ON THOMAS WILLIS'S CONCEPTS OF NEUROPHYSIOLOGY

[Part I]

by

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I. INTRODUCTION

IN previous papers we have dealt with problems of priority in relation to the circle of Willis* and the cranial nerves.[1, 2] We now turn to Willis's neurophysiological concepts and his endeavours to localize nervous and mental functions.

Willis dealt with these problems not only in *Cerebri Anatome* (1664), but also in later works, particularly *De Morbis Convulsivis* (1667) and *De Anima Brutorum* (1672). It is essential to draw from all his work, since his views were modified or amplified in his later publications. Of *De Anima* the second (pathological) discourse has been widely acknowledged (its importance has been extolled by Calmeil[4] and Vinchon and Vie[5]), but the first part has—on the whole—attracted less attention. This may be because neither on the neurophysiological nor on the psychological level did Willis make any major new contribution. The anatomical description of the brain seldom goes beyond that in *Cerebri Anatome*. Chapter 3, which contains valuable descriptions of the comparative anatomy of the oyster, lobster and earthworm,[6] was written primarily in order to explain the respiration of animals living in water or buried in earth. Thomas Hobbes, Locke, Berkeley, Hume and David Hartley were the chief architects of empirical psychology in England: none appears to have been appreciably influenced by Willis's writings, with the exception of Berkeley who, in *Siris*,[7] only referred to Willis's notion of the kindling of the blood when he discussed the remedial properties of tar water. Charleton, in *The Different Wits of Men*,[8] gives a more readable and more interesting account of the psychological (and some psychopathological) aspects. Charleton's concept of the 'ample' and 'narrow' mind foreshadowed Kretschmer's 'cyclothymic' and 'schizoid' temperaments: in the copy of this book in the British Museum, there is a slip saying that it has been consulted by Locke.

Nevertheless, the first discourse of *De Anima* is noteworthy because here Willis attempted to correlate anatomical and physiological data with what was known of psychological function: thus, it might be regarded as a precursor of the many physiological psychologies published later, a distinction which is usually reserved for David Hartley's *Observations on Man*.[9]

Chapters 1 and 2 of the first discourse of *De Anima* are of special interest to our present analysis, as they contain a historical review and provide the background of Willis's views on nervous function. As Cranefield[10] pointed out, the word 'Psychologie' (as it appears at the end of the

* We take this opportunity of admitting a regrettable (and wholly inexplicable) error when we stated[1] that Willis omitted the posterior cerebral artery in his circle. We are indebted to Professor W. Feindel[3] for drawing our attention to this mistake which fortunately has no bearing on our main argument.

second chapter) is used here for the first time in the English language in Pordage's translation. The Greek word (*ψυχολογία*) was, of course, familiar in Latin texts.

Comparing Willis's Latin texts with Pordage's *Practice of Physick* (1684), we have decided not to use the latter's translation without modifications. Although it has an 'old world charm',[10] the meaning is not always clear and—because of exaggerated anglicization of technical terms—much of the elegance and neatness of Willis's original Latin style is lost. We shall, therefore, refer to both the Latin text, choosing the *Opera Omnia* of 1676, and to *Practice of Physick*.

The following abbreviations will be used for frequently recurring references: C.A.=Cerebri Anatome; A.B.=Anatomy of Brain; M.C.=De Morbis Convulsivis; C.D.=Convulsive Diseases; D.A.=De Anima Brutorum; S.B.=Soul of Brutes.

II. GENERAL CONCEPT OF NERVOUS FUNCTION

Like Descartes, Willis believed that man has an immortal and an immaterial soul, but in addition he has also a corporeal soul which he shares with other animals. This corporeal soul is twofold: a flame which is enkindled in the blood, and a sensitive soul in the brain, represented by animal spirits which he compared with light, air or wind. These, he believed, are distilled from the blood in the cerebral and cerebellar cortex, and thence carried through the white matter, the brain stem and through the nerves into all organs, muscles and fibrous membranes. This concept Willis maintained through all his works; in *Cerebri Anatome* he described the procreation and diffusion of the animal spirits (for example, C.A. 50–1, A.B. 73 *et seq.*, C.A. 54, A.B. 78/9, C.A. 93–5, A.B. 103/4) where, adopting Descartes' analogy, he compares their continuous flow with 'the chest of an organ which receives the wind to be blown into all pipes'. These pipes are the nerves, but he has convinced himself that the 'white, smooth and round nerves' are not hollow like the veins and arteries; their structure is impervious to any pointed instrument; even with the help of a spectacle or the microscope no cavity can be seen, but they are 'furnished throughout with pores and passages like an Indian cane' (C.A. 95, A.B. 104). In other places, however, he compares the reservoirs of animal spirits in the muscles and membranes with watery bogs and lakes (C.A. 93/4, A.B. 103). The animal spirits move in a 'watery latex'. Without such a humor the spirits could not exist within the nervous system. This 'watery latex', he believes, is also of nutritive value (C.A. 100 *et seq.*, A.B. 108 *et seq.*). In this way he explains the muscular wasting paralysis, although the blood supply to the muscle is unimpaired.

The same nerves (and muscles) serve both motor and sensory function. It fell to Swammerdam[11] to write soon after Willis (though published only in 1737) that 'We very clearly find also by experiments, that the motion produced in the muscle by irritating the nerve . . . goes continually descending. The nerves designed for the senses . . . doubtless tend upwards. . . .' Galen also believed that different nerves served motor and sensory function, the former being harder than the latter. From the periphery, Willis considered that sense impressions were carried centrally, then collected and perceived in the sensorium commune, or, beyond this, elaborated into higher function, such as imagination, will

(appetite) and memory. From the common sensory, or indirectly, from higher stations, motor impulses return by the same pathways to the muscles, except for involuntary impulses which he thought originated in the cerebellum.

