The most important of all the organs: Darwin on the brain

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This article discusses Charles Darwin’s interest in topics that may broadly be defined as ‘neurological’ in character. Using published and manuscript materials, it examines the sources of Darwin’s knowledge of neurological matters and seeks to explain why questions concerning the relation of mind and brain both in humans and other animals were relevant to his wider concerns. The paper concludes with a discussion of Darwin’s impact on late 19th and early 20th century neurological thought. The 150th anniversary of the publication of the Origin of Species and the 200th of the birth of its author afford an opportunity to reflect on Charles Darwin’s relationship to neurology. The first section of this article considers the part played by what might broadly be defined as ‘neurological’ materials in the shaping of Darwin’s theory. The following section provides a brief review of the impact that Darwin’s ideas were to have upon subsequent neurological thought.

Neurological materials in Darwin’s theory

The first edition of the Origin contains only one reference to the brain in the form of the rhetorical question: ‘Why should the brain be enclosed in a box composed of such numerous and such extraordinarily shaped pieces of bone?’ (Darwin, 1859, p. 437) Darwin’s contention was that the intricacy of the construction of the skull—and the fact that a similar pattern was evident in all vertebrates—was far more intelligible on the hypothesis of descent from a common ancestor than on the assumption that all these species were the result of acts of special creation.

Nor is there much discussion of the human mind in the work. Indeed in the preamble to the chapter on ‘Instinct’ Darwin declares: ‘I must premise, that I have nothing to do with the origin of the primary mental powers, any more than I have with that of life itself. We are concerned only with the diversities of instinct and of the other mental qualities of animals within the same class’ (Darwin, 1859, p. 207). It is only in the ‘Conclusion’ that he ventures the opinion that: ‘In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history’ (Darwin, 1859, p. 488).

On this evidence, it might seem a reasonable conclusion that Darwin had little interest in psychology and still less in the nervous system. He appears happy to defer discussion of the implications for these fields of his theory to the ‘distant future’. This was, however, not the case. His private notebooks show that Darwin had for many years shown a keen interest in topics related to the human mind as well as in ‘neurology’, as the term was defined in the 19th century, to include the anatomy and physiology as well as the diseases of the nervous system.

Darwin was not himself a medical man. A brief sojourn at the Edinburgh school of medicine was enough to convince him that he was not suited to the more grisly aspects of the profession. His father, however, was a doctor who supplied his son with information drawn from his clinical experience that
helped to supplement Charles’s extensive reading. Thus Darwin noted that: ‘My F[ather]… says there is perfect gradation between sound people and insane’ (Notebook M p. 13; Barrett, 1987, p. 522). In later years, moreover, Darwin established an extensive network of contacts and correspondents, including such medical men as James Crichton-Browne, who were to supply him with further clinical, anatomical and physiological information relevant to his work and speculations.

From an early stage in the development of his thinking, Darwin recognized the need to incorporate man into his theory. In particular, it was necessary to show how human mental powers could be explained in terms of an evolutionary theory. If the human mind was deemed to be a special, unique divine creation then the thoroughgoing naturalism at which Darwin aimed would be fatally undermined. Darwin, therefore, sought evidence for what he called a ‘materialist’ understanding of the mental powers that would erode the distinction between human mental capacities and those found in the lower animals. This ‘materialism’ also entailed that mental faculties be shown to have a bodily basis.

While developing his ideas about the origin of species in the 1830s, Darwin devoted two notebooks—designated ‘M’ and ‘N’—to his speculations on man and mind (Gruber, 1974). The private jottings in these notebooks are sometimes difficult to decipher; a number of recurrent themes are, however, apparent. Thus Darwin repeatedly speculates about the relation of the mental powers in man and animals to ‘brain’.

For example, one of Darwin’s pre-occupations was with the related questions of whether animals possessed reason and of the distinction between instinct and ‘intelligence’. In the ‘N’ notebook, Darwin maintained the fact that there was evidence to suppose that animals possessed memory strengthened the supposition that they were rational beings. Like humans, animals were capable of learning and of modifying their behaviour in the light of past experience. Darwin noted that Jean-Baptiste Lamarck, in his *Zoologie Philosophique*, had suggested the possibility of a form of transmissible memory: ‘Habits becoming hereditary [sic] form the instincts of animals . . . almost identical with my theory . . . no facts, and mingled with much hypothesis’. The question then arose of what was the organic basis of this process. Darwin felt that there was a: ‘strong argument in favour of brain forming the instincts, — could brain make a tune on the pianoforte, yes if every individual played a little, and something destroyed bad brain’ (Notebook N p. 90–1; Barrett, 1987, p. 589).

