'The motions performed by these animals cannot surely be attributed to their material part alone; unless we shall deny them a soul altogether, and, with Descartes, refer all their actions to their corporeal machinery' (Whytt, 1751, p. 120).

The idea of a 'soul' or sentient principle operating in the nervous system that remains after loss of the encephalon was taken up by Jiri Prochaska (1749–1820). He resurrected the notion of the 'sensorium commune' which had been associated with the lateral ventricles in the ventricular doctrine,

but was now attributed by Prochaska to the brain and spinal cord (Fig. 5C): ‘what are the Sensorium commune, its functions, and its seat? “External impressions, which are made upon the sensorial nerves, are propagated rapidly through their whole length to their origin; where, when they have arrived, they are reflected according to a certain law, and pass into certain and corresponding motor nerves, through which, again rapidly propagated even to the muscles, they excite certain and determinate motions.” This place, in which, as in a centre, the nerves appropriated to sense as well as motion, meet and communicate, and in which the impressions of the sensorial nerves are reflected upon the motor nerves, is called the Sensorium commune—a term already received by most physiologists. The whole cerebrum and cerebellum certainly does not seem to belong to the composition of the sensorium commune: these parts of the nervous system appear to be rather the instruments which the mind uses immediately in the performance of the actions termed animal; but it seem not improbable that the sensorium commune, properly so called, extends to the medulla oblongata, the crura cerebri and cerebelli, even to part of the thalami optici, and to the whole spinal marrow, in a word, as widely as the origin of the nerves. That the sensorium commune extends to the spinal marrow, we learn from the motions remaining in decapitated animals, which could not take place without the consent and co-operation of the nerves arising from the spinal marrow’ (Procháska, 1784, p. 123). This work of Prochaska, in clearly associating some connection between sensory reception and motor action at the spinal cord level greatly helped in the development of the idea of a reflex. That this is so is made explicit in his insightful comment that: as, therefore, the principal function of the sensorium commune consists in the reflection of sensorial into motor impressions, it is to be observed, that “this reflection takes place whether the mind be conscious or unconscious of it” (Procháska, 1784, Part II, p. 127). ‘To these we must add all those motions which for some time remain in the body of a decapitated man, or other animal, and are excited by pinching the body, but especially the spinal marrow, which certainly occur without consciousness, and are governed by the residual part of the sensorium commune, which is in the spinal marrow. “all these actions arise from the organisation and physical laws proper to the sensorium commune, and are, therefore, spontaneous and automatic.” Those actions, which take place in the animal body with consciousness, are either such, that the mind has no power over its will, or such as the mind can coerce or impede at will: the former, as they are ruled by the sensorium commune alone, is as far as it does not depend upon the mind, are also automatic actions, not less than those which are performed unconsciously; such are sneezing from a stimulus applied to the nostrils, cough from a stimulus applied to the trachea, vomiting from irritation of the fauces, or from an emetic, tremor and convulsions in chorea S. Viti, and in the paroxysms of intermittent fever, etc. But the actions which the mind directs and moderates by its power, although the sensorium commune has

its part in producing them, we call, nevertheless, animal, not automatic’ (Procháska, 1784, Part II, p. 129).

We have seen that Aristotle proposed the existence of what he called *pneuma*, possibly analogous to an element derived from the stars, which was inhaled in breathing (see also Everson, 1995). This was drawn into the heart where it became *vital pneuma*, and distributed from there through blood vessels to initiate the activity of organs such as muscles. The problem of how the brain and spinal cord participate in the integrative action of the nervous system which accompanies behaviour arose with the discovery of nerves and their origins in the brain and spinal cord by Galen and his followers (Galen, 1821a,b, 1962, 1968). They retained the notion of *vital pneuma* generated in the heart, but were now required to modify Aristotle’s ideas by their discovery of spinal nerves and the importance of the integrity of these nerves in motor behaviour. Galen then suggested that when *vital pneuma* enters the brain it is converted there to *psychic pneuma*, from there it passes down both the cranial nerves and spinal cord and out of the spinal nerves to activate muscle. It is clear that Galen conceived of *psychic pneuma* as a fluid that either flowed along hollow tubes in the nerves or provided the substrate for the flow of a potency, somewhat akin to the modern concept of an action potential.

Descartes, we have seen, refined this notion by giving a specific description of the *vital pneuma* as composed of fine blood particles which, on reaching the brain were converted into much finer particles. As Descartes considered, he had described the specific composition of *psychic pneuma* he gave it the name *animal spirits*, although by spirits he did not mean to infer that these were anything other than very fine particles.

The discovery by Willis of reflexes gave rise to the problem of how animal spirits might participate in the integrative actions of the nervous system which accompany these reflexes. This difficulty was exacerbated by the realisation that reflexes could be performed by decorticate animals. For in this case, how could the production of animal spirits, dependant on the integrity of the brain, participate in reflex generation by spinal cords with their attached motor nerves in the absence of the brain? The solution of this problem was provided by Luigi Galvani (1737–1798). He showed that nerves could conduct electricity in a way similar to that which metallic wires conduct voltaic electricity and that the potential for generating this electricity in the nerves could be found in the nerves themselves (see Bennett, 1999). His key experiment in showing that nerves conduct electricity was one in which a frog’s exposed spinal cord—leg preparation was suspended in a sealed jar by means of a wire passed through the spinal cord and then through a seal at the top of the jar; lead shot was present in the bottom of the jar. A wire was then strung across the ceiling to pick up the charge from a frictional machine and convey it to the wire from which the spinal cord was strung by induction. This apparatus allowed for the unequivocal demonstration that when the machine sparked the legs twitched. From this, Galvani

concluded that the spinal cord and its attached nerves conduct electricity (Galvani, 1791). The discoveries of Galvani showed that there was no need for a store of animal spirits in the brain derived from psychic pneuma and used by the spinal cord and its attached nerves to control organs. Both spinal cord and nerves possessed the ability to generate the electricity needed to initiate reflexes independent of the brain.

4.2. *Bell and Magendie: identification of sensory and motor spinal nerves*

We have seen the confusion that was still present at the end of the 18th century concerning the idea of reflexes and the extent to which either the conception of the soul or the sensorium commune had to be evoked in relation to the function of the spinal cord in order to explain reflex action. This difficulty was to remain until a demarcation emerged between the sensory and motor functions of the posterior and anterior roots of the spinal cord at the beginning of the 19th century. This was due to Charles Bell (1774–1842; Fig. 7C), to whom the identification of the anterior roots as motor can be attributed and to Francois Magendie (1783–1855; Fig. 7B) who is responsible for the idea that not only are the anterior roots motor but the posterior roots are sensory. Much controversy attended the attribution of these discoveries, which will not be followed here.

Bell wrote to his brother in 1810 describing the following experiments.

Experiment 1: I opened the spine and pricked and injured the posterior filament of the nerves—no motion of the muscles followed. I then touched the anterior division—immediately the parts were convulsed.

Experiment 2: I now destroyed the posterior part of the spinal marrow by the point of a needle—no convulsive movement followed. I injured the anterior part and the animal was convulsed. It is almost superfluous to say that the part of the spinal marrow having sensibility comes from the cerebrum: the posterior and insensible part of the spinal marrow belongs to the cerebellum. Taking these facts as they stand, is it not most curious that there should, thus, be established a distinction in the parts of a nerve, and that a nerve should be sensible' (Bell, 1811). Bell confirmed his hypothesis that the anterior nerves were motor by a number of further ingenious experiments: in a paper, Bell describes the portio dura of the seventh nerve as a respiratory nerve of the face. By division of the nerve, the face is deprived of its consent with the lungs and all expression of emotion (Bell, 1821, p. 398). 'An ass being thrown, and its nostrils confined for a few seconds, so as to make it pant and forcibly dilate the nostrils at each inspiration, the portio dura was divided on one side of the head; the motion of the nostril of the same side instantly ceased. On division of the nerves, the animal gave no sign of pain: there was no struggle nor effect when it was cut across. The animal being untied, and corn and hay being given to him, he ate without the slight-

est impediment' (Bell, 1821, p. 80). On monkeys he wrote: 'on cutting the respiratory nerve on one side of the face of a monkey, the very peculiar activities of his features on that side ceased altogether. The timid motion of his eyelids and eyebrows were lost, and he could not wink on that side, like a paralytic drunkard, whenever he showed his teeth in rage' (Bell, 1821, p. 80). His brother-in-law (Shaw) comments were: 'before the operation, the creature was, of course, full of grinnings and grimaces at the liberties taken with him: the moment the Portio dura was severed, although his anger and jabberings did not cease, his face became passive and motionless like a mask.' These experiments established for Bell his claim to have discovered the motor function of the anterior roots.

It is of great interest that the arguments developed for the claim that the anterior roots are motor in function did not involve any reference to either the action of the soul or of a sensorium commune. The reason that dialogue on these issues came to be based on experimental observations without recourse to issues that were of such importance at the end of the 18th century is clear. Bell and Magendie's experiments did not involve disruption of the spinal cord or removal of the encephalon, so that questions as to how reflexes could be elicited without the brain did not arise. Rather their research centred on the effects of cutting nerves that lead from the brain and spinal cord to the peripheral parts of the body. Bell had satisfied himself by dissection that the anterior and posterior roots were continuous with particular columns of the spinal cord that were connected with the brain. Hence, there was no conflict between the idea that the soul resides only in (or interacts only with) the brain and the fact that severing the roots produced the effects observed.

In a remarkably incisive passage, Bell seems to have correctly understood the integrative power of the spinal cord in decapitated animals: 'the spinal marrow has much resemblance to the brain, in the composition of its cineritious and medullar matter. In short its structure declares it to be more than a nerve, that is, to possess properties independently of the brain. Another consideration presses upon us. Where many relations existing between the different parts of the frame, and necessary to their combined actions, established? There must be a relation between the four quarters of an animal. These combined motions and relations are not established in the brain, the phenomena exhibited on stimulating the nervous system of the decapitated animal sufficiently evince. They must, therefore, depend on an arrangement of fibres somewhere in the spinal marrow. Comparative anatomy countenances this idea, since the motions of the lower animals are concatenated independently of the brain and independently of the anterior ganglion. Such arguments induce me to believe that the brain does not operate directly on the frame of the body, but through the intervention of a system of nerves whose proper roots are in the spinal marrow' (Bell, 1834, 1835). In this passage, the requirement of a soul or a Sensorium commune in the spinal

cord is abandoned, even though animals without brains are being considered.

Bell does not seem to have made any reference to the posterior roots possessing a sensory function. This may be explicable by reference to the fact that most of his work was carried out on stunned rabbits. It was Bell's contemporary, Magendie who first made the distinction between motor and sensory nerves in relation to the anterior and posterior roots. The French Academy of Science in 1822 announced the following in its proceedings: 'Monsieur Magendie reports the discovery he has recently made, that if the posterior roots of the spinal nerves are cut, only the sensation of these nerves is abolished, and if the anterior roots are cut, only the movements they cause are lost' (Magendie, 1822). In a more complete description of the experiments, he comments that: 'I then had a complete view of the posterior roots of the lumbar and sacral pairs, and on lifting them up successively with the points of a small pair of scissors, I was able to cut them on one side, the spinal marrow remaining untouched. I was ignorant what might be the result of this attempt; I reunited the wound by a suture, and then observed the animal; I at first thought the member corresponding to the cut nerves, was entirely paralysed; it was insensible to the strongest prickings and pressures, it seemed to me also incapable of moving; but soon, to my great surprise, I saw it move in a manner very apparent, although sensibility was entirely extinct. A second and third experiment gave me exactly the same result; I began to think it probable that the posterior roots of the spinal nerves might have different functions from the anterior roots, and that they were more particularly destined for sensation' (Magendie, 1822, p. 88). In addition, I began to examine "the posterior roots" or the nerve of sensation. The following are the results of my observations: in pinching, pulling, pricking these roots, the animal gives signs of pain; "but it is not to be compared in intensity with that which occurs if the spinal marrow be only slightly touched at the part where these roots arise" (Magendie, 1822, p. 95). These experiments then established for Magendie the sensory nature of the posterior nerves.

Magendie also made important observations supporting the idea that the anterior roots were motor in function, independent of Bell, as illustrated in the following experiments: 'everyone knows that nux vomica determines both in man and animals, general and very violent tetanic convulsions. I was curious to ascertain if these convulsions would still take place in a member in which the nerves of motion had been cut, and if they would appear to be as strong as usual, a section of the nerves of sensation having been made. The result accorded entirely with the preceding; that is to say in an animal in which the posterior roots were cut, the tetanus was complete and as intense as if the spinal nerves had been untouched: on the contrary, in an animal in which I had cut the nerves of motion of one of the posterior members, the members remained supple and immovable at

the time when, under the influence of the poison, all the other muscles of the body suffered the most violent tetanic convulsions' (Magendie, 1822, p. 95). The experiments of Bell and Magendie provided the grounds for what became known as the Bell–Magendie hypothesis of spinal roots, which is best stated in Magendie's words as: "it is sufficient for me at present to be able to advance as positive, that the anterior and posterior roots of the nerves which arise from the spinal marrow, have different functions, that the posterior appear more particularly destined to sensibility, whilst the anterior seem more especially allied to motion" (Magendie, 1822, p. 91).

4.3. Marshall Hall: isolating sensation from sense in the spinal cord

Bell and Magendie had avoided becoming caught-up in the controversies as to whether the spinal cord contained a 'soul' capable of initiating motion independent of the cerebrum. This, as we have seen, was because the experiments they performed only involved cutting the spinal nerves. Nevertheless, the problem still remained as to how sensibility could be associated with the isolated spinal cord, where the word 'sensibility' was associated with the psychological attribute of feeling a sensation. This was largely solved by Marshall Hall (1790–1857; Fig. 7D) in the 1830s through his careful distinction between sensation and reflex action. He gave a full communication to the Royal Society in 1833 entitled, 'On the Reflex Function of the Medulla Oblongata and Medulla Spinalis' in which he stated 'a form of muscular motion subsists, in part, after the voluntary and respiratory motions have ceased by removal of the cerebrum and medulla oblongata, and which is attached to the medulla spinalis, ceasing itself when this is removed.' 'A lower animal after decerebration will remain motionless under a bell jar.' 'The absence of spontaneous motion proves the privation of volition. The excited motions of decapitated animals are dependent upon a principle different from sensation and volition.'

The animals experimented on were salamanders, frogs and turtles. In the first of these, the tail, entirely separated from the body, moved as in the living animal, on being excited by the point of a needle passed lightly over its surface. The motion ceased on destroying the spinal marrow within the caudal vertebrae. 'Three things', Hall observed, 'are plain from these observations. (1) The nerves of sensibility are impressible in portions of an animal separated from the rest; in the head, in the upper part of the trunk, in the lower part of the trunk. (2) The motions similar to voluntary motions follow these impression made upon the sentient nerves. (3) The presence of the spinal marrow is essential as the central and cementing link between the sentient and motor nerves' (Hall, 1832, p. 138). 'I conclude, then, that there is a property of the sentient and motor system of nerves which is independent of sensation and volition;—a property of the motor nerves independent of immoderate irritation;—a property

which attaches itself to any part of an animal, the corresponding portion of the brain and spinal marrow of which is entire.’

By 1837, Hall had given an account of the spinal cord as containing a reflex centre that operated in a non-sentient and non-volitional manner by contrast with the nerves of sensation which pass up to the brain and the motor nerves of volition that pass down from the brain. The results of this work are summarised by his statements (Hall, 1832, 1837a,b, 1843):

1. that reflexes do not involve sensation and therefore do not involve the brain;
2. that the ‘excito–motory property or power’ mediated by the ‘true spinal marrow’ is independent of the nerves which connect the spinal cord to the brain. So the ‘true spinal marrow’ is not to be thought as a group of nerve fibres;
3. the true spinal marrow does not possess sensation, volition or consciousness;
4. the true spinal marrow possesses its own excito or sensory nerves which are separate from the nerves of sensation and therefore not sentient;
5. the true spinal marrow possesses its own motor nerves that are not voluntary and therefore distinct from the nerves of volition;
6. generally, the spinal and cerebral nerves lie side by side in the same fasciculi;
7. experiments in which the nerve of one lower limb are stimulated generate movements of the upper limbs, as well as of the opposite lower limb, show that the excito–motor system is positioned next to the voluntary system of the cerebrum. However, the two systems are not independent as the excito–motor system can be modified during a volitional act. ‘The true spinal system is susceptible of modification by volition.’

These conclusions were revolutionary in as much as they clearly stated that sensory nerves exist that do not produce sensations and that motor nerves exist that do not merely mediate volitional acts. So reflex acts do not require a nervous arc from muscle to brain and then from brain to muscle, as Charles Bell had thought. Rather, the reflex arc required the following:

1. A nerve leading from the point or part irritated to and into the spinal cord marrow.
2. The spinal marrow itself.
3. A nerve or nerves passing out of or from the spinal marrow; all in essential relation or connection with each other (Hall, 1850).

Hall gave an example of how the true spinal marrow operated in his analysis of the stepping reflex: ‘in the actions of walking in man, I imagine the reflex function to play a very considerable part, although there are, doubtless, facts which demonstrate that the contact of the sole with the ground is not unattended by a certain influence upon the action of certain muscles.’

This work laid the foundations for and in some respects anticipated the contributions of Charles Sherrington later in the century. Following Hall, the notion of a spinal ‘soul’ and a spinal Sensorium commune was, in general, not accepted. This is made clear in the very influential textbook of Johannes Muller (1801–1858), *Elements of Physiology* (1835). In this, he states that ‘the spinal cord is a reflector’ ‘the phenomena of reflection are not dependent on the sensorium commune but on the motor apparatus of the central organ.’ In 1831, Johannes Muller confirmed the Bell–Magendie law experimentally. That Muller had grasped the full meaning of Marshall Hall’s work is evident from his description of the reflex as follows: ‘the view which I take of the matter is the following: irritation of sensitive fibres of a spinal nerve excites primarily a centripetal action of the nervous principle, conveying the impression to the spinal cord; if the centripetal action can then be continued to the sensorium commune, a true sensation is the result; if, on account of division of the spinal cord it cannot be communicated to the sensorium, it still exerts its whole influence upon the spinal cord; in both cases, a reflex action may be the result. In the first case, the centripetal action excites, at the same time, ‘sensation’; in the latter case, it does not, but is still adequate to the production of ‘reflex motion’, or centrifugal reflection’ (Muller, 1833, p. 153).

4.4. *Elaboration of the conception of the ‘true spinal marrow’*

Although Marshall Hall had, with his conception of ‘the true spinal marrow’, arrived at the correct view of the relationship between the brain and the spinal cord, there was still much resistance to the abandonment of the idea of the spinal ‘soul’. For instance, Eduard Pfluger (1829–1910) still argued in 1853 that the spinal cord was sentient and even possessed consciousness (see Pfluger, 1853). Likewise Friedrich Goltz (see Section 5.4) also subscribed to the view in 1869 that a spinal cord ‘soul’ exists so that a frog without a brain could still possess ‘soul faculties’. However, he was not consistent in this view, subscribing elsewhere in his 1869 work to the idea that the decerebrate frog possesses only simple reflex mechanisms, and does not possess any perception of sensations (Goltz, 1860). Claude Bernard, in his *Lecons sur la physiologie et la pathologie du systeme nerveux* of 1858 argued against Pfluger and in favour of Marshall Hall that spinal reflexes initiated by excitation of sensory nerves did not involve consciousness but simply that ‘the excitation carried by the sensory nerve reaches the cord, is then propagated by the cord to the anterior root and by the last to the muscles (Fig. 8B; see also Fig. 8D).’ Likewise (Vulpian, 1866; Bernard, 1858), in his *Lecons sur la physiologie du systeme nerveux* argued that the ‘soul’ was not involved in reflex spinal cord action, ridiculing this in his rhetorical remark ‘is it possible to admit the intervention of the ‘soul’ in decapitated salamanders and frogs?’