Willis pointed out that the existence of animal spirits, although sometimes 'palpable' (D.A. 34, S.B. 23), could only be proved by their effects. The animal spirits are the 'hypostasis' of the corporeal soul. 'In things to be known, the corporeal soul obeys the rational soul which presides over imagination; but not in things to be done, the corporeal soul inclining to the flesh.' He attempted to explain (though this 'seems very hard to be unfolded', D.A. 48, S.B. 32) how animals may perceive, discriminate between objects, have appetite, memory and other kinds of inferior reasons, without 'calling an immaterial soul into play'. Inborn instinct may play some part, but he had no doubt that brutes learn by experience through the same mechanisms which operate in man. 'A dog being struck by a staff, or by the flinging of a stone, perceives the hurt received by the senses, and easily retains the idea in his memory, but the instinct dictates to him that the like stroke may be shunned afterwards . . .' (D.A. 55, S.B. 38). Anatomy also suggested to Willis the similarity of these corporeal functions in man and in various species of animals for, 'We have noted little or no difference in the brain of either, as to the shape and exterior conformation of the parts, the size only excepted' (D.A. 65, S.B. 44). Willis, however, here forgot that in *Cerebri Anatome* he had indeed noted some differences, for example, with regard to the convolutional pattern (C.A. 50, A.B. 75/76) and to the quantitative relationship between cerebral cortical and white matter (C.A. 50/51, A.B. 76).

In chapters 8 and 9, the *passions* are discussed. He enumerated eleven, a number which approximated to that of Gassendi,[12] who described twelve. Descartes[13] and Hobbes[14] both proposed a larger number, though Descartes believed they could be reduced to six primary passions. Willis added little to the descriptions given by his predecessors except to introduce his own, anatomically more precise, interpretation of the 'commerces between the brain and praecordia' (D.A. 67, S.B. 45).

The rest of the first discourse of *De Anima*—apart from the final chapter on sleep—deals with the anatomical, physiological and psychological aspects of the higher senses of which he recognizes five, viz. touch or feeling, taste, smell, hearing, and sight. This section, in particular, conforms to the pattern of an early tract on 'physiological psychology'. What Willis said of the eye—'Many authors, both Physiceans and Mathematiceans, have already laboured so exactly that hardly anything can be added . . . it may be lawful for us to subjoin here our description of the eye, not taken from the writings of others, but by our own ocular inspection and observation . . .' (D.A. 116, S.B. 78)—applies also to the other senses. There are many details which are worthy of attention. Thus, in the chapter on *touch* or *feeling* we find his description of the reflex response to pain, proverbially known as 'where the pain is, there the finger will be' (D.A. 91, S.B. 91). He believed in differential receptors for different kinds of sensation; 'the sensitive soul using corporeal organs has many sensories fitted for much variety of objects, and divers representations of things; . . . both the conformation of the pores, as also the disposition of the animal spirits, are proportioned to the little bodies, sent in from the object, which are only of one kind, fitly to be received' (D.A. 84, S.B. 57). However, he added '. . . yet it is not to be thought that these fibres . . . are of a different kind of formation; for neither are there some fibres, by which heat or others by which cold, or others different from either, by which other tangible things are perceived; but the same fibres are everywhere alike and receive and distinctly carry the approaches of every object. . . . The reason of the difference is, because the fibres, though of the same nature and frame, enter into divers ways of contractions or wrinklings, from the various strokes of sensible things' (D.A. 90, S.B. 61). Similar views of the *unspecifity* of nerve fibres have been expressed by modern authors, for example Henry Head, Lorente de Nò and Le Roy Conel.

Smell Willis regarded as superior to *taste*, while to sight he gave the 'most noble' place. He observed that loss of smell may be accompanied by that of taste and that sweet substances tend to impair or pervert taste. Of the anatomy of the tongue, he does not mention its innervation by a branch (our glossopharyngeal) of the vagal nerve; only the trigeminal and the hypoglossal nerves are described. He omitted also the branch, in the petrosal canal, from the facial (and

vagal) nerves, our chorda tympani, which he had previously described (C.A. 117, A.B. 117) —though after Fallopius. Nor did he quote Malpighi's[15] description of the papillae of the tongue which was probably the outstanding contribution to the anatomy and physiology of taste at that time, confirmed by Bellini in a monograph the same year.[16] The chemical aspects in Willis's chapters on taste and smell are inferior to the clear and concise account by Boyle a few years later.[17] Although Fulton's[18] remark that Boyle's two tracts were the first on taste and smell in the history of physiological literature, is perhaps not quite correct, they were very successful, as testified by numerous reprints and translations into French and Italian.

The chapter on *Hearing* contains the famous description of paracusis (to which Willis's name has since been given (D.A. 108, S.B. 73)); it has its counterpart in the descriptions of toxic optic hyperacuity (D.A. 126, S.B. 86), found in a 'Man, indued with a hot brain, who after plentiful drinking of wine, was able to read distinctly in a very dark night. . . .' We also find a report of an 'Experiment made in a dog, in which after perforation of both drums, hearing remained unimpaired for a time, but wholly ceased after three months, after the sensory organ had succumbed to the superficial injury' (D.A. 107/8, S.B. 72). This experiment and its interpretation was severely criticized by Schelhammer,[19] certainly unjustly so, since Willis drew only very qualified conclusions from it: 'It is seen, that the drum is the preliminary, and as it were preparatory instrument of hearing, which receiving the first impression of the sound . . . directs it . . . towards the sensory organ, which is placed more inward: it performs a similar function with regard to hearing, as the coats of the eye, forming the pupil in respect of the sight. . . .' This analogy aroused Schelhammer's particular criticism (though in this instance also not quite justified).