These references to the capacities of the brain are somewhat cryptic. What is, however, striking is the degree of agency that Darwin ascribed to ‘brain’. Moreover, they suggest that Darwin saw the brain as a plastic organ undergoing constant transformation both within the lifetime of the individual and between generations, and upon which the collective experience of a species was imprinted. Darwin was to return to the question of how habit could be transformed into instinct in the first edition of the *Origin*, but without any explicit reference to the brain (Darwin, 1859, p. 209). The issue was important to his overall theory because he maintained that changes in instinctive behaviour could be as important as modifications of bodily structure to an organism’s chances of success in the struggle for existence. However, as the comments in Notebook N demonstrate, a modification of instinct that might lead to some selective advantage did also entail a change in the ‘corporeal structure’ of the brain. ‘Can we deny’, Darwin asked rhetorically, ‘relation of mind and brain. Do we deny the mind of a greyhound and spaniel, differs from their brains then can we deny that the grand child dug for mice from some peculiarity of structure of brain? — is this more wonderful than memory, affected by diseases. &c &c, double consciousness? What other explanation — can we suppose some essence’ (Notebook N p. 43e; Barrett, 1987, p. 575).

These last remarks demonstrate how the clinical materials that Darwin had gleaned from various sources figured in his attempts to arrive at naturalistic understanding of psychological phenomena. He derived some of his knowledge of the phenomenon of ‘double consciousness’, for example, from: ‘Dr. Hollands [sic] story of man in Delirium tremens hearing other man speaks’ (Notebook N p. 111; Barrett, 1987 p. 593). This was Henry Holland (1788–1873), a distant cousin and another member of the circle of medical acquaintances upon whom Darwin drew for information. Such pathological mental activity demonstrated, *inter alia*, that: ‘consciousness of personal identity is by no means a necessary part of man’s mind’. In the Notebook M, Darwin speculated on: ‘the possibility of the brain having whole train of thoughts, feeling and perception separate from the ordinary state of mind’ (Notebook M, p. 80; Barrett, 1987, p.538). As well as conscious thought—or what Darwin referred to as ‘the more energetic self’—‘brain’ was thus capable of maintaining several chains of complex unconscious mental activity, a faculty that explained, among other things, instinctive behaviour in both man and animals.

Other nervous disorders were also grist to Darwin’s mill. He maintained that: ‘a person twitching when a disagreeable thought occurs, is closely analogous to epilepsy and convulsion’ (Notebook M, p. 20; Barrett, 1987, p. 524). Both forms of involuntary movement were dependent on: ‘the action of brain’. The psychic aspect of the first category was merely incidental. In places, Darwin seemed to be groping his way towards a theory of cerebral reflexes, suggesting that: ‘the action of brain which gives sensation of pain, emits its power on the muscles in the twitching’. Conversely, he wondered: ‘whether there is any analogy between grief and pain—certain ideas hurting brain, like a wound hurts body’. Darwin noted that: ‘ears flow from both, as when one burns end of nose with a hot razor’ (Notebook N, p. 45; Barrett, 1987, p. 575).

Darwin was particularly fascinated by the case of ‘Mr Corbet’, one of his father’s patients. Darwin noted that as the result of a ‘paralytic stroke’ Corbet’s: ‘intellect [was] impaired’. In particular, he had lost the ability to comprehend spoken language while retaining the power of speech. Darwin remarked upon the selective nature of the cognitive deficit. Corbet: ‘could receive a new train through eyesight, though, not through hearing’. Thus, ‘when dinner was announced he could not understand it’. Corbet was, however, able to deduce that it was dinner-time when shown a watch (Notebook M, p. 9; Barrett, 1987, p. 521). As we shall see, Darwin was in his later writings to return to the significance of such cases for an evolutionary understanding of language.