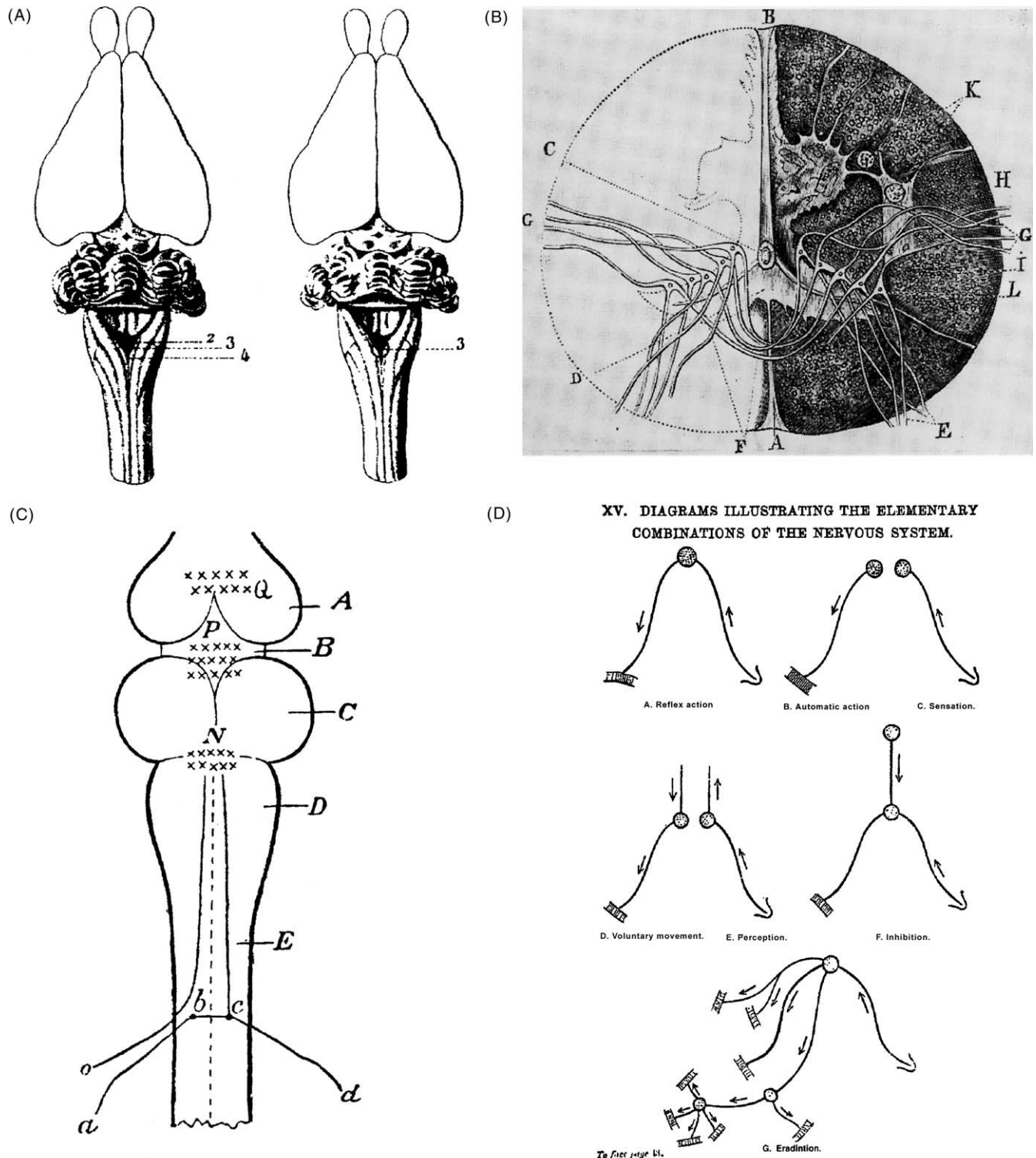


Fig. 8. Neural pathways of brain stem and spinal cord ascertained in the 19th century. (A) Location of the respiratory center in the medulla of young rabbits; drawing made by Alfred Vulpian for a memoir written of Marie-Jean-Pierre Flourens (1858) (see Olmstead, 1944). (B) Schema of the connections between the posterior and anterior roots of the spinal cord as taught to students in the days before the neuron doctrine and the theory of the synapse (from Bernard, C. *Leçons sur la Physiologie et la Pathologie du Système Nerveux*. J.B. Ballière, Paris, 1858). (C) Ivan Michailovich Sechenov's diagram illustrating reflex arcs in the spinal cord and brain of the frog. Letters a–d represents a spinal reflex arc with sensory (a–b), central (b–c) and motor (c–d) components. The reflex arc of the brain consists of the sensory nerve (o), the central component (N–c) and the motor efferent (c–d). P is the region in the brain stem where Schenov concluded the inhibitory apparatus. (D) Connections in the nervous system as taught to students in 1885 (from Pye-Smith, P.H. *Syllabus of a course of lectures on Physiology delivered at Guy's Hospital*. London: Churchill, 1885).

Ivan Sechenov (1829–1905) elaborated in detail in 1863 what he took to be the relationship between the ‘true spinal marrow’ and the brain as a consequence of his work on the reflexes of frogs (Fig. 8C): ‘in the decapitated animal the reflex apparatus for each point of the skin consists of the cutaneous nerve a entering the spinal cord and ending in cell b of the posterior horns; this cell is connected with another cell c, situated in the anterior half of the spinal cord and, together with cell b forms the so-called reflex centre; the motor fibre d issues from cell c and ends in the muscle. The reflex, being the product of the functioning of this apparatus, is none other than continuous excitation of a–d, always beginning with the stimulation of a in the skin. As to the reflexes of the brain, they are effected by a mechanism consisting of the following parts: cutaneous fibres terminating in the nervous centres N which produce the walking movements (as shown by Berezin, there is a difference between cutaneous fibres ending in the brain and in the spinal cord); path Nc along which the voluntary motor impulses proceed from the brain; and, finally, components c and d which enter the spinal mechanism. This apparatus is also brought into action by excitation of o, i.e. of the cutaneous nerve. Both reflexes are apparently, identical as to their origin so long as the excitation follows the above-mentioned path; they remain identical even when the inhibitory apparatus P comes into action, since this apparatus is effective for N as well as for bc and is located in the brain, in front of N’ (Sechenov, 1863, p. 15).

In 1879, Michael Foster (1836–1907) published the third edition of his great work *A Textbook of Physiology* in which he gave a succinct account of the relationship between spinal reflexes and the brain as follows: ‘the phenomena of reflex action have shown us that the cord contains a number of more or less complicated mechanisms capable of producing, as reflex results, co-ordinated movement altogether similar to those which are called forth by the will. Now it must be an economy to the body, that the will should make use of these mechanisms already present, by acting directly on their centres, rather than that it should have recourse to a special apparatus of its own of a similar kind. And from an anatomical point of view, it is clear that the white matter of the upper cervical cord does not contain a sufficient number of fibres, even of attenuated dimensions, to connect the brain, by afferent or efferent ties, with every sensory and motor nerve-ending of the trunk and limbs.’

Yet even in the last quarter of the 19th century the idea of a spinal cord soul still lingered and was considered by Foster in his textbook to be worthy of consideration, as in his comments that: ‘two entirely different questions are started; the one whether the spinal cord of the frog possesses intelligence, the other whether it possesses consciousness; and care must be taken to keep the two questions apart. Intelligence in the ordinary meaning of that word undoubtedly presupposes consciousness; but we are not at liberty to say that consciousness may not exist without intelligence.’

4.5. Implications of the conception of a reflex for the function of the cortex

Sechenov was a leading proponent of the idea that the brain was to be regarded as a site of reflex activity only. Since the distinctions of Marshall Hall had banished both the Sensorium commune and the ‘soul’ from the spinal cord, which was now conceived as working in a mechanical reflex mode only, the brain could be considered in the same way. He pointed out that the psychological attributes of humans, involving pleasure, fear, anger, etc. were all identified in terms of what humans say or do, and hence involve muscle contractions, whether of the larynx or of the limbs, that are part of a particular reflex. A reflex pathway was taken as constituting essentially afferent nerves bringing in sensory information, together with a central processing unit either in the spinal cord or the brain, leading to an efferent nerve that was responsible for the contraction of muscles. In willed movement, the afferent nerves were replaced by memory traces in the brain left by previous events that did involve afferent sensory inflow. In rational behaviour, an inhibition emanating from the brain itself exerted a control on the reflexes, letting them proceed or not. Sechenov summarises his considerations of the extension of the conception of the spinal reflex and its role in relation to the ‘true spinal marrow’ to the brain as follows (Sechenov, 1863).

‘The infinite diversity of external manifestations of cerebral activity can be reduced ultimately to a single phenomenon—muscular movement’ (Sechenov, 1863, p. 3). ‘Moreover, the reader will readily grasp that absolutely all the properties of the external manifestations of brain activity described as animation, passion, mockery, sorrow, joy, etc. are merely results of a greater or lesser contraction of definite groups of muscles, which, as everyone knows, is a purely mechanical act.’ (Sechenov, 1863, p. 3). ‘This idea of the mechanical nature of the brain, irrespective of these or other conditions, is a real find for the naturalist.’ ‘We have found that the spinal cord in the absence of the brain always, i.e. *inevitably*, produced movements when a sensory nerve is subjected to stimulation; this circumstance is regarded by us as the first sign of the mechanical nature of the functioning of the spinal cord in accomplishing movements. Further study of this question has shown, however, that the brain, too, may under definite conditions (but not always) act like a machine, its functioning being manifested in so-called involuntary movements’ (Sechenov, 1863, p. 8). ‘By means of absolutely involuntary learning of consecutive reflexes in all spheres of the senses the child acquires a multitude of more or less complete ideas of objects, i.e. elementary concrete knowledge. The latter occupies in the integral reflex exactly the same place as the sensation of fright in the involuntary movement; hence it corresponds to the activity of the central element of the reflex apparatus’ (Sechenov, 1863, p. 53). ‘We see, therefore, that my opponent is really under the delusion of his self-consciousness: his entire act is nothing but a psychical reflex, a series of

associated thoughts evoked by the first impulse to conversation and expressed in a movement which logically follows from the most powerful thought' (Sechenov, 1863, p. 105).

Fifty years later, the work of Ivan Pavlov (1849–1936) on the 'reflex' stimulation of the salivary glands, or the conditioned reflex, was interpreted as confirming Sechenov's 'for the salivary glands the rule is that all variations of their activity observed in physiological experiments are exactly duplicated in experiments with psychic stimulation, that is, those in which a certain object does not come into direct contact with the oral mucous membrane, but attracts the attention of the animal from some distance. For example, the sight of dry bread produces stronger salivary secretion than that of meat, although the latter, judged by the movements of the animal, stimulates a much more active interest. When the animal is teased with meat or any other edible substance, the salivary glands produce a very concentrated mucous; however, the sight of substances that the animal rejects causes a secretion of very liquid mucous from the same glands. In brief, the experiments with psychic stimulation represent an exact, however diminutive, copy of the experiments with physiological stimulation of the glands by means of the same substances' (Pavlov, 1907, 1928, p. 13).

5. The localisation of function in the cortex

5.1. Broca: the cortical area for language

Although the first experiments indicating a specialised area of the cortex for motor control were reported by Fritsch and Hitzig in 1870 (see Section 5.2) it could be claimed that the first evidence for cortical specialisation was that reported by Paul Broca (1824–1880; Fig. 9A) in 1861 for the uniquely human capacity for speech. In that year Broca reported the results of an autopsy on the cortex of one of his patients, a Monsieur Leborgne, who had suffered from loss of speech, that is, was aphasic. Broca found a lesion in the left anterior (frontal) lobe that he suggested was the language area of the cortex, subsequently known as Broca's area (Broca, 1861; Fig. 10A and B).

5.2. Fritsch and Hitzig: the motor cortex

There was little progress in the understanding of the function of the cortex for nearly 200 years between the death of Thomas Willis in 1675 and, as we shall see, the experiments of Fritsch and Hitzig about 1870. For example, the leading French physiologist of the day, Marie-Jean-Pierre Flourens (1794, 1867), claimed, as a consequence of his researches on pigeons (about 1824), that the cortex was only concerned with perception, intellectual abilities, and the will, not with motor action (Flourens, 1823). He showed in 1858 that the motor action involved in respiration could be delimited to the medulla, and did not involve the brain (Fig. 8A). Furthermore, according to Flourens, these functions of the cor-

tex could not be ascribed to different areas of the cortex, for this acted as a whole: 'all sensations, all perception, and all volition occupy concurrently the same seat in these organs. The faculty of sensation, perception, and volition is then essentially one faculty' (Flourens, 1823).

It is not until the second half of the 19th century that progress was made concerning the functions of the cortex with respect to motor control. In 1870, Gustav Fritsch (1838–1891; Fig. 9B) and Edouard Hitzig (1838–1907; Fig. 9C) published their monumental work *Über die elektrische Erregbarkeit des Grosshirns* (1870), in which they described the results of their experiments on stimulating the brains of dogs with galvanic currents that led them to the idea of a 'motor cortex' (Fig. 10F). In these experiments, the exposed cortex of dogs was excited at different sites with levels of electrical stimulation just detectable when applied to the human tongue. They found areas on the surface of the cortex that gave muscular contractions involving the face and neck on the opposite side of the dog to the hemisphere being stimulated as well as forepaw extension and flexion. On unilateral ablation of the forepaw area of the cortex, they observed that sensation was unaffected but the dog possessed impaired motor activity and posture. On this work, they commented that: 'a part of the convexity of the hemisphere of the brain is motor, another part is not motor. The motor part, in general, is more in front, the non-motor part more behind. By electrical stimulation of the motor part, one obtains combined muscular contractions of the opposite side of the body. These muscle contractions can be localised on certain very narrowly delimited groups by using very weak currents. The possibility to stimulate narrowly delimited groups of muscle is restricted to very small foci which we shall call centres' (Fritsch and Hitzig, 1870). Not only did this lead them to the hypothesis that a discrete area of the cortex possessed a motor function, but they also generalised this idea by suggesting that other functions of the cortex might also be found in specific areas of the cortex, thus: 'certainly some psychological functions, and perhaps all of them, in order to enter matter or originate from it, need circumscribed centres of the cortex' (Fritsch and Hitzig, 1870, p. 81; von Bonin, 1960). This conception of cortical localisation was the first major advance in our understanding of cortical function since the time of Willis.

Following this work of Fritsch and Hitzig on dogs, John Hughlings Jackson (1835–1911; Fig. 9D) reached similar conclusions concerning the existence of a motor cortex in humans, based on his observations on patients with epilepsy reported in 1863: 'in very many cases of epilepsy, and especially in syphilitic epilepsy, the convulsions are limited to one side of the body; and, as autopsies of patients who have died after syphilitic epilepsy appear to show, the cause is obvious organic disease on the side of the brain, opposite to the side of the body convulsed, frequently on the surface of the hemisphere' (Jackson, 1863). Of particular interest was the temporal pattern of contraction across muscle groups during seizures in spreading epilepsy. This led Hughlings Jackson

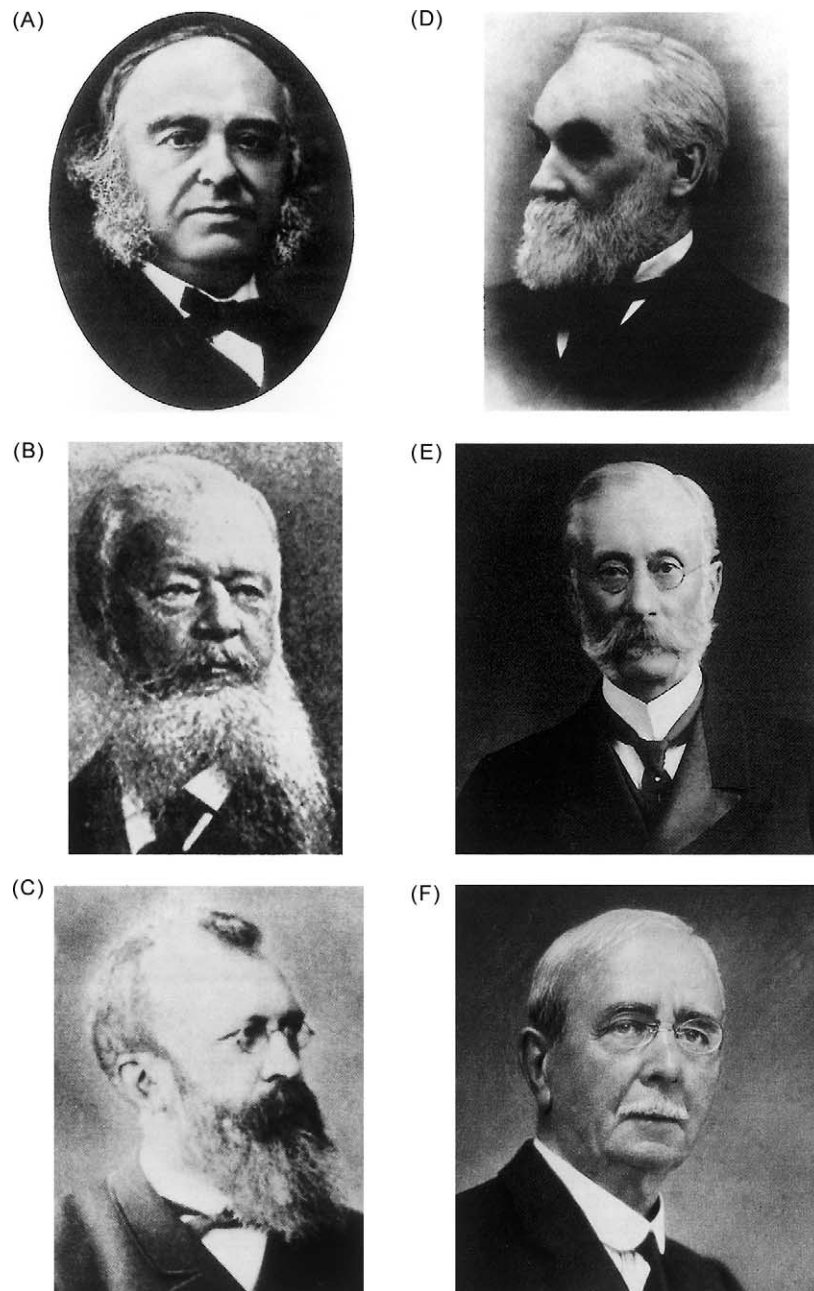


Fig. 9. Pioneers on the localization of cortical functions in the 19th century. (A) Paul Broca (1824–1880), whose association between aphasia and damage to the frontal cortex in M. Leborgne ‘Tan’, determined in 1861, which was the first cortical localization that was widely accepted (courtesy of the Academie de Medecine, Paris). (B) Gustav Fritsch (1838–1927) (C) Edouard Hitzig (1838–1907) (both B and C reproduced by kind permission of Dr. A.E. Walker, for whom Professor Stender of Berlin obtained the picture of Hitzig). (D) John Hughlings Jackson (1835–1911), who determined the existence of a somatotopically organized motor cortex as a consequence of his observations on epileptic seizures in his patients. (E) David Ferrier (1843–1928), a leader of the cortical localizationist movement at the end of the 19th century (courtesy of Yale Medical Historical Library, New Haven, CT). (F) Charles Scott Sherrington (1857–1952).

to speculate that the motor cortex must be organised along somatotopic lines, so that the hand, face and foot, which possess the greatest capacity for specialised movement, receive the largest representation in the motor cortex. These brilliant suggestions of Hughlings Jackson were confirmed by the work on primates by David Ferrier (1843–1928; Fig. 9E) in 1874. Using alternating current stimulation of discrete sites

on the cortex, he was able to delineate clearly the area of the cortex that produces the twitching of muscles as well as movements that in some cases resembled attempts at walking (Fig. 10E). On introducing small lesions into the motor area of the cortex which he had mapped, Ferrier showed that, in some cases, these resulted in a paralysis of the opposite hand and forearm, and in another case, to the paralysis of