It has been said that Willis's general concepts of nervous function were, to a large extent, derivations of Cartesian modifications of Galen.[20, 21, 22] There is no doubt that Willis was influenced by Descartes, as he himself repeatedly acknowledged. Descartes was the first modern philosopher to introduce a mechanistic interpretation of bodily function: the impact of his teaching upon all concerned with problems of biology and medicine was almost universal and few escaped from it entirely. There is, however, a difference between influence and total dependence. Even Foster had to make the important qualification that Willis's hypotheses, though derived from Descartes, were modified by more exact anatomical knowledge and occasionally by sound physiological deductions in which 'we may probably trace the influence of Lower and other of Willis's contemporaries. . . .'

Moreover, those who have emphasized Willis's dependence on Descartes have overlooked the even greater stimulus he received from Descartes' contemporary, Pierre Gassendi. It is the merit of Soury[23] to have drawn attention to Gassendi's influence, which has also been traced by Canguilhem,[24] Keele[25] and Cranefield.[10] In Willis's time Gassendi's reputation was almost equal to that of Descartes. His writings, however, were soon eclipsed by the greater lucidity and power of exposition of Descartes, Hobbes and Locke; otherwise Gassendi would have deserved a more lasting recognition.[26] His outstanding philosophical merit is the rediscovery of Epicurus who developed the atomistic philosophy of Democritus into a naturalistic concept with distinct positivist tendencies. The first Epicurean echo in Britain was heard in 1654, in Charleton's *Physiologica Epicuro-Gassendo-Charltonia*,[27] which contains, however, little of concrete interest to our problem. Boyle is often stated to have built his 'corpuscular' theory on the model of Epicurus. He was certainly acquainted with the ideas of Gassendi, although he also counted Bacon, Descartes and Helmont among those who

influenced him.[28] Gassendi is now believed to have anticipated Locke in the rejection of innate ideas.[29] A Catholic priest, he combined his Epicurean views with an impeccable formal acceptance of the dogmas of the Catholic Church. Some have discovered cynicism in this attitude, but it should be remembered that even the 'materialist' Hobbes was not an atheist, and medical men like Boyle and Sydenham combined a largely naturalistic outlook with devotion to Christianity.

The foregoing digression was necessary in order to understand better the fascination which Gassendi exerted on Willis throughout his working life. Gassendi professed to be the first French disciple of Francis Bacon, but he did not accept Harvey's discovery of the circulation of the blood. He had practical experience in anatomy and his knowledge of the brain was not shadowy, as was that of Descartes. While, in Descartes' view, the main function of the animal spirits takes place in the ventricles (in which the peripheral nerves terminate and where he wrongly located the pineal gland, the 'seat' of the immaterial soul), Gassendi[12] transferred this function to the substance of the brain. He also explained why Aristotle was wrong to ascribe perception to the heart. The following are translated quotations on these points:

'. . . Furthermore, that the common faculty of perception is rather in the brain than in the heart, is proved by the fact that the nerves originate in the brain, and not, indeed, in the heart. We have shown above that in this respect Aristotle was mistaken. The sensory faculty given to passing nerves is lost completely when they are themselves ligated, obstructed, burnt, cooled, severed, in that part to which the nerve goes and is distributed' (*op. cit.*, vol. II, p. 334).

Earlier (*op. cit.*, vol. II, p. 218), after describing the 'systole' and 'diastole' of the brain, and the motion caused by it, Gassendi had pointed out: 'Why should we not suspect that the ventricles are rather receptacles for the excretions of the brain than destined to elaborate the spirits? For what reasons could the animal spirits not be elaborated in the brain substance itself, and, particularly in the white and callous (callosa) matter around and near the sinus? Vital blood and the spirits flow in from all sides, through various branches of the cervical or carotid arteries, from which also arise those incorporated in the choroid plexus. . . . It does not seem plausible that such a mass (of brain substance) had been made only for the sake of dilatation and compression of the ventricles, but quite obviously has been made in order to give a new quality to the vital spirits and provide for their elaboration, after they have been received into the substance of the brain. To this task and duty could the motion of the brain, which is under consideration, be attributed . . .' (*op. cit.*, vol. II, pp. 326–7).

'In this respect, one has to assume that the animal spirits are created in that part of the brain from which the nerves take their origin, as they are soon seen to set forth throughout the softer substance as nerve fibres or channels and to develop into nerves filling the whole white matter and being distributed in all directions . . . I already said why a nerve or a fibre cannot be touched without exerting a certain pressure; nor can it be compressed without stimulating the spirit contained in it . . . nor can the spirit be stimulated without that it drives or repels the neighbouring one, also derived from the brain. . . . Nor can this one be repelled without influencing the whole series for the sake of continuity and repletion, and the emerging spirit jumps back* towards the very origin of the nerve and nerve fibre in the brain, with the result that the sensory faculty resident in the brain is put into operation, and the given fact is perceived, apprehended and recognized. . . . Indeed, one has to assume that the nerves are built