Darwin drew on personal experience to illustrate further the dependence of mental states on ‘physical action on the brain’. Sometimes his observations were of quite a general nature.
Thus he claimed: ‘it is an argument for materialism, that cold water brings on suddenly in head, a frame of mind, analogous to these feelings, which may be considered as truly spiritual’ (Notebook M, p. 19; Barrett, 1987, p. 524). Even in casual discourse Darwin took for granted that personality was determined by the peculiarities of an individual’s cerebral machinery. Thus, the bad temper of one acquaintance led him to the conclusion: ‘some part of the organization of his brain wants mending: nothing else will account for his manner of viewing things’ (Darwin to Charles Lyell, 9 August 1838, letter 424).

On other occasions, Darwin derived important insights from particular incidents in his own life. He noted that on 12 August 1838, while at the Athenaeum Club, he was: ‘very much struck with an intense headache after good days work which came on from reading review of M. Comte Phil, which made me endeavour to remember, and to think deeply . . .’. The headache was, however, easily cured by reading some lighter matter. Darwin was as interested in this ‘article by Boz’ as he had been in the more serious reading: ‘and read so intently as to be unconscious of all around, yet there was no strain on the intellectual powers — the difference is of a man wagging his foot and working with his toe to perform some difficult task’ (Notebook M, p. 81; Barrett, 1987, p. 539).

Perhaps the most important consequence that followed from recognizing the true role of ‘brain’ in shaping the mind was that it made possible to: ‘trace the causation of thought’. Darwin had a passing familiarity with the work of such classical psychologists as John Locke. But he was of the view that ‘to study metaphysics, as they have always been studied appears to me to be like puzzling at astronomy without mechanics’. He maintained that ‘the problem of the mind cannot be solved by attacking the citadel itself — the mind is function of body—we must bring some stable foundation to argue from’ (Notebook N, p. 5; Barrett, 1987 p. 564). Such a stable foundation was only to be found in the premise that mind was a function of the brain and could be scientifically studied in the same way as any other function. This insistence that the study of the human mind should seek a basis in the material organization of the body was not original to Darwin. Its roots can be found in the work of such 18th century figures as David Hartley, with whose work Darwin was acquainted. Moreover, the 19th century saw a new determination with which Darwin’s views accorded to erect a new, biologically informed, psychology

Darwin excluded such speculations from the first edition of the Origin of Species largely for strategic and prudential reasons. He realized that the thesis that species were not fixed but had evolved over time was sufficiently contentious without being mixed with the potentially incendiary claim that the human mind was in essence no different from the mental powers manifested by the lower animals and that all thought derived from the properties of the evolving brain.

In the later editions of the Origin, Darwin became somewhat less reticent about touching upon these issues in print. Thus in the 1861 edition he remarked that ‘if we look at the differentiation and specialization of the several organs of each being when adult (and this will include the advancement of the brain for intellectual purposes) as the best standard of highness of organisation, natural selection clearly leads towards highness . . .’ (Darwin, 1861, p. 134). The concomitant evolution of brain and intellect is simply taken for granted. In the sixth edition of 1872, Darwin tried to address the question of why, if greater intelligence was of obvious advantage in the struggle for life, all organisms had not evolved the mental powers enjoyed by man. He concluded that a definitive answer ‘ought not to be expected, seeing that no one can solve the simpler problem why, of two races of savages, one has risen higher in the scale of civilization than the other; and this apparently implies increased brain-power’ (Darwin, 1872a, p. 181).

But it is in The Descent of Man, and Selection in Relation to Sex (1871) that Darwin gave his fullest and most considered statement on neurological and psychological matters. He was at last ready to address the implications of his theory for our understanding of human nature. Much of the book is devoted to proving that ‘man bears in his bodily structure clear traces of his descent from some lower form’ (Darwin, 1871, p. 34). It was, according to Darwin, ‘notorious that man is constructed on the same general type or model with other mammals’. The brain, ‘the most important of all the organs, follows the same law’. Anatomists had shown that ‘every chief fissure and fold in the brain of man has its analogy in that of the orang . . .’ (Darwin, 1871 p. 10–1).