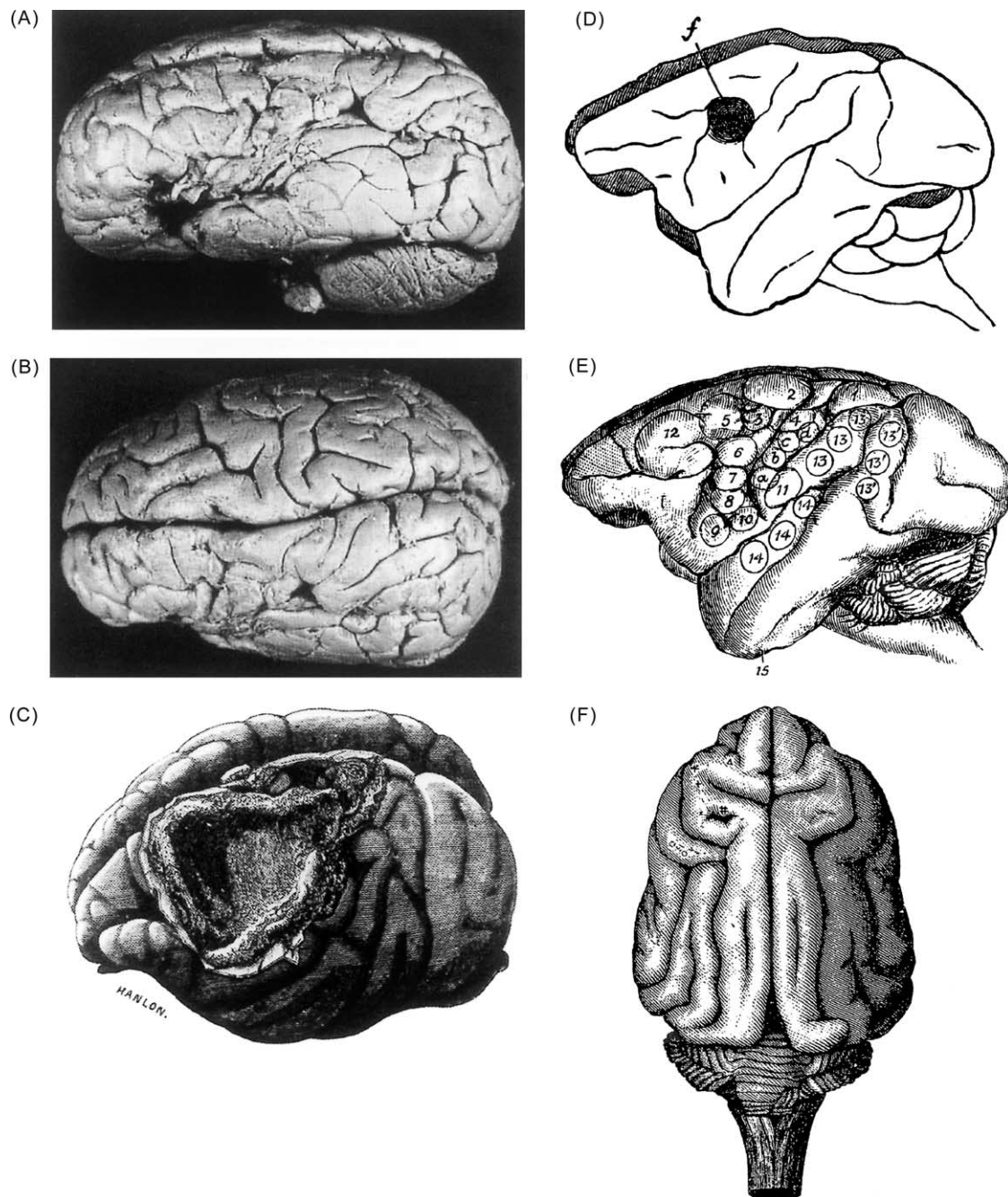


Fig. 10. Images of the human cortex involved in establishing localization of cortical functions. (A & B) Two photographs of the brain of Leborgne 'Tan' taken in 1861 (from the Musée Dupuytren. Courtesy of Assistance Publique, Hôpitaux de Paris). (C) Drawing showing the lesion of a monkey who became hemiplegic after cortical surgery; the monkey was presented at the International Medical Congress in 1881 by David Ferrier. (D) David Ferrier's (1886) diagram of the left hemisphere of the monkey brain showing the locus of the ablation that resulted in a paralysis of the biceps on the right side. (E) David Ferrier's (1886) diagram of the left hemisphere of the monkey brain showing the regions that gave rise to movements (circles with numbers) when electrically stimulated. (F) Drawing of the brain of a dog from Fritsch and Hitzig (1870); this figure shows the areas (triangle, cross, hatch marks) from which movements of the opposite side of the body were evoked with electrical stimulation.

the biceps muscle (Fig. 10D; see also Fig. 10C). By contrast, these animals showed normal sensitivity to touch and noxious stimuli. Such observations clearly pointed to a somatotopic organisation of the motor cortex (Ferrier, 1873/1874, 1876a,b). This work on primates was subsequently con-

firmed and extended by Victor Horsley (1857–1916) who, in 1887, showed that the precentral gyrus was predominantly motor and the post-central sensory, so that the motor cortex was to be found exclusively anterior to the Rolandic fissure (Beevor and Horsley, 1887, 1890, 1894).

5.3. *Electrical phenomena in the cortex support the idea of a motor cortex*

In 1875, Richard Caton (1842–1926) discovered that electrical oscillations could be recorded through two electrodes placed on the surface of the cortex of a monkey and that these oscillations were altered by various forms of sensory stimulation, as well as by anoxia and anesthesia. Caton comments that: in every brain hitherto examined, the galvanometer has indicated the existence of electrical currents. The external surface of the grey matter is usually positive in relation to the surface of a section through it. Feeble currents of varying direction pass through the multiplier when the electrodes are placed on two points of the external surface of the skull. The electric currents of the grey matter appear to have a relation to its functions. When any part of the grey matter is in a state of functional activity, its electric current usually exhibits negative variation. For example, on the areas shown by Dr. Ferrier to be related to rotation of the head and to mastication, negative variation of the current was observed to occur whenever those two acts, respectively, were performed. Impressions through the senses were found to influence the currents of certain areas, e.g. the currents of that part of the rabbit's brain which Dr. Ferrier has shown to be related to movements of the eyelids, were found to be markedly influenced by stimulation of the opposite retina by light (Caton, 1875, 1877, 1887). The electrical changes due to stimulation of the retina with light were later confirmed by Adolf Beck (1863–1942), adding credence to Caton's observations on the localisation of electrical activity during motor acts of the kind predicted by Ferrier's work (Beck, 1890).

5.4. *Challenges to the idea of a motor cortex*

In 1881, Friedrich Goltz (1834–1902) presented to the Medical Congress held in London dogs that had received lesions to their cortex. Goltz held that these should have severely reduced motor function if the idea of a motor cortex was correct. However, these dogs did not manifest such reduced function (Goltz, 1869, 1892). This challenged both the original work of Fritsch and Hitzig on dogs, involving galvanic stimulation of the cortex, and more directly the recent observations of Ferrier on the effects of lesions to the presumptive motor cortex of primates. In order to determine that the lesions of the cortex which Goltz had made did involve the motor region, members of the Congress were given parts of the nervous system of the operated dogs for histological examination. A cerebral hemisphere of one of these dogs was given to J.N. Langley, who subsequently reported his histological observations to the British Physiological Society (Langley, 1883). Langley was assisted in his full investigation by the young Charles Sherrington which resulted in Sherrington's first publication (Langley and Sherrington, 1884). Perhaps the most important outcome of this work was that it led to Sherrington's going to Goltz in Strasbourg to learn more about the techniques that Goltz was using in

these studies on the cortex, a subject which Langley did not usually work on.

6. **Charles Scott Sherrington: the integrative action of synapses in spinal cord and cortex**

6.1. *The integrative action of synapses in the spinal cord*

It is to Charles Sherrington (1857–1952; Fig. 9F) at the end of the 19th and the beginning of the 20th century that one must turn to find an experimental plan for elucidating the mechanisms of the 'true spinal marrow'. The thoroughness and methodical nature of Sherrington's researches on the subject are at a new level. These were not dependent on technical advances at the time so much as on the brilliance and clarity of his thinking, coupled with a formidable and indefatigable capacity for experiment. Sherrington first tackled the problem of the spinal origin of the efferent nerves innervating a particular muscle. 'For the study of the functions of the spinal cord, it is of importance to know accurately the positions of the central and peripheral structures between which the fibres of the spinal nerves constitute links' (Sherrington, 1892). He went on to show in that paper that 'the position of the nerve-cells sending motor fibres to any one skeletal muscle is a scattered one, extending throughout the whole length of the spinal segments innervating the muscle.' In 1905, his experiments indicated that stimulation of the afferent nerves of a particular muscle could produce contraction of that muscle independent of contraction of opposing muscles of the joint (Sherrington, 1905a,b). In 1910, he published his great paper, 121 pages long, on Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing (Sherrington, 1910). In this, he describes the flexion-reflex 'the flexion-reflexes excited by stimuli applied to the skin of the reacting limb itself are elicited best by nocuous stimuli. The flexion-reflex is here nociceptive and its significance is self-protection.' 'But reflex flexion can be elicited from the limb by application to it of stimuli non-nocuous in character, eminently by proprioceptive stimuli in the form of passive movement.' He also identifies the extension-reflex and the crossed-extension reflex by showing that if flexion in one limb is initiated by stimulation then an extensor movement often occurs in the contralateral homologous limb: 'the reflex movement elicitable from all exteroceptors of the limb except some at its attached base is (excluding extensor-thrust) primary flexion of the stimulated limb and extension of the contralateral limb.' Sherrington also established in this work a stepping reflex that is not due to contact of the foot with the ground.

'These skin stimuli though continuous and equable evoke the rhythmic alternating movement constituting stepping (in the decapitate preparation).' 'Faradisation of certain points in the exposed cross-section of the cord causes stepping of the ipsilateral hind limb with flexion at its opening phase, often accompanied by less vigorous stepping contralateral

hind limb converse in phase, but synchronous with that of the ipsilateral limb' and 'similarly the muscles employed in the extension phase of the step are those employed in the crossed-extension reflex, and the principles of simultaneous co-ordination of the musculature are the same as in that reflex.' 'No muscle which contracts in the flexion phase of the reflex step appears to contract in the extension phase. 'As for standing, Sherrington noted that: 'the decerebrate rigidity observable after mid-brain transaction is a tonic postural reflex; it is in fact reflex standing, i.e. "standing" purely reflexly maintained.' 'It is this tonic reflex which in part causes the decerebrate preparation to suppress the refractory periods characteristic of the reflex response of the limbs shown in the decapitate and spinal preparation. It, thus, changes rhythmic stepping movement into assumption and maintenance of an attitude, namely, standing.' 'Reflex standing employs contraction of the same muscles as contract in the extension phase of the step. In it as in the latter reflex the antagonists of the protagonist muscles are not contracting—there is some evidence that they are under tonic inhibition.' 'The prespinal mechanism involved in reflex standing co-operated also in the extension phase of the reflex step (in the decerebrate preparation). It also co-operates with the reflex stepping movements of the limbs amplifying their effectiveness by maintaining the erect posture of the body during the acts of walking, running, etc. In these acts, there is a grafting of proprioceptive reflexes executing the phasic flexions and extensions of the limb upon a tonic proprioceptive reflex

actuating the muscles which counteract gravity in the erect posture (*usustatus*) of the animal.'

In this great paper of 1910, as well as in earlier papers of 1897 and 1907, Sherrington laid down the conceptual scheme for the analysis of the role of the spinal cord in stepping and standing. In doing so he completed the research program initiated 80 years earlier by Marshall Hall with the consequence that the notion of a 'spinal soul' was finally eliminated from further consideration.

At the beginning of the 20th century, Sherrington established a number of other principles that were destined to play a major role in our understanding of spinal cord function. These include the following principles.

1. *The scratch reflex*: 'In the dog, when the spinal cord has been transacted in the neck, the scratch or scalptor reflex becomes in a few months prominent. A stimulus applied at any point within a saddle-shaped field of skin (Fig. 11C(A)) excites a scratching movement of the hind leg. The movement is rhythmic alternate flexion and extension at hip, knee, and ankle. Each flexion recurs at a frequency of about four times per second. The stimuli provocative (Sherrington, 1903) of it are mechanical, such as tickling the skin or pulling lightly on a hair' (Sherrington, 1947, p. 45).
2. *The concept of inhibition*: 'The striking correspondence observed (vide supra) between the reflex inhibition and the reflex contraction, when examined in

Fig. 11. Sherrington's elucidation of the principles of operation of the spinal cord. (A) Diagram indicating connexions and actions of two afferent spinal root-cells, α and αI , in regard to their reflex influence on the extensor and flexor muscles of the two knees. The α , root-cell afferent from skin below knee; αI , root-cell afferent from flexor muscle of knee, i.e. in hamstring nerve; ϵ and ϵI , efferent neurones to the extensor muscles of the knee, left and right; δ and δI , efferent neurones to the flexor muscles; E and EI, extensor muscles; F and FI, flexor muscles. The 'schalt-zellen' (V. Manokow) probable between the afferent and efferent root-cells are for simplicity omitted. The +ve sign indicates that at the synapse which it marks the afferent fibre α (and αI) excites the motor neurone to discharging activity, whereas the -ve sign indicates that at the synapse which it marks the afferent fibre α (and αI) inhibits the discharging activity of the motor neurones. The effect of strychnine and of tetanus toxin is to convert the minus sign into plus sign' (from Fig. 37 in Sherrington, 1947). (B) 'The final common path is, therefore, an instrument passive in the hands of certain groups of reflex paths. I have attempted to depict this very simply in the figure. There certain type-reflexes are indicated by lines representing their paths. The final common path (FC) selected is the motor neurone of the vasto-crureus of the dog or cat. Reflexes that act as 'allied reflexes' on FC are represented as having their terminals joined together next to the final common path. Reflexes with excitatory effect (+ve sign) are brought together on the left, those with inhibitory (-ve sign) on the right. Of the reflex pairs formed by the two reflexes which two symmetrical receptive points, one right and one left, yield in regard to the final common path, one of the pair only is represented, in order to simplify the diagram. To have a further indication of the reflexes playing upon FC, all that is required is to add to the reflexes indicated in the diagram for FC, a set of reflexes similar to those given in the diagram for FC I, for they must be added if the remaining members of the right and left reflex pairs from various parts of the body be taken into account. It is worth noting that in many instances the end-effect of a spinal reflex initiated from a surface point on one side is bilateral and takes effect at symmetrical parts, but is opposite in kind at those two parts, e.g. is inhibition at one of them, excitation at the other. Hence, reflexes initiated from points corresponding one with the other in the two halves of the body are commonly antagonistic. S stands for scratch-receptor, e and f are extensor and flexor muscles of knee, respectively' (from Fig. 44 in Sherrington, 1947). (C) Sherrington's classic picture of the areas for the scratch reflex in the dog: A shows the 'receptive field', as revealed after low cervical transection, a saddle-shaped area of dorsal skin, whence the scratch-reflex of the left hind limb can be evoked. Ir marks the position of the last rib; B shows a diagram of the spinal arcs involved; L, receptive or afferent nerve-path from the left foot; R, receptive nerve-path from the opposite foot; R α , R β , receptive nerve-paths from hairs in the dorsal skin of the left side; FC, the final common path, in this case the motor neurone to a flexor muscle of the hip; P α , P β , proprio-spinal neurones (from Fig. 39 in Sherrington, 1947). (D) Records from above downwards (read from left to right): FC, myograph curve of flexor muscle of hip (scratch-reflex). The vertical arc (preceding the response) coincides with the descent of the signal lines (S α , S β). Time in 1/5 s. Signal line S α : each descent of the line marks the period of stimulation of the skin belonging to arc R α (see (C)) of the shoulder skin. The strength of stimulus is arranged to be subminimal, so that a reflex response in FC is not obtained. Signal line S β : each descent of the line marks the period of stimulation, also subminimal of a point of shoulder skin 8 cm from R α . Though the two stimuli applied separately are each unable to evoke the reflex, when applied contemporaneously they quickly evoke the reflex. The two arcs R α and R β , therefore, reinforce each other in their action on the final common path FC (summation effect, immediate spinal induction) (from Fig. 38 in Sherrington, 1947).

one and the same type-reflex, allows the inference that the nerve-fibres from the receptive field of the reflex each divide in the spinal cord into end-branches (e.g. collaterals), one set of which, when the nerve-fibre is active, produces excitation, while another set, when the

nerve-fibre is active, produced inhibition (Sherrington, 1900, 1905a,b). The single afferent nerve-fibre would therefore in regard to one set of its terminal branches be *specifically excitator*, and in regard to another set of its central endings be *specifically inhibitory*. It would, in this

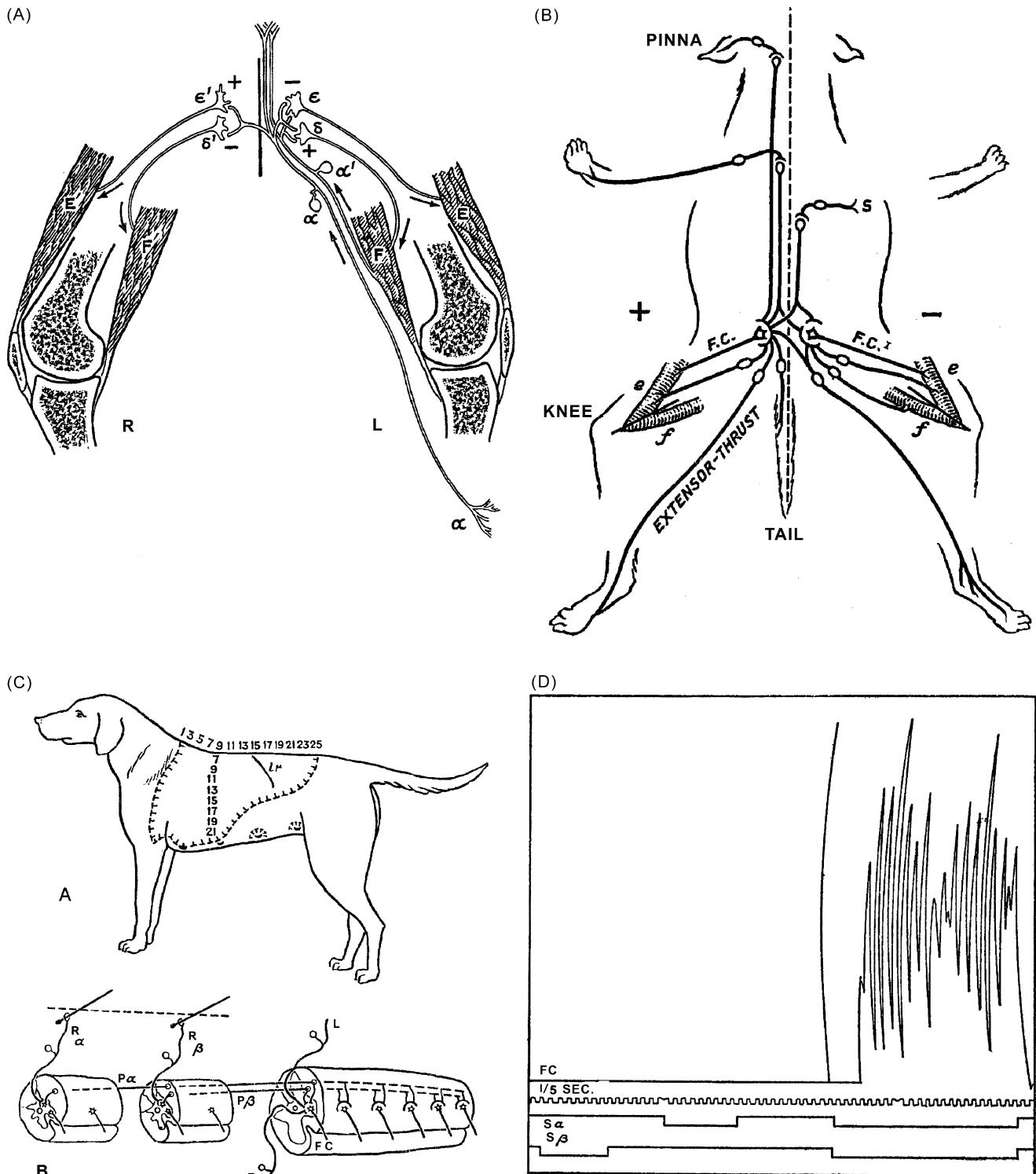


Fig. 11.

respect, be duplex centrally (Fig. 11A)' (Sherrington, 1947, p. 107).