* '. . . neque spiritus illeic sia urgeri, quin pellat, seu potius repellat vicinum instantem, ac pari ratione advenientem ex cerebro; neque iste porrò *repelli*, quin tota serie ob repletionem continuitatemque compulsa, spiritus exsistens ad ipsam originem nervi nervulique in cerebrum quasi *resiliat* ideò facultatem sentiendi residentem in cerebro hoc quasi resultu moveri, factumque attactum percipere, apprehendere seu cognoscere ac sentire . . .' (Gassendi, *op. cit.*, vol. II, p. 335; present writers' italics).

in such a way that they are covered by a double meninge, but interiorly they do not exhibit any appreciable cavity, but only a softer and, as is believed, a medullary substance derived from the brain. . . . As Galen has said, the nerve is nothing else but a small and somewhat harp brain; nor is the brain anything else but a very large and very soft nerve . . .' (*op. cit.*, vol. II, p. 335).

Gassendi's notion of sense perception being brought about by a 'jumping back' of the spirits has obviously influenced Willis, who uses the same word 'resilire'* repeatedly. Similar expressions occur in other places (e.g. in D.A. 53, S.B. 36). He also spoke of 'vestigia', again adopting an identical expression ('vestigia seu plicae') of Gassendi's (*op. cit.*, vol. II, p. 409). Willis also owes the inspiration of his much discussed and criticized *explosion theory* to Gassendi. This theory by which he tried to explain muscular contraction as well as convulsions had first been proposed by Willis in 1664. Since this hypothesis apparently had a mixed reception, Willis returned to it in the first chapter of his treatise on convulsive disease (1667) in a somewhat defensive mood, saying

'In the meantime that this opinion may not be thought altogether new, and that I have exposed it as a child of my own brain . . . I will show you the assertion of the famous Gassendus, which openly favours our hypothesis, and in some sort gave an occasion of it' (M.C. 4, C.D. 3). [And he quotes from Gassendi] 'but indeed the same fiery nature of the soul serves within the body, by its own mobility, in about the same way as a little flame of gunpowder does in a cannon. . . .'

Gassendi's concept of the *corporeal soul* exerted perhaps an even greater influence on Willis, who acknowledged this on many occasions:

'Peter Gassendus, skilful and truth-seeking Man, in his recent Experimental Philosophy, when he had enumerated very many instances, by which the cunning and wonderful sagacity of brute animals were declared . . . adds that these things could not deservedly be attributed to them, unless one granted them a certain kind of reason. . . . As commonly a two-fold memory, namely a sensitive and intellective, is distinguished, so nothing forbids to call reason sensitive and intellectual. . . . There is nothing more easily observed than that brutes do collect one thing out of another, or what is the same thing, do reckon or recount, and therefore are indued with reason' (D.A. 6, S.B. 4).

Willis's concept of the corporeal soul has often been criticized as a retrograde animistic step—in contrast to Descartes' animal spirits which were thought to be entirely physical and part of a machine. There is, however, another aspect to the matter: for Descartes the behaviour of animals was entirely mechanical; only man had an immaterial soul. Gassendi's and Willis's concept—seen from this angle—was much nearer to biological reality, and it appears to be a step in the direction where—much later—modern evolutionism was to arise.

Willis was not the first to place the origin of animal spirits into the cerebral and cerebellar cortex. As Grünthal[30] has shown, he was preceded by Sylvius (de Le Boe), who, in 1663, in the fourth book (already previously published in 1660) of his *Disputationes Medicae*,[31] briefly but quite clearly made that point. In §§29 and 30 of this book, he described how the spirits are distilled from the blood in the cortex, whence they are carried through the medullary substance

* 'impressio priorum, viz. *sensuum*, ratio formalis consistit in spirituum *retractione*, seu versus fontes suos *reflexu*. Ubicunque enim objecti sensibilis impressio radiosae huic contexturae infertur, statim aut tota compages, aut illius portio quaedam . . . *nutare*, ac *retroacta*, veluti *resilire*, in se et recedere cogitur' (C.A. 54; present writers' italics).

and the nerves to all parts of the body. They are, he added later (§36), responsible for the function of external and internal (imagination, reasoning power, judgement and memory) senses, for the interplay of emotions between the brain and the rest of the body, and for muscular contraction. In book 12 he returns to the animal spirits and their behaviour in health and disease. Although he was, like Willis, an iatrochemist, his interpretation of the function of the animal spirits was sober and restrained and far removed from the fanciful and often grossly anthropomorphic descriptions Willis was apt to give.

The concept of the *succus nutritivus* was much discussed and criticized during Willis's lifetime and immediately afterwards. Critics usually attacked Willis as the chief exponent of the hypothesis, although he himself referred to previous authors, without, however, giving names. There is no doubt that Glisson[32] not only accepted the nutritious qualities of the nervous juice, but also gave the same reason, viz. that atrophy of the muscle after a lesion of the nerve occurs without any impediment to the blood supply. Glisson upheld the *succus nutritivus* despite the fact that the nerves have no visible canals and no liquor appears on the surface of a dissected nerve. Among others who, preceding Willis, also spoke of the nutritious properties of nerve juice, we find Charleton[33] and Deusing.[34*]

III. CEREBRAL LOCALIZATION OF NERVOUS AND MENTAL FUNCTION

Willis connected the corpus striatum, his *sensus communis*, with sensory perception and motor control, the corpus callosum with imagination, cerebral cortex with memory, and the middle of the brain (probably meaning the basal ganglia and the corpora quadrigemina) with instinctual behaviour. The corpus striatum was concerned only with voluntary motion; involuntary movement was controlled by the cerebellum.