3. *The concept of a final common pathway*: 'The action of the principle of the final common path may be instanced in regard to "allied arcs" in the scratch reflex as follows. If, while the scratch-reflex is being elicited from a skin point at the shoulder, a second point distant, e.g. 10 cm from the other point, but also in the receptive field of the skin, be stimulated, the stimulation at this second point favours the reaction from the first point. This is well seen when the stimulus at each point is of subminimal intensity. The two stimuli, though each unable separately to invoke the reflex, yet do so when applied both at the same time (Fig. 11D). This is not due to overlapping spread of the feeble currents about the stigmatic poles of the two circuits used. Weak cocainisation of either of the two skin points annuls it. Moreover, it occurs when localised mechanical stimuli are used. It, therefore, seems that the arcs from the two points, e.g. $R\alpha$ and $R\beta$ (Fig. 11C(B)) have such a mutual relation that reaction of one of them reinforces reaction of the other, as judged by the effect on the final common path.

It is obvious that such reinforcement—immediate spinal induction—may occur in either of two ways. The diagram (Fig. 11C(B)) treats the final common path as if it consisted of a single individual neurone. The single neurone of the diagram stands for several thousand. It may be (I) that when the reflex is excited from $R\alpha$, only a particular group of the motor neurones composing the final common path is thrown into action, and similarly another particular group when the reflex is excited from $R\beta$. If the two groups in the final common path are separate groups, the explanation of the reinforcement shown in the muscular response may be by mechanical summation of contraction occurring in two separate fields of muscular tissue, the contraction of each too slight to cause perceptible movement by itself without the other. In other words, the reinforcement would be due not to the response in the set of neurones comprising the final common path (FC in Fig. 11C(B)), being neurone for neurone more intense under the combined stimulation of $R\alpha$ and $R\beta$ than under stimulation of either singly, but the result would arise from the number of neurones in action in FC being simply greater under the stimulation of the two skin points than under stimulation of one of them only (Sherrington, 1947, p. 121).

'The final common path is, therefore, an instrument passive in the hands of certain groups of reflex paths. I have attempted to depict this very simply in Fig. 11B. There certain type-reflexes are indicated by lines representing their paths. The final common path (FC) selected is the motor neurone of the vasto-crureus of the dog or cat. Reflexes that act as 'allied reflexes' on FC are represented as having their terminals joined together next to the final common path. Reflexes with excitatory effect (+ve sign) are brought together on the left, those with

inhibitory (–ve sign) on the right. Of the reflex pairs formed by the two reflexes which two symmetrical receptive points, one right and one left, yield in regard to the final common path, one of the pair only is represented, in order to simplify the diagram. To have a further indication of the reflexes playing upon FC, all that is required is to add to the reflexes indicated in the diagram for FC, a set of reflexes similar to those given in the diagram for FC I, for they must be added if the remaining members of the right and left reflex pairs from various parts of the body be taken into account. It is worth noting that in many instances the end-effect of a spinal reflex initiated from a surface point on one side is bilateral and takes effect at symmetrical parts, but is opposite in kind at those two parts, e.g. is inhibition at one of them, excitation at the other. Hence, reflexes initiated from points corresponding one with the other in the two halves of the body are commonly antagonistic. S stands for scratch-receptor, e and f are extensor and flexor muscles of knee, respectively' (Sherrington, 1947, p. 151).

4. *The relation between the brain and the common final pathway*: 'Are there in the body no reflexes absolutely neutral and indifferent one to another? But there are reflexes that do in the spinal dog appear neutral and indifferent to the scratch-reflex. For instance, a weak reflex of the tail may be obtained without any obvious interference between it and the scratch-reflex. But to show that reflexes may be neutral to each other in a spinal dog is not evidence that they will be neutral in the animal with its whole nervous system intact and unutilized. It is a cardinal feature of the construction of the higher vertebrate nervous system that longer indirect reflex arcs, attached as extra circuits to the shorter direct ones, all pass through the brain. With those former intact the number of reflexes neutral one to another might be fewer. In presence of the arcs of the great *projicient receptors* and the *brain* there can be few receptive points in the body whose activities are totally indifferent one to another. Correlation of the reflexes from points widely apart is the crowning contribution of the brain towards the nervous integration of the individual' (Sherrington, 1947, p. 148).

6.2. Sherrington: somatopic mapping of the motor cortex

Although Ferrier in 1886 had first located the motor cortex in primates as a distinct area (Fig. 10D), it was Sherrington and Grunbaum in 1902 who first gave a detailed description of the spatial extent of this area on the cortex of primates. They noted that: 'the "motor" area does not to any point extend behind the *sulcus centralis*. Feeble reactions can occasionally, under circumstances, be provoked by strong faradisation behind the *sulcus centralis*, but these are equivocal, and appear under conditions that exclude their acceptance as equivalent to "motor-area" reactions.' In this, Sherrington and Grunbaum clearly distinguished for the first time the motor area from the area 'behind

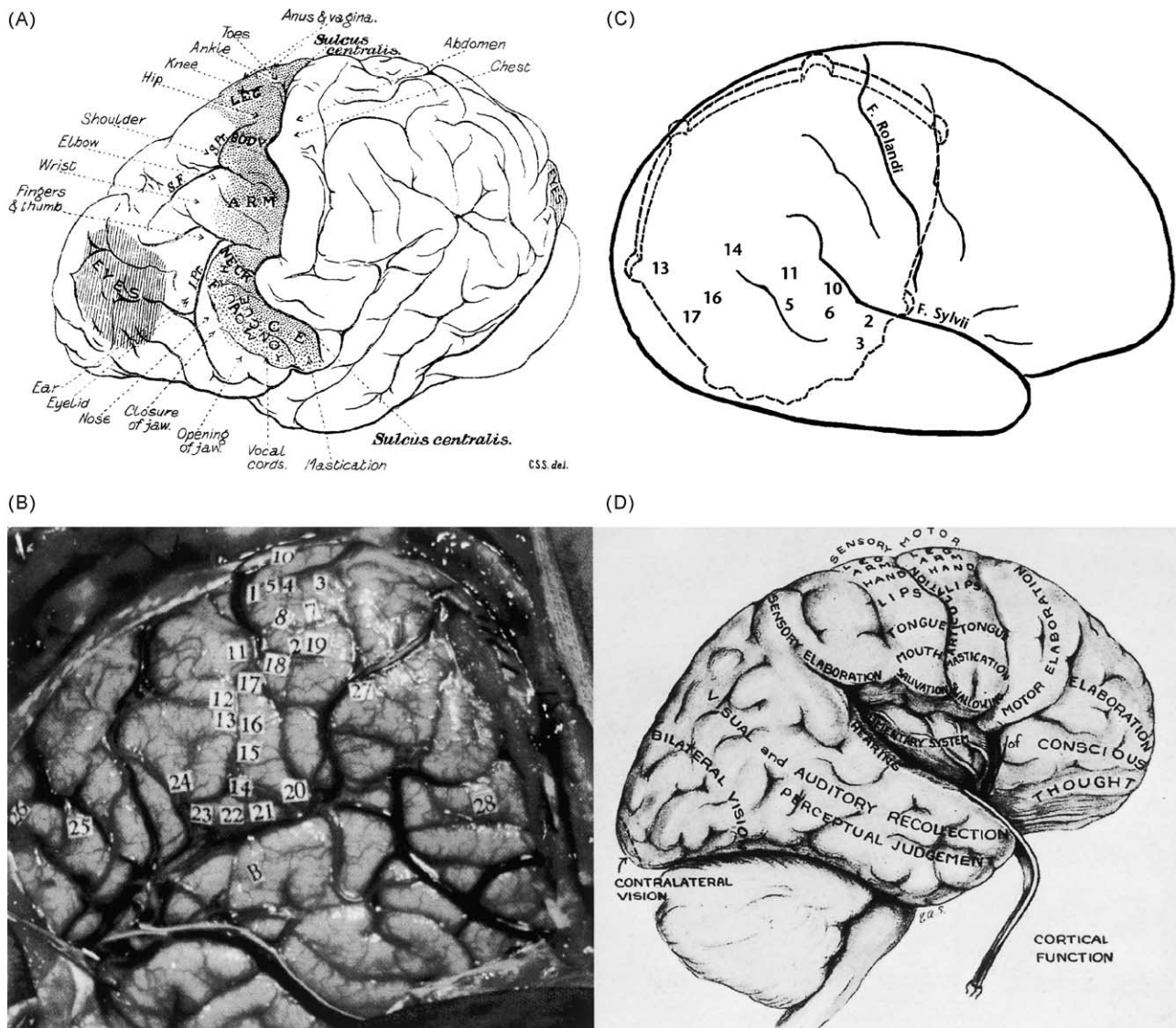


Fig. 12. The motor and somatosensory cortex in humans and other primates. (A) Brain of a chimpanzee (*Troglodytes niger*). Left hemisphere viewed from side and above so as to obtain as far as possible the configuration of the sulcus centralis area. The figure involves, nevertheless, considerable foreshortening about the top and bottom of sulcus centralis. The extent of the 'motor' area on the free surface of the hemisphere is indicated by the black stippling, which extends back to the sulcus centralis. Much of the 'motor' area is hidden in sulci. The names printed large, in enhanced black, on the stippled area indicate the main regions of the 'motor' area; the names printed small, outside the brain, indicated broadly by their pointing lines the relative topography of some of the chief sub-divisions of the main regions of the 'motor' cortex. But there exists much overlapping of the areas and of their sub-divisions which the diagram does not attempt to indicate. The shaded regions, marked 'eyes', indicate in the frontal and occipital regions, respectively, the portions of cortex which, under faradisation, yield conjugate movements of the eyeballs. But it is questionable whether these reactions sufficiently resemble those of the 'motor' area to be included with them. They are, therefore, marked in vertical shading instead of stippling as is the 'motor' area. S.F. = superior frontal sulcus; S.Pr. = superior precentral sulcus; I.Pr. = inferior precentral sulcus (from plate 4 in [Grunbaum and Sherrington, 1902](#)). (B) Effects of electrical stimulation of the brain of a human. The dura has been turned back to expose the cortex. The left temporal lobe is seen below the fissure of Sylvius. The numbered tickets dropped on the surface of the cortex, indicate points of positive response to electrical stimulation. A few of the patients responses during the operation are as follows (from Fig. VII-3 in [Penfield and Roberts, 1959](#)). Post-central gyrus—1: tingling right thumb and slight movement; 19: sensation in lower lip outside; 17: sensation right upper lip inside; 16: tingling in right side of tongue at the tip; 14: sensation in the "joint of the jaw and in the lower lip inside". Pre-central gyrus: 11: feeling in my throat which stopped my speech; 12: quivering of jaw in a "sidewise manner"; 13: pulling of jaw to right. (C) Further experiments on the effects of stimulation of the brain of a human. Broken line indicates craniotomy exposure. The responses to stimulation (thyatron stimulator) of the cortex of a woman were as follows: points 13 and 17—contralateral colored stars (points lie on visual (occipital) cortex). Points 14 and 16—complicated visual hallucinations, like the aura of her attack. At points near to 14 and 16, stimulation had the following effect. She stared suddenly and then cried: "Oh! I can see something come at me! Do not let them come at me!" She remained staring and fearful for 30s, although the stimulation was of much shorter duration. Points 11, 5, 10, 6, 2, and 3—auditory hallucinations that she heard the voices of her mother and brothers "yelling" at her in an accusing manner, producing terror and tears' (from Fig. 87 in [Penfield and Rasmussen, 1968](#)). (D) Functions of the human cortex. The illustration serves as a summary restatement of conclusions, some hypothetical (e.g. the elaboration zones), others firmly established. The suggestion that the anterior portion of the occipital cortex is related to both fields of vision rather than to one alone is derived from the results of stimulation (from Fig. 110 in [Penfield and Rasmussen, 1968](#)).

the *sulcus centralis* that we now know as somatosensory (Fig. 12A). In this work, they also identified what we now call ‘the frontal eye fields’, thus: ‘our observations indicate that the frontal region, yielding conjugate deviation of the eyeballs, presents such marked differences of reaction from the “motor” area of the Rolandic region that we hesitate to include it with the so-called “motor” cortex; it seems necessary to distinguish it in a physiological category separate from that. Spatially, it is wholly separated from the Rolandic “motor” area by a field of “inexcitable” cortex’ (Grunbaum and Sherrington, 1902; Fig. 12A). Their method of unipolar faradisation (alternating current) stimulation of the cortex allowed for much finer localisation than had been possible with double-point electrodes used up to this time. As they comment: ‘in the “motor” area we have found localised, besides very numerous actions, certain movements of the ear, nostril, palate, movements of sucking, of mastication, of the vocal cords, of the chest wall, of the abdominal wall, of the pelvic floor, of the anal orifice, and of the vaginal orifice.’ This led them to the discovery of the somatotopic organisation of the motor cortex, thus: ‘we find the arrangement of the representation of various regions of the musculature follow the segmental sequence of the cranio-spinal nerve-series for a very remarkable extent’ (Grunbaum and Sherrington (1902). This classic paper, published at the beginning of the 20th century, established without equivocation the conception of a motor cortex and, therefore, that different parts of the cortex are specialised for different functions.

7. The relation between cortex and mind: Sherrington, his contemporaries and proteges

We shall now turn to a consideration of how Sherrington, as well as his contemporaries and proteges, on whom he had a profound influence, regarded the problem of the relation between the mind and the cortex. As the purpose of this essay has been to trace the history of the integrative action of the nervous system up to the time of Sherrington, we shall not dwell here on the contributions of his proteges to this history. However, this essay would not be complete without a description of how, in the first half of the 20th century, the problems that beset an understanding of the integrative action of the spinal cord in earlier centuries were confronted by Sherrington and his colleagues when they in turn came to consider the integrative action of the cortex and the mind.

7.1. Sherrington

As we have seen, it was the brilliant research of Sherrington that finally revealed the true nature of the spinal cord as a reflex centre as well as the role of the cortex in the generation of reflexes. He also clarified the beautiful specificity of the localisation of function within the motor and somatosensory cortex. However, although the notion of a ‘spinal soul’ no longer figured in neurophysiology, the question of whether

a ‘cortical soul’ existed remained moot. Or, to put it more perspicuously, the question of the relationship between the mind and the cortex remained deeply puzzling. Sherrington considered this question, tackling it in his usual methodical manner by first considering it in a historical setting through the work of Jean Fernel and the beginnings of the conception of physiology and neurophysiology. Later, he took up the problem at length in *Man on his Nature*, his Gifford Lectures of 1937/1938.

Sherrington studied Fernel carefully, and read extensively in the works of philosophers, from Aristotle onwards. However, as we shall see, his grasp of philosophical problems and his understanding of the differences between scientific problems and philosophical ones was infirm. Despite acquaintance with Aristotle’s *De Anima*, he failed to see the depth and fruitfulness of the Aristotelian conception of the *psyche* and its bearing on the essentially conceptual questions that plagued him. He noted Aristotle’s ‘complete assurance that the body and its thinking are just one existence’, and that ‘the “oneness” of the living body and its mind together seems to underlie the whole (Aristotelian) description as a datum for it all’ (MN 189). Nevertheless, Sherrington did not probe the Aristotelian philosophical doctrine properly. Instead, he moved towards a Cartesian dualist conception of the relation between mind and body, unsurprisingly encountering the same insoluble problems as Descartes had. Using the term ‘energy’ to signify matter as well as energy, Sherrington held that ‘evolution has dealt with . . . us as compounded of “energy” and “psyche”, and has treated in us each of those two components along with the other. The two components are, respectively, on our analysis, an energy-system and a mental system conjoined into one bivalent individual.’²¹ ‘Energy’ (or matter) and mind are, he thought, ‘phenomena of two categories’ (MN 251).

‘Energy’, in his view, is perceptible, spatio-temporally locatable, subject to the laws of physics and chemistry. Mind, by contrast, is ‘invisible’, ‘intangible’, without ‘sensual (sensory) confirmation’ (MN 256). Sometimes Sherrington states that mind is ‘unextended’,²² at others he states that since mind has a location, it is inconceivable to him that it should lack a magnitude or be without extension. ‘Accepting finite mind as having a “where” and that “where” within the brain, we find that the energy-system with which we correlate the mind has of course extension and parts . . . Different “whereas” in the brain correlate with different mental actions . . . We have to accept that finite mind is in extended space’ (MN 249f). On the other hand, he remarks, more sapiently than he evidently realised, that the mind is not ‘a thing’ (MN 256). He conceived of mind as the agent of thought, the source of desire, zest, truth, love, knowledge, values—of all,

²¹ Sherrington (1951, p. 250); subsequent references in the text to this work will be flagged ‘MN’.

²² ‘So, our two concepts, space–time energy sensible (perceptible) and insensible (imperceptible) unextended mind, stand as in some way coupled together, but theory has nothing to submit as to how they can be so’, quoted by Eccles and Gibson (1979, p. 143) without a reference.

as he put it, ‘that counts in life’ (MN 256). It is, he wrote, ‘the conscious “I”’.²³ But this is misconceived. The mind is no more located in the head or brain than is the ability to walk or talk. It is neither extended, nor an unextended point, any more than the ability to score a goal is either extended or an unextended point. The mind is not ‘the conscious “I”’, since there is no such thing as ‘an I’, any more than there is such a thing as ‘a you’ or ‘a he’. I am not my mind—I *have* a mind, not as I have a car or even as I have a head or brain, but rather as I have eyesight or the ability to think.

How we should conceive of the conceptual relationships between mind, body (and brain), and person is a deep philosophical problem—the character of whose solution we have intimated. Sherrington was exceedingly unclear about the matter, not fully realising that this was not an empirical matter at all, but a purely conceptual one. Sometimes he seems to accept the mistaken idea that the mind has a body,²⁴ even though, to be sure, it is not *minds* that ‘have bodies’, it is *human beings*.²⁵ At other times he seems to go so far as to claim that the body (or at any rate parts of the body) has (or have) a mind—a part of the body that is sensitive has ‘mind only lent it, in the form of sensation by proxy’ (MN 187). But this is confused. What would a body do with a mind? *People* have minds, as indeed, they have bodies. ‘So much of the body as feels, has its sensations done for it’ by the brain, Sherrington argued, and so too, ‘the body’s thinking seems to be done for it, namely in the brain’ (MN 187), presumably by the mind. Here, too he was confused, since the brain does not ‘do’ sensations—there is no such thing as ‘doing’ sensations. But we have sensations *in* various parts of our sensitive body (parts that hurt, throb, itch, etc.)—and we would have no sensations, but for the normal functioning of the brain and nervous system. Similarly, *the body* has no thinking to do—there is no such thing as one’s body thinking. It is people who think, and their thinking is not done for them by their brain—they have to do their own thinking. There is no such thing as the brain’s thinking anything—although, of course, human beings would not be able to think, but for the normal functioning of their brain. That, to be sure, does not imply that one thinks *with* one’s brain, in the sense in which one walks with one’s legs or sees with one’s eyes.

Given this confused dualism, the question of the relation between the two entities cannot but arise. Sherrington asserted that no one doubts that there is, as he put it, ‘a liaison’ between brain and mind. But ‘the “how” of it we must think

remains for science as for philosophy a riddle pressing to be read’ (MN 190). ‘In all those types of organism in which the physical and the psychical coexist, each of the two achieves its aims only by reason of a *contact utile* between them. And this liaison can rank as the final and supreme integration completing its individual. But the problem of how the liaison is effected remains unsolved; it remains where Aristotle left it >2000 years ago. There is, however, one peculiar inconsistency which we may note as marking this and many other psychological theories. They place the soul in the body and attach it to the body without trying in addition to determine the reason why, or the condition of the body under which such attachment is produced. This, however, would seem to be a real question’ (Sherrington, 1947, p. xxiii).

It is curious to find Sherrington writing this, since he knew that the question of how the mind can interact with the body is *not* a question that can arise for Aristotle. Within the framework of Aristotelian thought, as we have seen (Section 1) the very question is as senseless as the question ‘how can the shape of the table interact with the wood of the table?’ Aristotle manifestly did not leave this as a problem within his philosophy. The problem arose within the framework of Plato’s dualist philosophy, which was refuted by Aristotle, but nevertheless informed neo-Platonism and, via St. Augustine, came to dominate Christian thought. To be sure, Thomas Aquinas adopted Aristotelian psychology and strove, with questionable coherence, to adapt it to Christian theology (Fernel’s reflections are very much the product of late medieval Aristotelianism). But Platonic dualism remained the most natural conception for popular Christianity, and it informed the Renaissance form of neo-Platonism. The relationship between mind and body is highly problematic for any form of dualism, and with the 17th century dominance of Descartes and the corresponding decline in the influence of Aristotelian philosophy, the problem of interaction came onto the agenda again, and has remained there ever since.

Sherrington contributed nothing towards its solution. He noted that science was impotent to solve the problem. ‘Life ... has resolved itself into a complex of material factors; all of it except one factor. There science stopped and stared as at an unexpected residue which remained after its solvents has dissolved the rest. Knowledge looking at its world had painfully and not without some disillusion arrived at two concepts; the one, that of energy, which was adequate to deal with all which was known to knowledge, except mind. But between energy and mind science found no ‘how’ of give and take ... To man’s understanding the world remained obstinately double’ (MN 200). Life and the processes of life, Sherrington observed, were explicable by physics and chemistry, but ‘thought escapes and remains refractory to natural science. In fact natural science repudiates it as something outside its ken’ (MN 229). This is, of course, untrue. For psychologists can and do study thinking—which is not in any sense ‘outside its ken’. But it is evident that what Sherrington meant was that thinking and thought are not

²³ Quoted in Eccles and Gibson (1979, p. 142).

²⁴ I have seen the question asked “why should the mind have a body?” The answer may well run, ‘to mediate between it and other mind’ (MN 206).

²⁵ The phrase ‘to *have* a body’ is indeed curious and misleading. We do not say of insentient things that they have a body (trees, for example, do not have bodies). We ascribe bodies only to ourselves and sometimes to higher animals. Only what leaves a corpse behind when it dies can be said to have a body (we do not say of a dead fish, for example, that it is the corpse (or the remains) of a fish). The use of the phrase earmarks not an empirical truth of some kind, but an attitude towards certain kinds of sentient creatures—paradigmatically towards human beings.

reducible to physics and chemistry. ‘For myself’, he wrote, ‘what little I know of the how of the one (i.e. the brain) does not, speaking personally, even begin to help me toward the how of the other (i.e. the mind). The two for all I can do remain refractorily apart. They seem to me disparate; not mutually convertible; untranslatable the one into the other’ (MN 247). On the matter of strict reducibility, at any rate, he is quite right.

Sherrington’s conception of the interaction between mind and body was Cartesian through and through (although without the commitment to the interactionist role of the pineal gland). ‘I would submit that we have to accept the correlation, and to view it as interaction: body → mind. Macrocosm is a term with perhaps too medieval connotations for use here: replacing it by “surround”, then we get surround ↔ body ↔ mind. The sun’s energy is part of the closed energy cycle. What leverage can it have on the mind. Yet through my retina and brain it is able to act on my mind. The theoretically impossible happens. In fine, I assert that it does act on my mind. Conversely my thinking ‘self’ thinks it can bend my arm. Physics tells me that my arm cannot be bent without disturbing the sun. My mind then does not bend my arm. If it does, the theoretically impossible happens. Let me prefer to think the theoretically impossible does happen. Despite the theoretical I take it that my mind *does* bend my arm and that it disturbs the sun’ (MN 248). ‘Reversible interaction between the “I” and the body’, he concluded, ‘seems to me an inference validly drawn from evidence’ (MN 250). This is a deep confusion—for it is not ‘the “I” that moves my arm when I move my arm, nor indeed is it my mind. I do so—and I am neither my mind, nor am I a ‘self’, an ‘ego’, or an “I”. I am a human being. However, how the puzzles here are to be fully unravelled is a philosophical task for another occasion.’²⁶

Sherrington was admirably candid in confessing his bafflement. But he did not realise that the root of the trouble is conceptual confusion—not empirical ignorance. And he was not aware of the revolution in philosophy that was taking place at that very time in Cambridge that would have enabled him to disentangle his confusions. His predicament was not unlike Descartes’s, 300 years earlier. Writing in his old age to Princess Elizabeth of Bohemia, who asked him how a thinking soul could move the animal spirits, the great philosopher and scientist confessed that ‘I may truly say that what your highness proposes seems to me the question people have most right to ask me in view of my published works.’

7.2. Edgar Adrian

Edgar Douglas Adrian (1889–1977) was a much younger contemporary of Sherrington’s, with whom he shared the Nobel Prize in 1932. His work is, in a way complementary to that of Sherrington’s, in as much as it gives an account of

the electrical activity in both motor and sensory nerve fibres that accompany reflex and other integrative actions of the nervous system. Adrian showed that there is only one kind of action potential in nerve fibres, whether these are motor or sensory. Furthermore, that the force of contraction and the intensity of sensation is graded as a consequence of different frequencies of action potential firing in the nerves as well as changes in the number of nerve fibres that are firing. He later turned his attention to the origins of electrical oscillations in the brain, and established that the Berger rhythm comes from the occipital part of the cortex.

The question ‘how is the brain related to the mind?’ puzzled Adrian no less than it puzzled others. But, unlike Sherrington, he was disinclined to speculate upon the nature of the mind, or upon the question of how brain activities are related to mental phenomena. His reflections on such questions are, therefore, relatively few, and expressed with considerable caution. Nevertheless, it is worth surveying them briefly, for they raise questions that still bewilder neuroscientists. Though Adrian did not commit himself to Cartesian dualism, as we shall see, Cartesian elements do creep into his cautious and tentative remarks.

In his lecture on consciousness in 1965, Adrian observed that, in general, natural scientists prefer to remain uncommitted on such questions as the relationship between mind and matter. However, he admitted, it is difficult for physiologists to maintain such Olympian detachment. Any neuroscientist concerned with studying the sense organs and the central nervous system can hardly avoid the problems that have always arisen in trying to relate physical events and activities in the body to mental activities. The problem can be put most starkly by reflecting on the fact that one might, according to Adrian, build a mechanical human being that behaved exactly as we do. For the ‘universal Turing machine’, he observed wittily, can ‘turn its band to any problem’, and a ‘man machine’ might be programmed to do anything we can do. What would, however, be missing ‘is ourself, our ego, the I who does the perceiving and the thinking and acting, the person who is conscious and aware of his identity and his surroundings.’²⁷

We are convinced, Adrian remarked, that we have an immediate awareness of ourselves, and that this is one thing that a machine could not copy.

This thought is, to be sure, Cartesian through and through. What differentiates man from *mechanical animate nature* is, according to Descartes, consciousness. As we have observed, Descartes assimilated consciousness to self-consciousness. For, as we have seen, he held that thought, which is the essential attribute of mind, is defined as ‘everything which we are aware of as happening within us, in so far as we have an awareness of it.’ Notoriously, Descartes held that the foundation of all knowledge was each person’s consciousness of his own thoughts, and

²⁶ See Bennett and Hacker (2002, Chapter 12).

²⁷ Adrian (1966, p. 240).

hence, his indubitable knowledge of his own existence. In this respect, Adrian followed Descartes. For, he observed,

I used to regard the gulf between mind and matter as an innate belief. I am quite ready now to admit that I may have acquired it at school or later. But I find it more difficult to regard my ego as having such a second hand basis. I am much more certain that I exist than that mind and matter are different.

Apart from those who are insane, ‘out of their mind’, one does not come across people who do not believe in their own individuality, though there are many who do not believe in the separation of mind and matter. Belief in one’s own existence seems to depend very little on deliberate instruction.²⁸

Moreover, Adrian continued, ‘in the study of the human ego, introspections are almost all we have to guide us.’ ‘Introspections’, presumably, reveal to us the sensory, perceptual and emotional contents of consciousness. This conception conforms with the venerable philosophical tradition that stems from Descartes and the British empiricists. It is a general conception that is still characteristic of much neuroscientific reflection on these matters, especially among those neuroscientists who think that ‘qualia’ are the mark of conscious life—a feature that seems irreducibly ‘mental’.

Adrian was exceedingly hesitant to commit himself to any firm doctrine concerning the nature of what he called ‘our ego’. He quoted the neurologist Francis Schiller, who claimed in 1951 that consciousness is a ‘logical construction’, and the ego ‘a convenient abbreviation, an abstract of the multiplicity of objects from which it is developed’—this, Adrian averred, ‘seems to me a reasonable position to have reached.’²⁹ For, he thought, ‘the physiologist is not forced to reject the old fashioned picture of himself as a conscious individual with a will of his own’, for the view embraced acknowledges some kind of validity to the introspective as well as to the physiological account, while admitting that the two are incompatible. What that implies, Adrian claimed, is that in the fullness of time the two accounts will have to be reconciled. But it would, he held, be absurd to suppose that the scientific account will not be altered.

7.3. John C. Eccles

After studying medicine at Melbourne University, John C. Eccles (1903–1997) went to Oxford in 1925 as a graduate student to work with Sherrington, who was at that time engaged in research with Liddell on the characteristics of the myotatic reflex (Liddell and Sherrington, 1924; Liddell and Sherrington, 1925) and with Creed on the flexion reflex (Creed and Sherrington, 1926). Eccles’s first experimental work was done with Creed. It was on the

subject destined to dominate his research for over 40 years: the mechanism of inhibitory synaptic transmission (Creed and Eccles, 1928). After completing his D.Phil. in 1929, he joined Sherrington’s research group, and developed a technical improvement of the torsion myograph (Eccles and Sherrington, 1930a) in preparation for a collaboration concerned with research on the flexion reflex and inhibition (Eccles and Sherrington, 1930b; Eccles and Sherrington, 1931). These experiments were to see the last flowering of Sherrington’s scientific genius at the age of 75. The work on the ipsilateral spinal flexion reflex introduced Eccles to the technique of first stimulating with just a threshold conditioning volley, then at later intervals with a subsequent test volley in order to tease out the time course of the central excitatory and inhibitory states (Eccles and Sherrington, 1930a). This approach, when applied to the mechanism of transmission in the spinal cord, gave a very precise measure of the time course of the central excitatory and inhibitory states, or as we now know, the excitatory and inhibitory post-synaptic potentials. This was shown by Eccles and his colleagues some 20 years later, when they made the first intracellular recordings of post-synaptic potentials in motoneurons (Brock et al., 1952). Subsequent studies of inhibitory synaptic transmission using intracellular electrodes were carried out by Eccles and his colleagues at successively higher levels of the central nervous system. This provided a functional microanatomy of the synaptic connections to be found in the cerebellum (Eccles et al., 1966), thalamus (Eccles, 1969) and hippocampus (Andersen et al., 1963). In this way Eccles completed the research program described by Sherrington in *The Integrative Action of the Nervous System* half a century earlier.

Eccles had entered the field of neuroscience as a result of an inspirational experience he had had at the age of eighteen that changed his life and aroused an intense interest in the mind–brain problem.³⁰ In 1970s, evidently stimulated by the work done by R.W. Sperry and co-workers in 1960s on the results of hemispherectomy, he turned at last to these philosophical questions of his youth, first in *The Self and Its Brain* (1977), a book he wrote together with the philosopher Karl R. Popper, and subsequently, in his Gifford lectures of 1977–1978, published in 1984 as *The Human Mystery*. He opened his Gifford lectures with a handsome tribute to Sherrington’s Gifford lectures 40 years earlier. Eccles remarked that the general theme of *Man on His Nature* had been the defence of a form of dualism—a doctrine that was, by the 1970s, antipathetic to established philosophy. Nevertheless, it was a doctrine that Eccles deeply admired, and, moreover, believed to have been given experimental confirmation by Kornhuber’s work on the electrical potential generated in the cerebral cortex prior to performing an intentional action and by Sperry’s work on split brain patients. Hence, he aimed, in his own Gifford lectures, to defend Sherrington’s conception, to ‘define the

²⁸ Adrian (1966, p. 241).

²⁹ Adrian (1966, p. 246).

³⁰ Eccles (1977, p. 357).

mind–brain problem more starkly’,³¹ and to bring to bear on the problem these most recent findings in neuroscience.

The general framework for Eccles’s reflections was furnished by Popper’s revival of a misconceived idea of the great 19th century mathematical logician Gottlob Frege.³² Frege distinguished between the perceptible ‘outer world’ of physical objects, the private ‘inner world’ of mental entities, and a ‘third realm’ of thoughts (propositions) that are imperceptible by the senses, but nevertheless public and shareable. Popper followed suit, distinguishing between World 1 of physical things, World 2 of mental things and World 3 of thoughts, theorems, theories, and other *abstracta*. The conception is confused, since although we distinguish material objects from mental states, and both from propositions or theorems, these are not ‘worlds’ in any sense whatsoever. Furthermore, neither mental states nor propositions are denizens of a distinct ‘world’. There is only *one* world, which is described by specifying whatever is (contingently) the case. We do indeed talk of people’s mental states of cheerfulness or depression, or of their having toothache. But this does not imply that cheerfulness, depression or toothache are peculiar mental entities that exist in an ‘inner world’. These nominals (‘cheerfulness’, ‘depression’, ‘toothache’) merely provide an indirect way of talking of people *being* cheerful, depressed and of their tooth’s hurting—it introduces no new entities, merely new ways of talking about existing entities (e.g. about people and how things are with them). Similarly, we talk of propositions, theorems and other *abstracta*—but this too only appears to introduce new entities, and is really no more than a convenient way of talking about what is or might be said, asserted, or proven, etc. There is absolutely no need to succumb to Platonism and conjure new entities into existence and new worlds for them to inhabit. All talk of expressions standing for ‘abstract entities’ is a misleading way of saying that expressions that look as if they stand for concrete entities do not do so at all, but rather fulfil quite different functions.

Popper’s three-world doctrine impressed Eccles and he formulated his dualism in terms of it. World 1—the material world of the cosmos, he declared, consists of mere material things and of beings that enjoy mental states. The latter, being a subset of the entities in World 1, he refers to as ‘World 1_M’. It stands in reciprocal causal interaction with World 2 by means of what he terms ‘the liaison brain’ (HM 211).

Research done by Kornhuber and coworkers on changes in electrical potential antecedent to a voluntary movement had revealed that the so-called readiness potential began up to 800 ms before the onset of the muscle action potential, and led to a sharper potential, the pre-motion positivity, beginning at 80–90 ms prior to the movement. The patterns of neuronal discharges eventually project to the appropri-

ate pyramidal cells of the motor cortex and synaptically excite them to discharge, so generating the motor potential (a localised negative wave) just preceding the motor pyramidal cell discharge that initiates the movement. The question on which Kornhuber’s research seemed to throw light was: ‘how can willing of a muscular movement set in train neuronal events that lead to the discharge of pyramidal cells of the motor cortex and so to the activation of the neuronal pathways that lead to the muscle contraction (HM 214). It is striking that Eccles took these discoveries to betoken empirical confirmation of mind–brain interaction of a kind (but in a different location) that had been envisaged by Descartes. He argued as follows:

What is happening in my brain at a time when the willed action is in the process of being carried out? It can be presumed that during the readiness potential there is a developing specificity of the patterned impulse discharges in neurons so that eventually there are activated the pyramidal cells in the correct motor cortical areas for bringing about the required movement. The readiness potential can be regarded as the neuronal counterpart of the voluntary intention. The surprising feature of the readiness potential is its very wide extent and gradual build up. Apparently, at the stage of willing a movement, there is a very wide influence of the self-conscious mind on the pattern of module operation. Eventually, this immense neuronal activity is moulded and directed so that it concentrates onto the pyramidal cells in the proper zones of the motor cortex for carrying out the required movement. The duration of the readiness potential indicates that the sequential activity of the large numbers of modules is involved in the long incubation time required for the self-conscious mind to evoke discharges from the motor pyramidal cells. . . . It is a sign that the action of the self-conscious mind on the brain is not of demanding strength. We may regard it as being more tentative and subtle, and as requiring time to build up patterns of activity that may be modified as they develop (HM 217).

So, Eccles conceived of what he called ‘the dualist-interactionist hypothesis’ (HM 217) as helping to ‘resolve and redefine the problem of accounting for the long duration of the readiness potential that precedes a voluntary action.’

Descartes, as we have noted, conceived of the mind as operating upon the pineal gland to generate the minute fluctuations in the animal spirits (the equivalent of neural transmitters) in the ventricle in which he thought the pineal gland was suspended. This, he held, enabled the acts of will of the mind to affect the motions of the animal spirits, which are then transmitted to the muscles. But the question of *how* an immaterial substance could actually interact causally with a material object such as the pineal gland to produce the appropriate minute motions was left totally unanswered. In much the same way Eccles thought that the ‘self-conscious mind’ interacts causally with the pyramidal cells of the motor cortex, gradually (rather than instantaneously) getting

³¹ See Eccles (1984); subsequent references in the text to this book will be flagged ‘HM’.

³² Frege (1984).

them to discharge. But the question of *how* an immaterial entity such as the mind can interact causally with neurons was left equally unanswered.

Both thinkers erred in conceiving of the mind as an entity of any kind. Had they heeded Aristotle in thinking of the mind not as an entity but as an array of powers or potentialities, they would have been much closer to the truth and would not have become enmeshed in insoluble problems of interaction. For it makes no sense to ask how one's abilities to do the various things one can do interact with one's brain.

Both thinkers erred in imagining that voluntary movements are movements produced or caused by antecedent acts of will.³³ For although there are such things as acts of will, namely, acts performed with great effort to overcome one's reluctance or aversion, or difficulties in acting in adverse circumstances, obviously the vast majority of our ordinary voluntary actions involve no 'act of will' in this sense at all.

The idea that voluntary movement is caused by an antecedent act of willing is confused. If willing were an act, then it itself would have to be voluntary, for were it not voluntary then the movement it allegedly causes would not be voluntary either. But if it is voluntary, then it would have to be preceded by another act of willing to will—which is absurd (since there is no such thing as willing to will) and also launches us on an vicious regress. Moreover, such inner acts of willing are mere fictions. It would be foolish to suppose that, for example, behind each utterance of a sentence (each word of which is voluntarily uttered) lie a multitude of acts of willing to utter each word. We are not aware of any such inner goings-on, nor is it by reference to such hypothesised acts that we determine, either in our own case or in the case of other people, that a certain act was voluntary.³⁴

Eccles was further confused over the object of the alleged act of will, which is variously characterised as (i) a muscular movement, (ii) an action or (iii) a movement of a limb. It is, of course, possible to intend to move, e.g. to flex, a muscle—but that is something we rather rarely intend to do, and although the movement of muscles is involved in all our positive, physical acts (by contrast with acts of omission and mental acts), what we intend, and what we voluntarily perform, are actions (such as raising our arm, writing a letter, saying something, picking up a book, reading a book, and so on) and not the constitutive muscle movements of these actions, of which we are largely unaware. But it is easy to see why a neuroscientist who is attracted to dualism should confuse the objects of the will. For according to the dualist conception, the mind has causally to affect the brain, and the

causal powers of neural events in the brain causally affect muscle contraction.

This raises yet a further insoluble problem for the dualist. The 'self-conscious mind' is supposed to influence the pattern of module operation, gradually molding and directing it so that it concentrates onto the pyramidal cells in the proper zones of the motor cortex for carrying out the intended movement. But how does the 'self-conscious mind' know which pyramidal cells to concentrate on and how does it select the proper zones of the motor cortex? For it would need such knowledge in order to execute such actions. And it is certainly not knowledge of which the self-conscious mind is conscious. To these questions there can be no answers, any more than the 19th century innervationist ideomotor theories of voluntary movement, favoured by such eminent scientists as Helmholtz and Mach (and psychologists such as Bain and Wundt) could answer the question of how the mind, in addition to having images of kinaesthetic sensations that allegedly accompany voluntary movements, directs the currents of energy going from the brain to the appropriate muscles (there must be appropriate feelings of innervation—of 'impulse' or 'volitional energy', they thought, otherwise the mind could never tell which particular current of energy, i.e. the current to this muscle or the current to that one, was the right one to use).

A second piece of empirical research encouraged Eccles in his advocacy of interactionist dualism. Sperry's discoveries concerning the capacities of split-brain patients was striking. He himself took it to vindicate some form of mind–brain interactionism:

Conscious phenomena in this scheme are conceived to interact with and to largely govern the physiochemical and physiological aspects of the brain process. It obviously works the other way round as well, and thus, a mutual interaction is conceived between the physiological and the mental properties. Even so, the present interpretation would tend to restore the mind to its old prestigious position over matter, in the sense that the mental phenomena are seen to transcend the phenomena of physiology and biochemistry.³⁵

It is, therefore, unsurprising that Eccles thought Sperry's work had dramatic implications. 'It is my thesis', he wrote, 'that the philosophical problem of brain and mind has been transformed by these investigations of the functions of the separate dominant and minor hemispheres in the split-brain subjects (HM 222).' The 'most remarkable discovery', Eccles held, was that all the neural activities in the right hemisphere 'are unknown to the speaking subject, who is only in liaison with the neuronal activities in the left (dominant) hemisphere.' To be sure, the right hemisphere is 'a very highly developed brain', but it 'cannot express itself in language, so is not able to disclose any experience of consciousness that we can recognise.' The dominance

³³ This error is still common among neuroscientists, and informs the research of Benjamin Libet and co-workers.