These views on localization of function were frequently developed by Willis, both in *Cerebri Anatome* and *De Anima*.

'As often as a sensible impression, such as a visual stimulus, arrives from the periphery it turns inwards like an undulation of water and is transferred to the corpora striata where the sensation received from outside becomes a perception or internal sense. If, however, this impression is carried further and penetrates the corpus callosum, imagination takes the place of sensation. If after this the same undulation of the spirits strikes against the cortex, as it were the outermost banks, it imprints there a picture or character of the object which, when it is later reflected from there revives the memory of the same thing'† (C.A. 54/55, A.B. 79).

Garrison[35] who, on the whole, is a just judge of Willis, says of his attempts at localization that he was 'giving free rein to his fancy' and employed 'faulty reasoning due in part to the clumsiness of (his) experimental technique and his ignorance of the actual anatomy of his laboratory animals. . . .' This criticism overlooks the important fact that such an attempt was made at all by Willis.

It is intriguing to analyse how far Willis was guided by pure speculation, and how much by observation or by plausible argument. The corpus striatum as the common sensory was

* Malpighi[15] mentioned also among early protagonists of the *succus nutritivus* the names of Fortius and Bachius, but, so far, we have been unable to trace these references.

† Willis gave a similar description in D.A. 36/37, S.B. 24/25. Here he compares the corpus striatum to an objective and dioptric glass and the corpus callosum to a whitened wall. Foster quoted this latter version, although he did not adopt Pordage's translation.

suggested to him because 'no other similarly striated part was found in the whole encephalon' (C.A. 62, A.B. 83). He saw also that these bodies were located between the cerebrum and its appendix (viz. medulla) and that ascending and descending pathways run through them facilitating interchange of function. The smelling and optic nerves, he believed, terminated in the corpus striatum and thalamus respectively. The cerebral cortex as the seat of the creation of animal spirits was suggested to him by its rich vascularity, in contrast to the white matter: it was also their resting place and the store house of engrams giving rise to memory. He had observed that 'these folds and convolutions are more numerous and larger in man than in any other animal, without doubt because of various and multiple activities of the higher faculties; and they vary in an uncertain and somewhat arbitrary manner, just as the activities of animal function are free and changeable, and not made only for one purpose. In quadrupeds they are fewer and in some, like the cat, are found of uncertain figuration and arrangement, the reason why this animal hardly thinks anything else or remembers except what instinct and necessity suggest. In the smaller quadrupeds and also in birds and fishes the cerebral surface is plane and even, and lacks gyri and sulci altogether; the reason why animals of this kind comprehend fewer things and only those of one kind. . . .' However, the white matter is of even greater comparative significance: it is the 'emporium' and he had observed that 'animals which excel in memory, imagination and volition, are supplied with a larger cerebral white matter, as can be seen in man and the more perfect quadrupeds: and animals which seem to have lesser use of these faculties, such as the smaller quadrupeds, birds and fishes, have a larger cortex and only a minimal white matter' (C.A. 50/51, A.B. 75/76).

While the cerebral cortex shows wide-ranging variety, the cerebellar cortex, he found, was of unvarying uniformity in the brains of animals and humans; this was one reason why he suggested for it the control of involuntary movement. Other reasons included the observation —in human pathology and in animal experiments—that lesions in the posterior regions of the brain almost invariably proved fatal, with signs of cardiac and respiratory disturbance; and furthermore his assumption that the intercostal and vagal nerves took their origin from the cerebellum. It should be remembered that at that time pons and medulla were regarded as part of the cerebellum.

However plausible these localizations were at the time of Thomas Willis, it was to be expected that they would be superseded by later discoveries. Some were entirely arbitrary as, for example, the connection of the cerebral cortex with sleep—an assumption difficult to reconcile with memory, which he also allocated to the cortex.* There remain, however, two of these localizations which have proved of *lasting* value: one, the association of *voluntary* motor action and of sensation with the region of the *corpus striatum*; the other of *autonomic function* with the *cerebellum*.

Corpus striatum. We give here only a brief account of Willis's contribution in this field, as a fuller description will be published elsewhere.[41] Although Willis did not discover the corpus striatum—Vesalius[42] had already provided an accurate illustration of it (in Fig. 7, Book 7)—he gave the first detailed description in *Cerebri Anatome*. He found that 'If these bodies are longitudinally

* The crucial point is that, for the first time, important mental function (in addition to the procreation of the spirits) was allocated to the cerebral cortex. During the seventeenth and eighteenth centuries, emphasis on cortical function was not maintained. Pourfour du Petit[36] made a hesitant attempt at connecting the parietal cortex with motor function. In 1740, Swedenborg emphasized the importance of cortical function, adopting Malpighian ideas.[37] This publication was of little influence, and Swedenborg's major work remained in manuscript until resuscitated by Tafel.[38] In this, Swedenborg expressed surprisingly mature thoughts on cortical and other brain function; he also acknowledged his debt to previous workers, including Willis. At the beginning of the nineteenth century, Gall and Spurzheim's short-lived, but historically important, cortical phrenology aroused much interest (and controversy), but it was not until Hughlings Jackson and Fritsch and Hitzig's experimental research that modern investigation of cortical function began in earnest.[39, 40]

dissected, they appear to be marked by medullary and shiny striae. . . . And it is worth mentioning that in the whole of the encephalon no other part is encountered which is similarly striated' (C.A. 62, A.B. 83). He also noted that, near the two roots of the fornix 'a transverse medullary tract, resembling a larger nerve, extends from one striate body to the other, and, so to speak, unites these and effects their mutual communication' (C.A. 63, A.B. 84). This is, without doubt, the *anterior commissure*, which he also illustrated in Fig. 7 of *Cerebri Anatome*. In this, Willis was not quite without predecessors. Eustachius[43] (though published only in 1714) had illustrated a transversal structure joining together the anterior pillars of the fornix (Table 17, Fig. 6); and Riolan[44] mentioned in a similar position, a 'funiculus transversalis', resembling the optic nerve in calibre and colour. Willis was the first to describe clearly the bundle as uniting the corpora striata, i.e. as a cerebral commissure. Subsequently, it was observed by Malpighi[15] and by Vieussens[45] who, acknowledging Willis's previous work on the third ventricle, introduced the term 'commissure' for it.