³⁴ It is also worth noting that Eccles wrote of 'voluntary intention' (see the earlier quotation), apparently supposing that intending is an act, which may be voluntary or involuntary. But intending is not an act, and there is no such thing as a voluntary (or involuntary) intention. Moreover, not every voluntary act is intentional (e.g. most of one's hand gestures while talking are voluntary, but not intentional).

³⁵ Quoted by Eccles (1977, p. 374) without a reference.

of the left hemisphere, he argued, is due to its verbal and ideational abilities, and ‘its liaison to self-consciousness (World 2)’ (HM 220). For what Sperry’s work shows, Eccles averred, is ‘that only a specialised zone of the cerebral hemispheres is in liaison with the self-conscious mind. The term liaison brain denotes all those areas of the cerebral cortex that potentially are capable of being in direct liaison with the self-conscious mind.’³⁶

Descartes thought that the pineal gland was the point of contact of the mind and brain, and that the mind apprehends what is before the eyes of the body in virtue of the images that come from the two eyes and are united on the pineal gland. Eccles thought that the liaison brain was the point of contact with the mind, where the nerve impulses from the sense organs are, in some sense, made available to the mind. But there is an interesting difference between the two doctrines. Descartes thought that the pineal gland itself, i.e. a part of the brain, fulfils the task of the Aristotelian and scholastic *sensus communis*, the task of synthesising and unifying the data of the separate senses. In this respect, his thought was more up to date than Eccles’s, since contemporary neuroscientists think likewise that the ‘binding problem’ is solved by the brain (rather than by the mind).³⁷ For Singer’s discoveries of coherent oscillatory firings in disparate parts of the brain concomitant with perceptual experience suggest that the simultaneity of these manifold neuronal activities and their connections to other areas of the cortex are necessary conditions for a perceiver to have the kind of unified perceptual experience we have (Engel et al., 1997). Eccles, by contrast, defended what he called ‘the strong dualist hypothesis’ that:

The self-conscious mind is actively engaged in reading out from the multitude of active modules at the highest levels of the brain, namely in the liaison areas that are largely in the dominant cerebral hemisphere. The self-conscious mind selects from these modules according to attention, and from moment to moment integrates its selection to give unity even to the most transient experience. Furthermore, the self-conscious mind acts upon these modules, modifying the dynamic spatio-temporal patterns of the neuronal events. Thus, the self-conscious mind exercises a superior interpretative and controlling role upon the neuronal events both within the modules and between the modules.

A key component of the hypothesis is that the unity of conscious experience is provided by the self-conscious mind and not by the neuronal machinery of the liaison ar-

reas of the cerebral cortex. Hitherto it has been impossible to develop any neurophysiological theory that explains how a diversity of brain events comes to be synthesised so that there is a unified conscious experience . . . My general hypothesis regards the neuronal machinery as a multiplex of radiating and receiving structures (modules). The experienced unity comes, not from a neurophysiological synthesis, but from the proposed integrating character of the self-conscious mind. I conjecture that in the first place the *raison d’être* of the self-conscious mind is to give this unity of the self in all its conscious experiences and actions (HM 227f).

How does the mind engage in this activity of synthesis (or binding)? Eccles suggested that:

The mind plays through the whole liaison brain in a selective and unifying manner. The analogy is provided by a searchlight. Perhaps a better analogy would be some multiple scanning and probing device that reads out from and selects from the immense and diverse patterns of activity in the cerebral cortex and integrates these selected components, so organising them into the unity of conscious experience . . . Thus, I conjecture that the self-conscious mind is scanning the modular activities in the liaison areas of the cerebral cortex . . . From moment to moment it is selecting modules according to its interests, the phenomena of attention, and is itself integrating from all this diversity to give the unified conscious experience (HM 229).

The metaphors are striking, and have echoes in current neuroscientific theory.³⁸ Nevertheless, Sperry’s discoveries have none of the dramatic implications Eccles imputed to them.

First, the phenomena were misdescribed. It is not just the neural activities of the right hemisphere that are unknown to the subject—all the activities of the brain are unknown to subjects, who do not, after all, perceive their own brains (and even if they could, do not have electron microscopes for eyes). It is true that the right hemisphere cannot express itself in language, any more than the right leg—because

³⁶ Eccles (1977, p. 358).

³⁷ See, for example, Crick (1995, p. 22, p. 232) and Kandel and Wurtz (2000, p. 492, p. 502). Unfortunately their formulation of the binding problem is vitiated by their commitment to the representationalist idea that what the brain has to do is to generate an internal image or representation, rather than to make it possible for the animal to perceive directly the objects in its environment. For a critical discussion of some of the ways in which the binding problem is formulated, see Bennett and Hacker (2001).

³⁸ So, for example, Crick called his theory of attention ‘the searchlight hypothesis’, since, he claimed, the reticular complex and the pulvinar promote only a small proportion of the activity of the thalamus on its way to the cortex, and this activity can be likened to a searchlight that lights up a part of the cortex. Crick suggested that the thalamic reticular complex and the pulvinar interact with the brain stem and with cortical mechanisms to reach a salient decision as to which neuronal groups that are active will be ‘brought into consciousness’ by the spotlight of attention (Crick, 1984). Similarly, the notion of a scanning device or ‘monitor’ in the brain has been invoked by Weiskrantz in connection with his investigations of blind sight. In his view, the awareness a normally sighted person has of whether he sees something in his visual field and of what he sees results from the operation of a neural monitoring system. Conscious experience, according to Weiskrantz, is the product of the monitoring function of the brain (Weiskrantz, 1987). It is interesting that whereas Crick and Weiskrantz apply these metaphors to the brain, Eccles applied them to the mind. Arguably, for different reasons, both conceptions are misguided.

there is no such thing as *a part* of a human being expressing itself in language. It is human beings that express themselves (or fail to express themselves) in language. So the left hemisphere cannot ‘express itself in language’ either. The right hemisphere is not able ‘to disclose any experience of consciousness’ that we can recognise because there is no such thing as a subordinate part of a person being conscious. It is human beings (and other animals) who are conscious (or unconscious), and conscious *of* (or not conscious of) various things.³⁹ The left hemisphere is equally lacking in ‘any experience of consciousness’. Finally, the left hemisphere has no ‘verbal and ideational abilities’, although the verbal and ideational abilities of normal human beings are causally dependent upon the normal functioning of the left hemisphere.

Secondly, the so-called self-conscious mind is not an entity of any kind but a capacity of human beings who have mastered a reflexive language. They can, therefore, ascribe experiences to themselves and reflect on the experiences thus ascribed.⁴⁰ But the ‘self-conscious mind’ is not the sort of thing that can intelligibly be said to be ‘in contact with’ the brain (let alone with something denominated ‘the liaison brain’).

Thirdly, Eccles’s main hypothesis is unintelligible. If the self-conscious mind were, *per impossibile*, ‘actively engaged in reading out’ from areas in the dominant hemisphere, and ‘selecting from these modules according to attention’, then the self-conscious mind would have to perceive or be aware of the neural modules in question (otherwise how could it ‘read them out’?), and know which ones to select for its purpose (otherwise the wrong ones might constantly be selected). Or, to put matters more lucidly, for any of this story to make sense, human beings would have to be aware of the neural structures and operations in question, and, from moment to moment, decide which ones directly to activate, and, of course, have the capacity to do so. But we possess no such knowledge and no such capacity.

Finally, the idea that the *raison d’être* of the ‘self-conscious mind’ is to engender the unity of the self (or, as our contemporaries would put it, ‘solve the binding problem’) is confused. For any talk of a person, or of a being as having a mind, already presupposes the unity of experience and cannot be invoked to explain it.

Eccles’s dualism was misconceived. Contemporary neuroscientists are eager to dissociate themselves from his doctrines and to dismiss his ideas as silly. This is misguided. Eccles had the courage to face difficult problems and to pursue his ideas about them to their logical conclusions. That these are wrong is true, and much can be learnt from the errors in question. It is, however, a sad mark of how lit-

tle many neuroscientists have learnt from Eccles’s struggles that they apparently believe that the problems that Eccles’s interactionist dualism was designed to answer can be solved by substituting the brain for Eccles’s ‘self-conscious mind’. Problems about how the mind can bring about movements of the muscles and limbs by acts of will are not solved by supposing, as Libet does, that it is the brain that decides what muscles and limbs to move. Although it is misguided to suppose that the mind is in liaison with the left hemisphere, it is no less misconceived to suppose, as do Gazzaniga⁴¹ and Crick⁴², that the hemispheres of the brain know things, have beliefs, think and guess, hear and see. For these are functions of human beings and other animals, not of brains or half brains (which enable human beings to exercise those functions). And, as we have noted, although it is confused to suppose the mind to scan the brain, it is equally confused to suppose the brain to scan itself in order to generate awareness or self-consciousness. In short, the lessons that *can* be learnt from Eccles’s failure have largely yet *to be* learnt.

7.4. Wilder Penfield

Wilder Penfield (1891–1976) was born in Spokane, Washington. After graduating from Princeton in 1913, he won a Rhodes Scholarship to Oxford and entered the School of Physiology there to begin his medical studies under the inspiring influence of Sherrington. He followed Sherrington’s interest in histology and in particular neurocytology. After obtaining his BA in physiology at Oxford, he went to the Johns Hopkins Medical School, where he finished his medical degree in 1918. His first research concerned changes in the Golgi apparatus of neurons after axonal section. In 1924, Penfield began to study the healing processes of surgical wounds in the brain. On Sherrington’s advice, he spent some time in Madrid working with Pio del Rio-Hortega, learning to use the histological methods of his brilliant teacher Ramón y Cajal. To this end, surgical specimens of brain scars were collected from patients who had been operated on for post-traumatic epilepsy.

Penfield was aware of the studies on cortical localisation in the primate brain that Sherrington had carried out, and which have been described earlier. In 1928, he went to Breslau to work with Otfried Foerster to learn his method of gentle electrical stimulation of the cortex in epileptic patients while they were under local anaesthesia during the excision of epileptogenic scar tissue. During these procedures he learnt the method of operating under local anaesthesia, using electrical stimulation to identify the sensory and motor cortex to guide the surgical excision. This technique was to be used to singular effect by Penfield in Montreal where, in 1934, he established the famous Montreal Neurological Institute at McGill University, which was devoted to the study and surgical treatment of focal epilepsy. Such stimulation made

³⁹ The misdescriptions of split brain patients’ abilities and their exercise is rife among neuroscientists (including Sperry, Gazzaniga and Crick). That it is misguided and altogether unnecessary is argued in detail in Bennett and Hacker (2002, Chapter 13).

⁴⁰ This controversial claim cannot be defended here, but we shall address it in another forum.

⁴¹ Gazzaniga (1997).

⁴² Crick (1994).

it possible to locate exactly the position of the sensori-motor cortex or of the cortex subserving speech so that these vital areas could be spared during the surgical excision. In some instances, the stimulation might activate the more excitable epileptogenic cortex and reproduce a portion of the patient's habitual seizure pattern. This enable the surgeon to identify the site of the physiologically deranged epileptic focus. Penfield's mastery of these procedures was subsequently summarised in a series of monographs on brain surgery for epilepsy.

Penfield noted in 1938 that stimulation of certain parts of the temporal cortex in patients occasionally excited the vivid recall of previous experiences. It became evident that almost half of the patients afflicted with epilepsy had seizures that could be shown to originate in one or the other temporal lobe. This work on temporal lobe epilepsy led to very important observations in regard to the hippocampus and memory function as well as the localisation of the cortex subserving it. By 1951, Penfield together with Milner, showed that removal of one hippocampus on the medial aspect of the temporal lobe resulted in severe memory disorder in patients who were later found to have damage to the hippocampus on the opposite side. Thus, the bilateral loss of function of the hippocampus led to the complete inability of these patients to remember any post-operative occurrence. This memory loss was not accompanied by any loss of intelligence or of attentive capacity. Penfield's analyses of the electrical stimulation of the cortex of 1132 conscious patients undergoing brain surgery greatly extended our knowledge of functional localisation, especially with regard to memory and to that most human of capacities, speech.

Already in his student days, Penfield had had a 'sense of wonder and a profound curiosity about the mind'. When he turned from the study of the animal to the human brain, his 'planned objective', he later wrote, was 'to come to understand the mechanisms of the human brain and to discover whether, and perhaps how, these mechanisms account for what the mind does.'⁴³ Studying under Sherrington, he came to 'the realisation that the brain was an undiscovered country in which the mystery of the mind of man might some day be explained.' He was, of course, fully aware of Sherrington's views on the relation of mind and brain. In the final paragraph of the foreword to his great book *The Integrative Action of the Nervous System* (1906), Sherrington had remarked 'that our being should consist of two fundamental elements offers, I suppose, no greater inherent improbability than that it should rest on one only.' Penfield, however, took the view that the neuroscientist should endeavour to explain the behaviour of animals, including human behaviour, on the basis of neuronal mechanisms alone. Only if that failed, he thought, should one have recourse to alternative forms of explanation. And throughout his career as a neurosurgeon, he retained this methodological commitment.

Towards the end of a long life dedicated to neurosurgery and neurology, Penfield published a small volume entitled *The Mystery of the Mind* (1975). This was, he wrote, 'the final report of my experience'—an overview of what he had achieved in respect of his youthful objective. 'The nature of the mind', he averred, 'presents the fundamental problem, perhaps the most difficult and most important of all problems' (MM, p. 85). What he wished at last to do, he wrote in the Preface, was to 'consider the evidence as it stands, and ask the question *do brain mechanisms account for the mind?* Can the mind be explained by what is now known about the brain?' (MM, p. 13). Referring explicitly to the above quoted remark of Sherrington's, Penfield judged that 'the time has come to look at his two hypotheses, his two "improbabilities". Either brain action explains the mind, or we must deal with two elements' (MM, p. 4). Despite his methodological commitment, Penfield found himself driven towards a Cartesian view not unlike that of his great teacher. 'For my own part', he wrote, 'after years of striving to explain the mind on the basis of brain-action alone, I have come to the conclusion that it is simpler (and far easier to be logical) if one adopts the hypothesis that our being does consist of two fundamental elements . . . Because it seems to me certain that it will always be quite impossible to explain the mind on the basis of neuronal action within the brain, and because it seems to me that the mind develops and matures independently throughout an individual's life as though it were a continuing element, and because a computer (which the brain is) must be programmed and operated by an agency capable of independent understanding, I am forced to choose the proposition that our being is to be explained on the basis of two fundamental elements. This, to my mind, offers the greatest likelihood of leading us to the final understanding toward which so many stalwart scientists strive' (MM 80). What led him to this conclusion? Two features in particular had impressed Penfield. First, given his specialisation in epilepsy cases, he was unsurprisingly impressed by the phenomena of epileptic automatism. Second, he was powerfully struck by the responses elicited from patients in reaction to electrode stimulation during surgery.

A patient, suffering an epileptic seizure that has induced automatism, will often continue to execute whatever more or less stereotypical tasks he was engaged in. He will, however, be in a fugue condition, i.e. after recovery he will remember nothing of what he had done during the seizure. Penfield interpreted automatism as showing that the epileptic seizure disconnected the mind from what he called, following Hughlings Jackson,⁴⁴ 'the brain's highest mechanism' (a precursor of Eccles's 'liaison brain').

He took it that the brain, during the period of automatism, is controlling the behaviour of a 'human automaton' in accordance with antecedent 'programming' by the mind. Just as the programming of a computer comes 'from without', so too the programming of the brain, which is, Penfield

⁴³ Penfield (1975); subsequent references in the text to this volume will be flagged 'MM'.

⁴⁴ Jackson (1873).

claimed, a biological computer, is effected by the mind via the brain's highest mechanism. Purpose comes to it from outside its own mechanisms. Short-term programming obviously serves a useful purpose, making possible automatic continuation of routine tasks, and this is visibly and strikingly manifest during periods of such epileptic seizures.

That this highest mechanism, most closely related to the mind, is a truly functional unit is proven by the fact that epileptic discharge in gray matter that forms a part of its circuits, interferes with its action selectively. During epileptic interference with the function of this gray matter, ... consciousness vanishes, and with it goes the direction and planning of behaviour. That is to say, the mind goes out of action and comes into action with the normal functioning of this mechanism.

The human automaton, which replaces man when the highest brain-mechanism is inactivated, is a thing without the capacity to make completely new decisions. It is a thing without the capacity to form new memory records and a thing without that indefinable attribute, a sense of humour. The automaton is incapable of thrilling to the beauty of a sunset or of experiencing contentment, happiness, love, compassion. These, like all awarenesses, are functions of the mind. The automaton is a thing that makes use of reflexes and skills, inborn and acquired, that are housed in the computer (MM, p. 47).

Though Penfield ventured no testable hypotheses about how this interaction occurs, he claimed that the highest brain mechanism is, as it were, the mind's executive. It accepts directions from the mind, and passes them on to the various mechanisms of the brain (MM 84). The mind directs the brain in action. It has no memory of its own. But the contents of the stream of consciousness are recorded in the brain (as seems evident from the inadvertent retrieval of long lost memories during cortical stimulation of the brain during operations). So, when the mind needs to retrieve a memory, in a flash it opens the files of remembrance in the brain through the highest-brain mechanism (MM 49).

Reflection on some of the phenomena consequent on cortical stimulation during operations led Penfield to similar conclusions. So, for example, a patient, whose 'speech cortex' was interfered with by an electrode, exhibited exasperation when he could not identify a picture of a butterfly. On withdrawal of the electrode, he said "now I can talk butterfly. I could not *get* the word "butterfly", so I tried to *get* the word "moth"!" It is interesting to see how Penfield construed and explained this temporary impairment of the patient's normal identificatory capacities.

It is clear that while the speech mechanism was temporarily blocked he could perceive the meaning of the picture of a butterfly. He made a conscious effort to "get" the corresponding word. Then, not understanding why he could not do so, he turned back for a second time to the interpretative mechanism ... and found a second concept that

he considered the closest thing to a butterfly.⁴⁵ He must then have presented that to the speech mechanism, only to draw another blank (MM 52).

According to Penfield, concepts are stored away in the mind's concept-mechanism in the brain, from which the mind selects the concept it requires. That concept is then presented in the stream of consciousness, and if the mind approves of the selection, the highest brain mechanism flashes this non-verbal concept to the speech mechanism, which, when functioning normally, will present to the mind the word that is appropriate for the concept (MM 53).

Penfield was equally impressed by the fact that when neural stimulation to the brain caused a hand movement, the patient invariably responded 'I did not do that. You did'. And equally, when cortical stimulation caused vocalisation, the patient said 'I did not make that noise. You pulled it out of me'. It was striking that no form of electrical stimulation to the cortex could induce a patient to believe or to decide (MM 77). It is not surprising that Penfield drew the conclusion that belief and volition are functions of the mind.

A man's mind, Penfield concluded, is the person (MM 61). It is the mind that is aware of what is going on, that reasons and decides, and that understands (MM 75f). The person walks about the world (*sic*), depending always upon his 'private computer' (i.e. his brain), which he programs continuously (MM 61). The highest brain mechanism is the meeting place of mind and brain, the psycho-physical frontier (MM 53). The mind, in making decisions, causes the highest brain mechanism to send neuronal messages to other mechanisms in the brain, and data stored in the brain are admitted to consciousness. How is interaction effected? Here, Penfield speculated that there must be a second form of energy (other than the electrical energy that is used by the highest brain function to innervate the nervous system) which is available to the mind. This, he conjectured, must be made available to the mind in its waking hours by the highest brain mechanism.

The mind vanishes when the highest brain mechanism ceases to function due to injury or due to epileptic interference or anaesthetic drug. More than that, the mind vanishes during deep sleep. What happens when the mind vanishes? There are two obvious answers to that question; they arise from Sherrington's two alternatives—whether man's being is to be explained on the basis of one or two elements (MM 81).

Penfield thought it preposterous to suppose that the mind is merely a function of the brain, and so ceases to exist when it 'vanishes' in sleep or epileptic automatism and is recreated afresh each time the highest brain mechanism functions normally. Rather, he concluded, the mind is 'a basic element', and has a 'continuing existence'. 'One must assume', he wrote (MM 81), that although the mind is silent, when it

⁴⁵ Penfield obviously meant that it was the closest thing to the concept of a butterfly.

no longer has its special connection to the brain, it exists in the silent intervals and takes over control when the highest brain mechanism goes into action.' So, the highest brain mechanism switches off the power that energises the mind whenever one goes to sleep, and switches it on again when one awakens.

Is the explanation improbable, Penfield queried. It is not so improbable, to my mind, as is the alternative expectation (explanation)—that the highest brain mechanism should itself understand, and reason, and direct voluntary action, and decide where attention should be turned and what the computer must learn and record, and reveal on demand (MM 82).

Penfield's neo-Cartesianism is no advance over that of Sherrington and Eccles. But if we are to learn anything from his errors, we must not simply dismiss them as misguided and move on to other matters. That will merely ensure that we learn nothing from his endeavours. We must ask what went wrong, what drove one of the greatest neurosurgeons and neurologists of all times to embrace such a misconceived view of the mind and brain?

It should be noted that there are at least two fundamental unquestioned presuppositions that Penfield shares with Sherrington and Eccles. The first is a Cartesian conception of the mind. Like Descartes, Penfield conceives of the mind as an independent substance (or, as he puts it, 'a fundamental element' that has 'continuing existence'). Like Descartes, he identifies the person with the mind, rather than with the living human being. Like Descartes, he takes the mind to be the bearer of psychological attributes,⁴⁶ and consequently conceives of human beings as subjects of psychological predicates only derivatively. And like Descartes, he takes the mind to be a causal agent that can bring about changes in the body by its actions.

The second presupposition is that the question which so deeply disturbs him, namely, whether brain mechanisms account for the mind, whether the mind can be explained by reference to what is known about the brain, is an empirical question. Like Sherrington, Penfield conceives of the matter as a choice between two different empirical hypotheses. Either we can explain everything the mind does, e.g. thinks and believes, reasons and concludes, has wants, forms intentions and purposes, and decides to act, by reference to neural states and events, or we must conceive of the mind as an independent substance in immediate causal interaction with the brain and, hence, with the body. The choice between these two hypotheses is to be determined by the evidence that supports them severally and by their relative explanatory powers.

Both presuppositions are misconceived. The mind, as we have already intimated, is not a substance of any kind. Talk

of the mind is merely a *façon de parler* for talk about human powers and their exercise. We say of a creature (primarily of a human being) that it *has a mind* if it has a certain range of active and passive powers of intellect and will—in particular conceptual powers of a language-user that make self-awareness and self-reflection possible. The idioms that involve the noun 'mind' have as their focal points thought, memory and will. And they are all readily paraphrasable into psychological expressions in which the word does not occur. So, for example, to hold, keep or bear something in mind is to retain it in memory; to call or bring something to mind is to recollect it; and for something to be, go or pass out of mind is for it to be forgotten. To speak one's mind or to let someone know one's mind is to tell him what one thinks or opines; to turn one's mind to something is to be thinking of or to be preoccupied with it; and to be of one mind with another is to agree in judgement. To be minded or to have it in mind to do something is to intend to do it; to have half a mind to do something is to be inclined or tempted to do it; to be in two minds whether to do something is to be undecided; to make up one's mind is to decide and to change one's mind is to reverse one's decision or judgement.⁴⁷

A person is not identical with his mind. A mind is something (but not some *thing*) a person is said to *have*, not to *be*. In having a mind, an animal (that is thereby also a person, and a bearer of rights and duties) has a distinctive range of capacities. And it is obvious both that an animal cannot be identical with an array of capacities, and that if a human being loses enough of those distinctive capacities, he can cease to be a person (and exist only in a 'vegetative state'). It is not the mind that is the subject of psychological attributes, any more than it is the brain. It is the living human being—the whole animal, not one of its parts or a subset of its powers. It is not my mind that makes up its mind or decides; it is not my mind that calls something to mind and recollects; and it is not my mind that turns its mind to something or other and thinks—it is I, *this* person. Hence, too, the mind is not a causal agent that brings about changes in the body and its limbs by its actions. On the contrary, it is human beings that deliberate, decide and act, not their minds.

Consequently, Penfield's second presupposition is misguided. Whether we can 'account for the mind' in terms of the brain alone, or must account for the (supposed) activities of the mind (e.g. thought, reasoning, wants and purposes, intentions and decisions, voluntary and intentional action) by reference to the mind itself, conceived of as an independent substance and, therefore, causal agent is not a matter of choice between two empirical hypotheses. If these were empirical hypotheses, then either could in principle be true, i.e. both would present intelligible possibilities, and it would be a matter of empirical investigation to discover which is actually the case. But that is not how it is at all.

⁴⁶ Indeed, to explain what the mind or spirit is, Penfield quotes Webster's Dictionary: 'the element . . . in an individual that feels, perceives, thinks, wills and especially reasons' (MM 11).

⁴⁷ For a more detailed investigation of this point, see [Bennett and Hacker \(2001\)](#).

First, it is not the mind that thinks and reasons, wants things and has purposes, forms intentions and makes decisions, acts voluntarily or intentionally. It is the human being. We do indeed characterise a person as having a clear, rigorous or decisive mind. But these are merely ways of characterising the person's *dispositions* in respect of thought and will. If we want to understand why a normal person reasoned the way he did, thought what he did, has the goals and purposes that he has, and why he decided as he did, formed such-and-such intentions and plans, and acted intentionally, no neurological account will clarify for us what we wish to be clarified. To this extent Penfield was right. Where he was wrong was in the supposition that what we need is an explanation in terms of the activities of the person's mind—where the latter is conceived of as an agent with causal powers. Rather, what we want is an explanation in terms of the person's reasoning, hence too by reference to what he knew or believed, and, in the case of practical reasoning, by reference to his goals and purposes. And if our explanation renders his reasoning intelligible, no further information about neural events in his brain can add anything. All a neural explanation could do would be to explain how it was *possible* for the person to reason cogently at all (i.e. what neural formations must be in place to endow a human being with such-and-such intellectual and volitional capacities), but it cannot rehearse the reasoning, let alone explain its cogency.

Similarly, if we are puzzled by a person's actions, if we wish to know why A signed a cheque for £200, no answer in terms of brain functions is likely to satisfy us. We want to know whether A was discharging a debt, making a purchase, donating money to charity, or betting on a horse—and once we know which of these is in question, we may also want to know what A's reasons were. A description of neural events in A's brain could not possibly explain to us what we want to have explained. If we wish to know why A caught the 8.15 a.m. to Paris, a description of neural events cannot in principle satisfy our need for an explanation. But the answer that he had a committee meeting there at 2.00 p.m. that was to decide upon such-and-such a project for which A is responsible may give quietus to our curiosity. If A has murdered B, we may wish to know why. We may be given a reason, and still remain dissatisfied, wishing to understand more—but what more we wish to understand is most probably A's motive, not what neural events occurred at the time of the killing. We want to know whether he killed B out of revenge or out of jealousy, for example, and that requires a quite different narrative from anything neuroscientific investigation could produce. Explanation of action by redescription, by citing agential reasons, or by specifying the agent's motives (and there are other forms of explanation of related kinds) are not replaceable, even in principle, by explanations in terms of neural events in the brain. This is not an empirical matter at all, but a logical one. The type of explanation is categorially different, and explanations in terms of agential reasons and motives, goals and purposes, are not reducible to explanations of muscular contractions

produced as a consequence of neural events. But equally, such explanations are not couched in terms of the activities of the mind, conceived as an independent substance with causal powers of its own. In this sense, Penfield's dilemma is a bogus one. He was perfectly right to think that one cannot account for human behaviour and experience in terms of the brain alone—but wrong to suppose that the idea that one might be able to do so is an intelligible empirical hypothesis as opposed to a conceptual confusion. He was also wrong to suppose that the alternative is accounting for human behaviour and experience in terms of the causal agency of the mind, and wrong again in thinking that that too is an empirical hypothesis. There is no need whatsoever to impale oneself on either of the horns of Penfield's dilemma.

Once these presuppositions are jettisoned, it becomes easier to see that the explanation of human behaviour in terms of the interaction of the mind (conceived as an independent substance) and the brain is misconceived. It is not a false empirical hypothesis, but a conceptual confusion. For in as much as the mind is not a substance, indeed not an entity of any kind, it is not *logically possible* for the mind to function as a causal agent that brings about changes by acting on the brain. That is not an empirical discovery, but a conceptual clarification. But it is equally mistaken to suppose that substituting the brain for the Cartesian mind is any the less confused. That too is not an empirical hypothesis, but a conceptual muddle, which likewise stands in need of conceptual clarification.

Consequently, Penfield was mistaken to think that what so impressed him, namely the phenomena of epileptic automatism and the various facts that characterise electrode stimulation of the brain, constitute empirical support for a dualist hypothesis.

Epileptic automatism does not show that the mind has become disconnected from the 'highest brain mechanism' to which it is normally connected, and by which it is supplied with energy of an as yet unknown form.⁴⁸ What it shows is that during an epileptic seizure, as a consequence of the abnormal excitation of parts of the cortex, the person is temporarily deprived of some of his normal capacities (including memory, the ability to make decisions, emotional sensitivity, and a sense of humour), while other capacities, in particular capacities for routine actions, are retained. The phenomena are indeed striking, but they amount to a dissociation of capacities that are normally associated, not to a disconnection of substances that are normally connected. They do not show that the brain is a computer or that the mind is its programmer. The brain is no more a computer than it is a central

⁴⁸ It is striking to compare Penfield's conception on this matter with Descartes's remarkable simile in his *Treatise on Man*: 'when a *rational soul* is present in this machine (namely the body) it will have its principal seat in the brain, and reside there like the fountain keeper who must be stationed at the tanks to which the fountain's pipes return if he wants to produce, or prevent, or change their movements in some way . . . ' (AT XI, 131). Here, the tank is the ventricle in which the pineal gland is allegedly suspended, the pipes are the nerves, and the water the animal spirits.

telephone exchange (the previously favoured analogy), and the mind is no more a computer programmer than it is a telephonist. It is perfectly true that the capacity to continue routine tasks unreflectively is useful (and the expression ‘short term programming’ is an apt *metaphor* here). It is also true that the purposes pursued by a person are not the purposes of the person’s brain. But it does not follow that they are the purposes of the person’s mind. They are the purposes of the person—and they are to be understood in terms of facts about human life, social forms of life, antecedent events, current circumstances, agential beliefs and values, and so forth, not in terms of neural events and mechanisms. But it is, of course, true that but for the normal functioning of the brain, a human being would not have and would not be able to pursue the normal kinds of purposes that we do pursue.

The various phenomena that characterise electrode stimulation of the brain are similarly misconstrued by Penfield. The case of interference with the ‘speech cortex’ does not show that there is any such thing as a ‘concept mechanism’ in the brain that stores non-verbal concepts that can be selected by the mind and then presented to the speech mechanism to be matched to the word that represents the concept. That is picturesque mythology, not an empirical theory. Words are not names of concepts, and do not stand for concepts, but rather express them. Concepts are abstractions from the use of words. The concept of a cat is what is common to the use of ‘cat’, ‘chat’, ‘Katze’, etc. The common features of the use of these words is not something that can be stored in the brain or anywhere else independently of a word (or symbol) that expresses the concept. The patient whom Penfield describes could not think of the word ‘butterfly’ with which to identify the object in the picture presented to him. He knew that the object belongs to a class which resembles a different class of insects (viz. moths), and tried, equally unsuccessfully to think of the word for members of the second class. This temporary incapacity is incorrectly described as knowing the concept but being unable to remember the word for it. The supposition that the mind might be presented with non-verbal concepts from which to choose presupposes that there is some way of identifying non-verbal concepts and distinguishing one from the other independently of any words or symbols that express them. But that makes no sense.

It is certainly interesting that Penfield found that electrode stimulation could not induce either belief or decision. But this does not show that believing and deciding are actions of the mind, any more than it shows that they are not actions of the brain. It is true that they are not actions of the brain—but that is not an empirical fact that might be shown to be so by an experiment. Rather, there is no such thing as the brain’s believing or deciding (any more than there is such a thing as checkmate in draughts). But it is also true that they are not actions of the mind either. My mind does not believe or disbelieve anything—I do (although, to be sure, that is no action). Nor does it decide—it is human beings that decide and act on their decisions, not minds.

Penfield objected vehemently to the suggestion that the mind is a function of the brain, and supposed that if it were, then the mind would cease to exist during sleep or epileptic automatism. The suggestion is unclear, but one may surely say that the distinctive capacities of intellect and will of a creature that has a mind are a function of the creature’s brain (and of other factors too). It does not follow (as Penfield evidently feared it would) that the behaviour and experience of such a creature in the circumstances of life is explicable in neural terms. But nor does it follow that the mind ceases to exist during sleep or epileptic seizure—any more than one’s knowledge and beliefs, intentions and projects cease to exist when one is asleep. Penfield was rightly impressed by the fact that ‘the mind develops and matures independently throughout an individual’s life as though it were a continuing element.’ But he was misled by his unquestioned assumption that the mind is a kind of agent. Had he thought of the mind in more Aristotelian terms as a set of powers or capacities he would have been closer to the truth and less prone to conceptual illusion. For the continuous possession of capacities is not interrupted by sleep or by epileptic automatism, even though the agent cannot exercise some of his normal capacities during the seizure. And the developing unity of a person’s mind is not the development of a substance distinct from the human being himself, but rather the emergence of a determinate character and personality, an intellect with certain distinctive characteristics and a will with a coherent array of preferences—all of which are traits *of the person*.

Penfield thought that a form of Cartesian dualism is more probably correct than what he conceived to be the alternative, namely, ascribing understanding, reasoning, volition and voluntary action, as well as decision to the brain itself. It is very striking and important that the strategy that Penfield conceived to be altogether improbable is precisely the route that is currently adopted by the third generation of neuroscientists, who ascribe psychological functions to the brain. Penfield thought that this route is *improbable*. It is not improbable, it is impossible, i.e. it is logically incoherent to ascribe psychological attributes and conscious functions to the brain. But Penfield was wrong to suppose that the only alternative to this strategy is dualism.

8. Conclusion: in the shadow of Descartes

All of Sherrington’s contemporaries and students who struggled to understand the function of the cortex within the Cartesian paradigm have passed away. The following generation of neuroscientists (such as Blakemore, Crick, Damasio, Edelman, Libet, Young and Zeki) adamantly repudiate Cartesian dualism. They tend to conceive of themselves as liberated from the Cartesian legacy in virtue of substituting the integrative action of the brain for the immaterial Cartesian soul or mind. In this way, they take themselves to be free from the errors of Sherrington and his

pupils in much the same way as Sherrington himself freed neuroscience from the idea of a spinal soul. However, appearances here are deceptive. We should like to suggest that Descartes's influence continues to be deep and pervasive and that he still casts a long shadow across contemporary cognitive neuroscience. More than four centuries after Descartes's birth, neuroscientists still labour under one form or another of his world picture, even while claiming to reject it.

Contemporary neuroscientists rightly reject the Cartesian conception of the mind as an immaterial thinking substance that stands in reciprocal causal relations to the brain. What Descartes had tried to explain in terms of interaction between an immaterial mind and a material body, contemporary neuroscientists try to explain in terms of interaction of the brain and body. This amounts to substitution of grey glutinous matter for an immaterial thinking substance. But this, by itself, does not free cognitive neuroscience from the shadow of Descartes. All it does is replace Cartesian mind/body dualism by a brain/body dualism that is isomorphic with it. Merely allocating to the brain the functions that Cartesian thought allocated to the mind leaves intact the fundamental logical structure of the Cartesian conception human nature.

To be sure, in suggesting that current neuroscience involves a form of brain/body dualism, we are fully aware of the fact that the brain is no less a material entity than is the body. The duality in question is not a duality of distinct kinds of substance. What we have in mind is different.

First Descartes attributed psychological attributes *to the mind* current neuroscientists attribute psychological attributes *to the brain*. In order to explain a human being's psychological attributes (such as perception, memory and volition), Descartes thought that it is actually the mind that perceives, thinks, feels passions and wills, and that when we ascribe such attributes to human beings, we do so derivatively. Similarly, contemporary neuroscientists think that it is the brain (or the hemispheres of the brain) that sees and hears, thinks, knows and remembers, feels emotions and makes decisions, and that the ascription of such psychological attributes to human beings is derivative.

Secondly, Descartes appealed to the psychological attributes of the mind in order to explain the behaviour of human beings. Current neuroscientists who think that the integrative action of the brain explains sensation, perception, memory and voluntary movement appeal to the alleged psychological attributes of the brain to explain the behaviour and experience of the human being.

For example, Crick explains visual experience by reference to the brain's beliefs, guesses and interpretations (Crick, 1995, p. 30, p. 32f, p. 157). Edelman attributes to the brain the ability to manipulate rules, form concepts and categorise its own activities (Edelman, 1994, p. 109, p. 130). Blakemore holds that the brain knows things, reasons inductively, constructs hypotheses on the basis of arguments. Young held that the brain poses questions and constructs hypotheses (Blakemore, 1977, p. 91). Attributes that Descartes ascribed to the mind, current neuroscientists ascribe to the

brain (Bennett, 1997). Just as Descartes explained voluntary action, on the one hand, and perception on the other, in terms of the causal interaction of the thinking mind and the body, mediated by the pineal gland, current neuroscientists explain the same phenomena in terms of the causal interaction of the thinking (hypothesising, categorising, reasoning) brain and body.

The Cartesian error that is perpetuated by current neuroscientists is the mistake of ascribing to part of a creature attributes which can logically be ascribed only to the creature as a whole. We have dubbed this 'The Mereological Fallacy' in neuroscience (mereology being the logic of part/whole relations) (Bennett and Hacker, 2001). It is a Cartesian error to suppose that it is the mind that feels pain, perceives, thinks and reasons, remembers and wills to act. For it is not the mind that feels a headache or a toothache, but the person whose head or tooth aches (the mind has neither head nor teeth). It is not the mind that sees (it has no eyes) or hears (it has no ears) but the living human being. And it is not the mind that thinks, reasons, remembers and forms intentions but the person.

It is equally mistaken to suppose that the brain knows (as Blakemore⁴⁹ supposes), believes (as Crick suggests), constructs hypotheses (as J.Z. Young⁵⁰ held), makes subtle classifications, comparisons, and logical decisions (as Richard Gregory⁵¹ claims). These are attributes of *human beings* (and, in respect of some of these attributes, of other animals)—not of their minds or of their brains. It is not the brain that is conscious or unconscious, but the person whose brain it is. It is not the brain that knows, believes or guesses things, but the knowledgeable, credulous, conjecturing *human being*. Human endeavour can be explained by reference to the thoughts, hopes, fears and desires of the person, but not by reference to the psychological attributes of his brain, since the brain has, and can have, no psychological attributes.

The extent to which contemporary cognitive neuroscience is still entrapped in the Cartesian web is evident not only from the fact that the mereological fallacy is rife and from the widespread appeal, in neuroscientific explanation to the alleged psychological attributes of the brain. It is also evident in the current mystification of consciousness. It was Descartes who redrew the boundaries of the mind in reaction against the Aristotelian conception and who, in so doing, redefined the mental in terms of consciousness. It is altogether unsurprising that contemporary neuroscience should find the idea of consciousness a profound mystery, and that eminent neuroscientists should concentrate so much of their theoretical efforts to explaining it. For within the current framework of thought, consciousness cannot but be mysterious—an apparently epiphenomenal accompaniment of the honest workings of the material (but thoughtful) brain. It can only

⁴⁹ Blakemore (1977).

⁵⁰ Young (1978).

⁵¹ Gregory (1973).

cease to seem mysterious if one breaks much more radically with the Cartesian paradigm than current neuroscientists have done (Bennett and Hacker, 2001).