Although Willis's part in the discovery of the anterior commissure was recognized by Ridley,[46] Mangetus,[47] Santorini,[48] Charles Bell[49] and Burdach,[50] it is not mentioned in the comprehensive historical works of Portal[51] and Haller.[52] Nor have we—so far—been able to trace a reference to it in the usual modern texts of the history of anatomy and medicine.

Willis also made an interesting *comparative* observation in the brains of birds, in which he found that the corpus striatum—instead of being confined to the anterior end of the medulla—extended throughout the hemisphere, whereas the corpus callosum was situated 'near the thalami where two ventricles stood out which were surrounded by a white and medullary substance . . .' (C.A. 63/64, A.B. 84). Although Willis's explanation of a transposition of the corpus striatum and the corpus callosum is no longer tenable, a relatively large extent of the striatal complex in birds was confirmed, at the beginning of the present century, by Edinger and his associates,[53, 54] Rose,[55] Ariens Kappers[56] and Huber and Crosby.[57]

In 1672 Willis returned to the subject of the corpus striatum, as he said, to fill in the gaps in his previous account. Fig. 8 of *De Anima* clearly depicts the internal capsule, and in the legend of this figure the letter H indicates 'The posterior border of the same striatum in which the optic striae and indeed other medullary processes are sent from the orbicular prominences [our corpora quadrigemina]' (D.A. 65, S.B. 44). The first description of the internal capsule is usually attributed to Vieussens,[45] who gave it the name 'geminum semicirculare centrum'. Haller, however, already recognized that Willis 'correctly illustrated the centrum geminum semicirculare'. Willis also noticed that, in post-mortem examinations of patients afflicted with 'long and severe paralysis . . . these bodies were less firm, discoloured, like the dregs of oil, and the striae much obliterated' (C.A. 63, A.B. 84). This is probably the first account of involvement of the region of the internal capsule in hemiplegia. In his 'neurological chronology', Riese[58] reserves this merit for Morgagni; but this was a hundred years after Willis, whose name does not appear in Riese's tables.

In 1672 Willis used a new type of dissection (later perfected by Vieussens):

'By gently scraping with the point of a penknife . . . we removed everywhere the softer and darker substance . . . the whiter and more hard being left.' In scraping off the surface of these structures he went so deep as to obtain the appearances 'also in the lower parts' (legend to Fig. 6, D.A. 42, S.B. 28). He described, among others, a 'medullary shoot reaching above the testes and nates [our corpora quadrigemina], and going under the pineal Kernel, tending towards the chambers of the optic nerves' (D.A. 38, S.B. 26). Thus, he may well have traced the pathways of the sensory lemnisci into the ventral nuclei of the thalamus.

Autonomic nervous system. The anatomy and function of the vagal and intercostal (sympathetic) nerves, their control by the cerebellum, and their role in emotional life, were among Willis's central interests, and he has devoted many pages of both *Cerebri Anatome* and *De Anima* to this subject. Sheehan[59] has given a full account of Willis's place in the history of the autonomic system to which the present writers have added a few points.[2] Here we shall let Willis speak for himself:

'But the office of the Cerebel seems to be for the animal spirits to supply some nerves; by which involuntary actions (such as the beating of the heart, continuous respiration, the concoction of the aliment, the protrusion of the chyle, and many others), which are made after a constant manner unknown to us, are performed whether we will or not. . . . Wherefore whilst the brain is varied by irregular convolutions, sulci or gyri, the design of this is one of the folds and lamellae, disposed in an orderly series (C.A. 74, A.B. 91). . . .

'We shall take notice in the second place, that the anomalous motions of the spirits inhabiting the cerebel, are wont also, by reason of the force of the affections, to be transmitted from thence to the brain; for as often as a violent passion, such as joy, sadness, anger, fear, or of any kind, is conceived in the brain, presently the impression of the same being brought through the by-paths of the prominences (i.e. our corpora quadrigemina) into the cerebel, disturbs the spirits destined to the vital or merely natural function in their very fountain, and for that reason presently induces notable changes in the organs of those functions (C.A. 80, A.B. 95).

'Among the nerves which are seen to belong to the cerebel, and to perform its offices, lastly follow the eighth or wandering pair, which indeed has its origin out of the common trunk of the medulla oblongata near the place where the last process of the cerebel terminates . . . we take notice that this nerve is bestowed chiefly on the praecordia, the acts of which are involuntary, and are performed without our care or knowledge, in sleep as well as in waking . . . from hence it may certainly be well concluded, that the oeconomy of the cerebel only concerns the involuntary function (C.A. 85, A.B. 98).

'The beginnings of the intercostal nerve are two or three shoots recurrent from the nerves of the fifth and sixth pair, and united into the same trunk . . . by this ramification it comes about, that there are very quick commerces and consent between the conceptions of the brain and the affections of the praecordia, also between the actions and passions almost of all the parts of the whole body, which belong to the involuntary function. For in that the trunk of the intercostal nerve proceeds from the nerves of the fifth and sixth pair near their beginning, that is a sign that both the influence of the animal spirits and the instincts for the performing of motions are derived chiefly into it from the cerebel, from whose annular process the aforesaid pairs of nerves arise' (C.A. 137, A.B. 131).

Willis, like Eustachius before him, was wrong in regarding the intercostal (sympathetic) nerve as an off-shoot of the fifth and sixth cranial nerves, but as we have pointed out,[2] both those workers described the cephalic portion of the sympathetic nerve and its close proximity to the third, fifth, sixth and ninth nerves.

The sympathetic (and parasympathetic) relations of the trigeminal nerve interested Willis in relation to weeping, laughing and other expressive phenomena in the region of the face. 'The parts of the face and mouth, composed into a mournful aspect, aptly answer to this

affection of the praecordia; the reason for which we have shown elsewhere, because the nerves which contract the praecordia are intimate relations, and rejoice in mutual sympathy with those, which pathetically compose the face in laughing and weeping. . . . But as to the organs which perform these kind of affections, we have elsewhere observed that there happens in man, otherwise than in brutes, a wonderful consent between the praecordia and the parts of the mouth and face, by reason of the origin of the intercostal nerve, so that as soon as sadness possesses the breast, presently the aspect of the face corresponds with the same perturbation' (D.A. 120, S.B. 80/81).

He gave similar consideration to the double innervation by vertebral (spinal) and vagal or intercostal nerves of the viscera serving digestion, excretion and genital function. 'These plexuses placed near the entrance of the chief excretory passages, serve for the opening and shutting them: a vertebral branch comes to either as a subsidiary; by which it comes to pass that besides increasing the forces of the spirits, their acts become in some measure spontaneous. . . . Without doubt whatever of sense or motion is made during the venereal act, is owed to the influence of the spirits through the nerves. In men the delightful ejaculation of the genital humor, and in women the no less pleasant reception of the same depends on the action of those nerves. Lastly, from the same plexus another nerve . . . is distributed on both sides into the bladder and its sphincter. . . . Certainly by these nerves the business of passing water is performed, but when at any time the same is painful, the sense of trouble is impressed on them' (C.A. 151/2, A.B. 140).

He also had some remarkable things to say (though expressed in a crude, mechanical manner) about *vasomotor* innervation: 'We may observe that from the aforesaid plexus of the wandering pair numerous shoots and fibres are distributed into the auricles of the heart and all the blood vessels belonging to the heart . . . which fibres, creeping along like ivy, thickly cover the coats of the vessels, and enter them in very many places . . . we may lawfully suppose that these nerves, as if they were reins put upon these blood-carrying vessels, do sometimes dilate, and sometimes bind them hard together for the determining the motion of the blood according to the force of the passions . . .' (C.A. 126, A.B. 123/24). He repeated this on p. 132 (A.B. 127) and added '. . . Sometimes the bronchi themselves are constricted by the convulsion of the nerves, and are hindered in their motion, so that they cannot take in and send forth the air after its due manner, as may be seen in asthmatical fits.'

These examples certainly confirm Sheehan's claim that Willis was a pioneer in the development of our knowledge of autonomic function. Furthermore, they substantiate Vichon and Vie's conclusion that he laid a factual basis for a modern physiology of emotion. Willis also made a notable contribution to psychosomatic medicine; perhaps one even more solid than that of Harvey[60] on whom Hunter and Macalpine[61] bestow this merit.

Neuburger,[62] and following him Grünthal,[30] regarded the cerebellar theory as erroneous, however fertile it may have proved for the future direction of experimental research. We have emphasized how relatively small this error was. If one substitutes the medulla for the cerebellum (of which it was thought to be a part) and the hypothalamus for the corpora quadrigemina (thought by Willis to be concerned with instinct) 'the error would indeed be small and we would be very close to our modern ideas of the cerebral control of the autonomic system'.[2]

Willis extended his ideas on the localization of involuntary movement also to psychopathological phenomena, especially incubus (nightmare), and the hysterical and hypochondrical passions. This is what he had to say about *incubus*: 'Wherefore we think the fit of the nightmare to be induced, because in sleeping, a certain incongruous matter is instilled into the cerebel, together with the nervous juice, which cause a certain torpor in the first spring of the spirits and compel them gradually to cease from the offices of their functions; so that the vital actions suffer a short eclipse, during which, partly from a strife of the obstructed praecordia, and partly from the

blood very much congested and stagnating in them, that weight or a sense as it were of a great bulk lying on them, is caused' (D.A. 200/1, S.B. 143).

Of the autonomic aspects of *hysteria*, he wrote: '. . . We doubt not to assert the passions commonly called hysterical to arise most often, because the animal spirits occupying the beginning of the nerves within the brain, are affected by a stroke . . . and get to themselves an heterogeneous and explosive copula, which they carry far away with themselves, into the channels of the nerves . . . they enter into explosions, and therefore stir up convulsive motions. . . . When therefore the animal spirits within the nerves of the wandering pair and intercostals, are imbued from their origin, even to their utmost ends, with an heterogeneous and explosive copula, they at length, either from mere fullness, or by an irritation somewhere made, are stirred up to explosions; in which affection, if any spirits leap forth towards the white matter of the brain, they induce the vertigo, the inflation and other accidents of the head' (M.C. 105/6, C.D. 71).