References

- Ackrill, 1979. Aristotle's definition of psuche. In: Barnes, et al. (Eds.), *Articles on Aristotle: Psychology and Aesthetics*, Vol. 4. Duckworth, London, pp. 65–75.
- Adrian, E.D., 1966. Consciousness. In: Eccles, J.C. (Ed.), *Brain and Conscious Experience*. Springer, Berlin, pp. 240–246.
- Andersen, P., Eccles, J.C., L  yning, Y., 1963. Recurrent inhibition in the hippocampus with identification of the inhibitory cell and its synapses. *Nature* 198, 540–542.
- Beck, A., 1890. Die bestimmung der localisation der Gehirn- und Ruchensmarken funktionen vermittelt der elektrischen Erscheinungen. *Centralbl. Physiol.* 4, 473–476.
- Beevor, C.E., Horsley, V., 1887. A minute analysis (experimental) of the various movements produced by stimulating in the monkey different regions of the cortical centre for the upper limb, as defined by Professor Ferrier. *Philos. Trans. R. Soc. Lond.* 178, 153–167.
- Beevor, C.E., Horsley, V.A., 1890. A record of the results obtained by electrical excitation of the so-called motor cortex and internal capsule in an orang-outang (*Simia satyrus*). *Philos. Trans. R. Soc. Lond.* 181, 129–158.
- Beevor, C.E., Horsley, V., 1894. A further minute analysis by electrical stimulation of the so-called motor regions (facial area) of the cortex cerebri in the monkey, *Macacus sinicus*. *Philos. Trans. R. Soc. Lond.* 185, 39–81.
- Bell, C., 1811. Idea of a New Anatomy of the Brain, submitted for the observations of his friends. Strahan & Preston, London, privately circulated. Reprinted 1936 in *Medical Classics*, Vol. 1. pp. 105–120 and preceded by quotations from some of his letters. Reprinted in *Sir Charles Bell, His Life and Times* by Gordon-Taylor, G., Walls, E.W., 1958. Livingstone, Edinburgh, pp. 218–231.
- Bell, C., 1821. On the nerves giving an account of some experiments on their structure and functions, which lead to a new arrangement of the system. *Philos. Trans. R. Soc. Lond.* 111, 398–424.
- Bell, C., 1834. On the functions of some parts of the brain, and on the relations between the brain and nerves of motion and sensation, and on the relations between the brain and nerves of motion and sensation. *Philos. Trans. R. Soc. Lond.* 124, 471–483.
- Bell, C., 1835. Continuation of the paper on the relations between the nerves of motion and of sensation, and the brain; more particularly on the structure of the medulla oblongata and the spinal marrow. *Philos. Trans. R. Soc. Lond.* 125, 255–262.
- Bennett, M.R., 1997. *The Idea of Consciousness*. Harwood Academic Publishers, Sydney.
- Bennett, M.R., 1999. The early history of the synapse: from Plato to Sherrington. *Brain Res. Bull.* 50, 95–118.
- Bennett, M.R., Hacker, P.M.S., 2001. Perception and memory in neuroscience: a conceptual analysis. *Prog. Neurobiol.* 65 (6), 499–543.
- Bennett, M.R., Hacker, P.M.S., 2002. *Philosophical Foundations of Neuroscience*. Blackwell Publishers, Oxford, in press.
- Benton, A.L., Joynt, R., 1960. Early descriptions of aphasia (Antonio Guainero's *Opera Medica*, 1481). *Arch. Neurol.* 3, 205–222.
- Bernard, C., 1858. *Leçons sur la Physiologie et la Pathologie du Système Nerveux*. Bailli  re, Paris.
- Blakemore, C., 1977. *Mechanisms of the Mind*. Cambridge University Press, Cambridge, p. 91.
- Broca, P., 1861. Remarques sur le si  ge de la facult   du langage articul  , suivies d'une observation d'aph  mie (perte de la parole). *Bulletins de la Soci  t   Anatomique* (Paris), Vol. 6. pp. 330–357, pp. 398–407; translated as 'remarks on the seat of the faculty of articulate language, followed by an observation of aphemia'. In: von Bonin, G. (Ed.), 1960. *Papers Presented on the Cerebral Cortex*. Charles C. Thomas, Springfield, IL, pp. 49–72.
- Brock, L.G., Coombs, J.S., Eccles, J.C., 1952. The recording of potentials from motoneurons with an intracellular electrode. *J. Physiol.* 117, 431–460.
- Caton, R., 1875. The electrical currents of the brain. *Br. Med. J.* 2, 278.
- Caton, R., 1877. Interim report on investigation of the electric currents of the brain. *Br. Med. J.* 1 (Suppl. L), 62–65.
- Caton, R., 1887. Researches on electrical phenomena of cerebral grey matter. In: *Proceedings of the Transactions of the Ninth International Medical Congress*, Vol. 3. pp. 246–249.
- Creed, R.S., Eccles, J.C., 1928. The incidence of central inhibition on restricted fields of motor units. *J. Physiol.* 66, 109–120.
- Creed, R.S., Sherrington, C.S., 1926. Observations on concurrent contraction of flexor muscles in the flexion reflex. *Proc. R. Soc. Lond. B* 100, 258–267.
- Crick, F., 1984. Function of the thalamic reticular complex: the searchlight hypothesis. *Proc. Natl. Acad. Sci. U.S.A.* 81, 4586–4590.
- Crick, F., 1994. *The Astonishing Hypothesis*. Simon and Schuster, London, p. 170.
- Crick, F., 1995. *The Astonishing Hypothesis*. Touchstone, London.
- Damasio, A., 1999. *The Feeling of What Happens*. Heinemann, London, p. 320.
- Eccles, J.C., 1969. *The Inhibitory Pathways of the Central Nervous System*. The Sherrington Lectures IX, Liverpool University Press, Liverpool.
- Eccles, J.C., 1977. In: Popper, K.R., Eccles, J.C. (Eds.), *The Self and Its Brain*. Springer, Berlin, pp. 357–374.
- Eccles, J.C., 1984. *The Human Mystery*. Routledge, London, p. 3.
- Eccles, J.C., Gibson, W.C., 1979. *Sherrington—His Life and Thought*. Springer, Berlin.
- Eccles, J.C., Sherrington, C.S., 1930a. Improved bearing for the torsion myograph. *J. Physiol. Lond.* 69, Pi.
- Eccles, J.C., Sherrington, C.S., 1930b. Reflex summation in the ipsilateral spinal flexion reflex. *J. Physiol.* 69, 1–28.
- Eccles, J.C., Sherrington, C.S., 1931. Studies on the flexor reflex. VI. Inhibition. *Proc. R. Soc. Lond. B* 109, 91–113.
- Eccles, J.C., Llin  s, R., Sasaki, K., 1966. The inhibitory interneurons within the cerebellar cortex. *Exp. Brain Res.* 1, 1–16.
- Engel, A.K., Roelfsma, P.R., Fries, P., Brecht, M., Singer, W., 1997. Role of the temporal domain for response selection and perceptual binding. *Cerebral Cortex* 7, 571–582.
- Everson, S., 1995. Psychology. In: Barnes, J. (Ed.), *The Cambridge Companion to Aristotle*, Cambridge University Press, Cambridge, pp. 168–194.
- Fernel, J., 1542. *De Naturali Parte M  dicine*. Simon de Colines, Paris.
- Ferrier, D., 1873/1874. The localization of function in the brain. *Proc. R. Soc. Lond.* 22, 228–232.
- Ferrier, D., 1876a. Croonian lecture: experiments on the brain of monkeys (second series). *Philos. Trans. R. Soc. Lond.* 165, 433–488.
- Ferrier, D., 1876b. *The Function of the Brain*. Smith Elder and Company, London.
- Frege, G., 1984. The thought. In: *Collected Papers on Mathematics, Logic and Philosophy*. Blackwell Science, Oxford, pp. 351–372.
- Flourens, M.-J.-P., 1823. *Recherches Exp  rimentales sur les Propri  t  s et les Fonctions du Syst  me Nerveux dans les Animaux Vert  br  s*. J.B. Bailli  re, Paris.
- Fritsch, G., Hitzig, E., 1870.   ber die elektrische Erregbarkeit des Grosshirns. *Arch. Anat. Physiol. Wiss. Med. Leipzig* 37, 300–332; see translation on the electrical excitability of the cerebrum. In: von Bonin, G. (Ed.), 1960. *Papers Presented on the Cerebral Cortex*. Charles C. Thomas, Springfield, IL, pp. 73–96.
- Furley, D., 1999. Aristotle the philosopher of nature. In: Furley, D. (Ed.), *From Aristotle to Augustine: History of Philosophy*, Vol. IV. Routledge, London, p. 16.
- Galen, C., 1821a. Commentaries on Hippocrates Book on Nourishment III. 1 Kuhn (1821–1833), Vol. XV. p. 257.

- Galen, C., 1821b. The Differentiation of Symptoms. 3 Kuhn (1821–1833), Vol. VII. pp. 55–56.
- Galen, C., 1854a. The Movement of Muscles I. Daremberg (1854–1856), Vol. II. p. 323.
- Galen, C., 1854b. The Sites of Diseases III. 14 Daremberg (1854–1856), Vol. II. p. 579.
- Galen, C., 1854c. Use of Parts IX. 14 Daremberg (1854–1856), Vol. I. pp. 597–598.
- Galen, C., 1854d. Use of Parts VIII. 6 Daremberg (1854–1856), Vol. I. pp. 541–543.
- Galen, C., 1859. The Sites of Diseases IV. 3 Daremberg (1854–1856), Vol. II. p. 590.
- Galen, C., 1962. On anatomical procedures IX. In: Lyons, M.C., Towers, B. (Eds.), *Galen on Anatomical Procedures* (Duckworth, W.H.L., trans.). Cambridge University Press, Cambridge, pp. 13–14.
- Galen, 1968. *De usu partium* (May, M.T., trans.). On the Usefulness of the Parts of the Body. Cornell University Press, Ithaca, NY, pp. 341–342.
- Galvani, L., 1791. *De viribus electricitatis in motu musculari commentarius*. De Bononiensi Scientiarum et Atrium Instituto atque Academia commentarii, Vol. 7, pp. 363–418 (for trans. see Foley, M.G., 1954. Galvani: Effects of Electricity on Muscular Motion. Burndy Library, Norwalk).
- Gazzaniga, M.S., 1997. *The New Cognitive Neurosciences*. MIT Press, Cambridge, p. 1393.
- Goltz, F.L., 1869. Beiträge zur Lehre den Funktionen der Nervenzentren des Frosches'. Hirschwald, Berlin.
- Goltz, F.L., 1892. Der Hund ohne Grosshirn. Siebente Abhandlung über die Verrichtungen des Grosshirn. (The dog without a brain. Seventh treatise on the functions of the brain). *Arch. Ges. Physiol.* 51, 570–614.
- Gregory, R.L., 1973. The confounded eye. In: Gregory, R.L., Gombrich, E.H. (Eds.), *Illusion in Nature and Art*. Duckworth, London, p. 50.
- Grunbaum, A.S.F., Sherrington, C.S., 1902. Observations on the physiology of the cerebral cortex of some of the higher apes (preliminary communication). *Proc. R. Soc. Lond.* 69, 206–209.
- Hall, M., 1832. These motions independent of sensation and volition. In: Alexander Walker (Ed.), *Proceedings of the Committee of Science, Zoological Society on Documents and Dates of Modern Discoveries in the Nervous System, 1839*. Facsimile Reprint 1973. Scarecrow Reprint Corp., Metuchen, NJ.
- Hall, M., 1837a. *Memoirs on the Nervous System*. J.B. Ballière, London.
- Hall, M., 1837b. On the True Spinal Marrow, and on the Excito–Motor System of the Nerves. Lectures given before the Royal Society, private printing.
- Hall, M., 1843. *New Memoir on the Nervous System*. J.B. Ballière, London.
- Hall, M., 1850. Synopsis of the Diastaltic Nervous System or the System of the Spinal Marrow and Its Reflex Arcs, As the Nervous Agent in All the Functions of Ingestion and of Egestion in the Animal Economy. Croonian Lectures, Mallett, London.
- Jackson, J.H., 1863. Convulsive spasms of the right hand and arm preceding epileptic seizures. *Med. Times Gazette* 2, 110–111.
- Jackson, J.H., 1873. On the anatomical, physiological and pathological investigations of epilepsies. *West Riding Lunatic Asylum Med. Rep.* 3, 315–319.
- Kandel, E., Wurtz, R., 2000. Constructing the visual image. In: Kandel, E., Schwartz, J.H., Jessell, J.M. (Eds.), *Principles of Neural Science*, McGraw-Hill, New York, pp. 492–502.
- Kenny, A.J.P., 1993. *Aquinas on Mind*. Routledge, London.
- Langley, J.N., 1883. Report on the parts destroyed on the right side of the brain of the dog operated on by Professor Goltz. *J. Physiol.* 4, 286–309.
- Langley, J.N., Sherrington, C.S., 1884. Secondary degeneration of nerve tracts following removal of the cortex of the cerebrum in the dog. *J. Physiol.* 5, 49–65.
- Liddell, E.G.T., Sherrington, C.S., 1924. Reflexes in response to stretch (myotatic reflexes). *Proc. R. Soc. Lond. B* 96, 212–242.
- Liddell, E.G.T., Sherrington, C.S., 1925. Further observations on myotatic reflexes. *Proc. R. Soc. Lond. B* 97, 267–283.
- Magendie, F., 1822. Expériences sur les Fonctions des Racines des Nerfs Rachidiens'. *J. Physiol. expér. path.*, Paris No. III, 2 August 1822, pp. 276–279. In: Craneffeld, P. (Ed.), *Documents and Dates of Modern Discoveries in the Nervous System, 1839* (Alexander Walker, Eng. trans.). Facsimile Edition 1973, Scarecrow Reprint Corp., Metuchen, NJ, pp. 87–91.
- Mistichelli, D., 1709. *Trattato dell'Apoplessia*. Roma; A de Rossi alla Piazza di Ceri (C.D. O'Malley, trans.; How do we know this?). In: Clarke, E., O'Malley, C.D., 1968. *The Human Brain and Spinal Cord*. University of California Press, Berkeley, CA, pp. 282–283.
- Muller, J., 1833. These motions sometimes sensitive and always involuntary; partial return to the doctrine of Whytt. In: Alexander Walker (Ed.), *From the Manual of Physiology in Documents and Dates of Modern Discoveries in the Nervous System, 1839*. pp. 153–154.
- Craneffeld, P. (Ed.), Facsimile Edition 1973. Scarecrow Reprint Corp., Metuchen, NJ.
- Nemesius, 1955. *The Nature of Man* (Telfer, W. (Ed.), trans.; Cyril of Jerusalem and Nemesius of Emesa) Westminster Press, Philadelphia.
- Pavlov, 1907. *Untitled Nobel Oration*. In: *Les prix. Nobel en 1904*. Norstedt & Söner, Stockholm.
- Pavlov, I., 1928. *Lectures on Conditioned Reflexes* (Gantt, W.H., Eng. trans.). International Publications, New York.
- Penfield, W., 1975. *The Mystery of the Mind: A Critical Study of Consciousness and the Human Brain*. Princeton University Press, Princeton, p. 1.
- Penfield, W., Rasmussen, T., 1968. *Cerebral Cortex of Man: Clinical Study of Localization and Function*. Hafner, New York.
- Pfluger, E.F.W., 1853. *Die sensorischen Functionen des Rückenmarks der Wirbelthiere nebst einer neuen Lehre über die Leitungsgesetze der Reflexionen*. Berlin, Hirschwald (The Sensory Functions of the Spinal Cord of Vertebrates, Together with a New Theory of the Laws of Transmission of Reflexes).
- Pourfour du Petit, F., 1727. Mémoire dans lequel il est démontré que les nerfs intercostaux fournissent des rameaux qui portent des esprits dans les yeux. *Mémoires de Mathématique et de Physiologie. Histoire de l'Académie Royale des Sciences*, pp. 1–19.
- Procháska, J., 1784. *De functionibus systemis nervosi, et observationes anatomico-pathologicae*. In: Gerle, W. (Ed.), *Adnotationum Academicarum*, Prague (Laycock, T., Eng. trans.; A Dissertation on the Functions of the Nervous System). In: Unzer and Procháska on the Nervous System. Sydenham Society, London, 1851.
- Rahman, F., 1952. *Avicenna's Psychology* (Eng. Trans.; Kitab al-Najab, Book III). Oxford University Press, London (Chapter VI).
- Sechenov, I.M., 1863. In: Gibbons, G. (Eds.), *Reflexes of the Brain* (Belsky, S., trans.; from Russian). MIT Press, Cambridge, MA.
- Sechenov, I.M., 1863. *Reflexes of the Brain* (Subkov, A.A., Eng. Trans.; *Medizinsky Vestnik. Sechenov's Selected Works*). State Publication House, Leningrad, Moscow, 1935.
- Sherrington, C.S. 1900. *Schafer's Textbook of Physiology*, Vol. II.
- Sherrington, C.S., 1903. Qualitative difference of spinal reflex corresponding with qualitative difference of cutaneous stimulus. *J. Physiol.* XXX, 39–46.
- Sherrington, C.S., 1905a. On reciprocal innervation of antagonistic muscles: seventh note. *Proc. R. Soc. Lond. B* LXXVI, 160–163.
- Sherrington, C.S., 1905b. On reciprocal innervation of antagonistic muscles: eighth note. *Proc. R. Soc. Lond. B* 76, 269–297.
- Sherrington, C.S., 1892. Notes on the arrangement of some motor fibres in the lumbo-sacral plexus. *J. Physiol.* XIII, 621–772.
- Sherrington, C.S., 1910. Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing. *J. Physiol.* XL, 28–121.
- Sherrington, C.S., 1947. *The Integrative Action of the Nervous System*. Cambridge University Press, Cambridge.
- Sherrington, C.S., 1951. *Man on His Nature*, 2nd Edition. Cambridge University Press, Cambridge.
- Singer, C.J., 1952. *Vesalius on the Human Brain*. Oxford University Press, London.

- Stuart, A., 1739. Lecture III of the Croonian lectures. *Proc. R. Soc. Lond.* 40, 36–48.
- Vesalius, 1543. *De humani corporis fabrica* (Basel, 1543, Bk. VII, Chi.). p. 623.
- Vesalius, A., 1542. On the Workings of the Human Body. *De Humani Corporis Fabrica*. J. Oporini, Basilaee.
- von Bonin, G., 1960. In: *Papers presented on the Cerebral Cortex*. Charles C. Thomas, Springfield, IL.
- Vulpian, A., 1866. *Lecons sur la physiologie générale et comparée du système nerveux. faites au Musée d'Histoire Naturelle*. J.B. Ballière, Paris.
- Weiskrantz, L., 1980. Varieties of residual experience. *Quart. J. Exp. Psychol.* 32, 365–386.
- Weiskrantz, L. 1986. *Blind sight: A Case Study and Implications*. Oxford University Press, Oxford.
- Weiskrantz, L., 1987. Neuropsychology and the nature of consciousness. In: Blakemore, C., Greenfield, S. (Eds.), *Mindwaves*. Blackwell Science, Oxford, pp. 307–320.
- Whytt, R., 1751. Documents relative to the spinal marrow, etc. Sensation the cause of a conservative motion in the whole or in the separated parts of animals—involuntary motion. The centre of this being the brain or spinal marrow. From An Essay on the Vital and other Involuntary Motions of Animals, Works, Edition 1768. p. 152, p. 162, p. 203. In: Alexander Walker (Ed.), *Documents and Dates of Modern Discoveries in the Nervous System*, 1839. pp. 112–122. Facsimile Edition 1973, Scarecrow Reprint Corp., Metuchen, NJ.
- Willis, T., 1664. In: Feindel, W. (Ed.), *The Anatomy of the Brain and Nerves* (trans. *Cerebri anatome*). Tercentenary Facsimile Edition, Vol. II. McGill University Press, Montreal, 1965.
- Willis, T., 1672. *De anima brutorum* (Eng. trans.; Two discourses concerning the soul of brutes, which is that of the vital and sensitive of man). Facsimile of Translation (Pordage, S., 1683). *Scholars' Facsimiles & Reprints*, Gainesville, FL, 1971.
- Willis, T., 1683. *Cerebri anatome cui accessit nervorum descriptio et usus* (Pordage, S., Eng. trans.; illustrated by Sir Christopher Wren. Flesher, London, 1964 (Chapter X)). Dring, Harper and Leigh, London.
- Young, J.Z., 1978. *Programs of the Brain*. Oxford University Press, Oxford, p. 119.