Again in 1670, answering Highmore who ascribed hysteria to an affection of the lung, he added: 'How many hysterical women do I myself not know who, on the occasion of a violent passion, have suddenly fallen down speechless, the attack undoubtedly proceeding from an eclipse of the animal faculties? This has quickly been succeeded by respiration, not of a difficult and laborious character, as seen in congestion and infarction of the lung, but instantly suppressed and almost imperceptible, with asphyxia and cadaverous appearance. Then, after an interval, spasms have begun to arise in the limbs, also the viscera to be inflated, as if a spherical mass were ascending and the praecordia to be fiercely agitated . . .' (*Affectionum quae dicuntur hystericae*, 5). 'Distress of the heart, palpitation, a rapid pulse, shortness of breath, profound sighing and the like; of these, I say, most relate chiefly to the nervous system and are justly considered convulsive, as one will be able to infer from the following experiment; namely, if in any live animal you ligate the trunk of the nerves belonging to the praecordia, viz. the vagus and intercostal, immediately the aforementioned symptoms, together with dyspnoea and a sense of suffocation will arise, imitating the type of hysterical attack' (*op. cit.*, 9).

'Most of the abdominal plexuses, but especially the lowest, and that related to it, the greatest of the mesentery, are often affected in the passions commonly called hysterical, as shall be presently described. Therefore if at any time such distempers proceed from the womb, the cause is manifest by which the aforesaid plexuses are drawn into consent. . . . Furthermore that symptom, very frequent in those kind of fits, namely a globe is perceived to be carried from the bottom of the belly which therefore is thought to be an ascent of the womb: I saw that it is nothing else than most cruel convulsions of these plexuses. Indeed often in women, and sometimes also in men, I have known when the convulsive affection has invaded, that a bulk in the hypogastrium has been seen to arise, then about the midst of the abdomen so great a swelling to follow, that it could not be hindred or pressed down. . . .'

'. . . This distemper often takes its rise from a sudden fear, great sadness or anger, or other violent passion, in which the spirits inhabiting the brain are strongly affected besides . . . the manner of the fits clearly evinces the same, insofar as a fulness of the head, a vertigo, a sparkling of the eyes, a ringing noise of the ears, begin in many the hysterical fits, and often conclude them. Besides I have opened some women dead of other diseases, though while they were sick, very obnoxious to hysterical passions, in whom the womb being very well, I have found in the hinder part of the head, the beginnings of the nerves, moistened and wholly drowned with a sharp serum . . .' (M.C. 105, C.D. 71).

'After these things are acted in the lower and middle regions, at length the distemper reaches to the head, by the passage of nerves . . . produce dimness of vision, and often symptoms very like the epilepsy, sometimes the spirits there exploded rush into the beginnings of other nerves . . . wherefore hysterical people towards the end of the fit often laugh, or weep, or talk idly . . .' (M.C. 107, C.D. 72).

These examples, we believe, convincingly demonstrate the relationship of the hysterical passions with the autonomic sphere. They also show that Willis exonerated the uterus as the exclusive cause of the hysterical passions, repeatedly stressing that the condition may occasionally be encountered in men (although

men were more prone to hypochondria, a related condition due to the spleen and its (autonomic) connections with the brain). The description of hysteria in men is usually attributed to Sydenham, but as Lord Brain has pointed out,[63] the true discoverer of the 'passio hysterica' was Shakespeare and the 'patient' King Lear.

Hunter and Macalpine[61] rightly emphasize that some of the alleged hysterical cases would now be diagnosed as organic disease, as epilepsy or, perhaps, its temporal lobe variety. Undoubtedly the concept of hysteria accepted by others as well as Willis was wider in the seventeenth century and must have included many conditions besides epilepsy. Nevertheless, the quotations given above show that Willis was thoroughly familiar with some outstanding hysterical manifestations which are unmistakable to the modern psychiatrist. Hunter and Macalpine also point out that Willis's concept of hysteria was too narrowly based upon the convulsion; they contrast his notion with that of Sydenham,[64] who, in their opinion, gave a clearer clinical description of hysteria, thereby exerting a greater influence. By classifying the 'hysterical passions' together with epilepsy under convulsive diseases, Willis obviously exposed himself to this criticism. However, it is only fair to emphasize that Willis encompassed far more than what we now call a hysterical fit. Vinchon and Vie give an impressive list of Willis's descriptions, which include movements in the lower belly, ascension of a sort of globe, rumbling of the bowels, vomiting, distension of the hypochondrium, belching of air, impeded respiration, suffocation, vertigo, disordered eye movements, laughter, tears, absurd confabulations, aphonia, akinesia, feeble pulse, cadaverous complexion and so forth.[5] Our quotations tend to confirm this wider range. Perhaps this disagreement has arisen because of Willis's double use of the adjective 'convulsive' both in a pathogenic and in a clinical sense. He obviously attributed to the *animal spirits* a convulsive or explosive 'copula' which could produce the varied manifestations listed above, and by no means convulsions only in a clinical sense.

Sydenham's 'Epistolary Dissertation' undoubtedly exerted a greater influence on the understanding of hysteria, but, as Leigh[65] has pointed out, this was probably because of his simple, earthy style, quite unlike that of Willis who, 'despite his originality, and perhaps because of his mechanistic approach, was so sadly distorted by his own theorizing'. It is, however, interesting to note how many of Willis's pathogenic theories were incorporated in Sydenham's essay.

Part II will be published in the April Issue.

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