This morphological uniformity notwithstanding, Darwin recognized, however, that ‘it may be urged that, as man differs so greatly in his mental power from all other animals, there must be some error in this conclusion’ (Darwin, 1871, p. 34). He was, therefore, obliged to show how the human mind could also be viewed as something that had evolved from more primitive types.

To achieve this goal, Darwin relied on his previous contention that the growth of mind was dependent on the progressive development of its material substrate. No-one, he averred, ‘doubts that the large size of the brain in man, relatively to his body, in comparison with that of the gorilla or orang, is closely connected with his higher mental powers’ (Darwin, 1871, p. 145). He claimed that the same dependency between intellectual power and cerebral mass was evident elsewhere in the animal kingdom, even among insects. The ant’s ‘cerebral ganglia’, although tiny, were much larger than those of other insects, which explained their evident superior ‘intelligence’. Indeed, according to Darwin, ‘the brain of an ant is one of the most marvellous atoms of matter in the world, perhaps more marvellous than the brain of man’ (Darwin, 1871, p. 145).

Darwin acknowledged that ‘little is known about the functions of the brain’ (Darwin, 1871, p. 38). This paucity of solid information did not, however, prevent him from speculating about how the changes this organ had undergone in the course of evolutionary time might have impacted upon the psychological performance of the organism. For instance, he suggested that ‘intelligent’, as opposed to purely instinctive action, may have become more prominent in the course of evolutionary time in part because ‘as the intellectual powers become highly developed, the various parts of the brain must be connected by the most intricate channels of intercommunication; and as a consequence each separate part would perhaps tend to become less well fitted to answer in a definite and uniform, that is instinctive, manner to particular sensations or associations’ (Darwin, 1871, p. 38). As this
passage suggests, Darwin saw the interaction between behaviour and its material substrate to be complex in nature. He relied on the assumption that new mental habits that altered the organization of the brain could become hereditary traits.

This reciprocal action between structure and function was particularly evident in the case of the evolution of language. The capacity for spoken and written language had in western culture long been seen as a distinctive trait that humans alone possessed. It was, moreover, viewed as a spiritual faculty rather than as a physiological function. As part of his overall strategy, Darwin sought to subvert both these assumptions and to show that language could also be understood as one outcome of the evolutionary path that the human brain had followed.

The question of the origin of language had, especially during the enlightenment period, been a subject of intense speculation. This debate continued into the 19th century. Darwin's correspondence shows that he took a keen interest in this 'marvellous problem', as he did in so many other topics. In November 1862, for instance, he wrote that he had 'read with much interest' the philologist, Max Müller's Lectures on the Science of Language. He noted, however, that Müller's views on the 'first origin of language seems the least satisfactory part' (Darwin to J. D. Hooker, 4 November 1862, Letter 3795).

A later letter makes clearer Darwin's objections to Müller's preferred solution to the 'marvellous problem' of the origin of language. He complained that Müller was 'dreadfully afraid of not being thought strictly orthodox', and consequently made unnecessary concessions to the biblical account of the birth of language. Moreover, Müller was not a supporter of the theory of evolution; Darwin detected 'covert sneers at me' within the book (Darwin to Crichton–Browne, 18 November 1862, Letter 3796). What especially divided Müller from Darwin was that the former was determined to insist on a special status for man within the universe. In particular, Müller maintained that language was an attribute that distinguished humans from all other living beings. 'Language', Müller insisted, 'is our rubicon, and no brute will dare to cross it' (Müller, 1862 p. 340).

But Darwin was determined to cross this rubicon. Human language, far from being a unique gift from God, had, Darwin contended, evolved from the more rudimentary forms of communicative behaviour that humans shared with the lower animals. The faculty of 'articulate language' owed: 'its origin to the imitation and modification, aided by signs and gestures, of various natural sounds, the voices of other animals, and man's own instinctive cries' (Darwin, 1871, p. 56). Relying on what was known of the habits of contemporary primates, Darwin suggested that these sounds had at first been especially prominent in the mating behaviour of our ancestors. Later, however, these creatures would have begun to find vocal communication serviceable in a wider range of contexts. In Darwin's view, 'it does not appear altogether incredible, that some unusually wise ape-like animal should have thought of imitating the growl of a beast of prey, so as to indicate to his fellow monkeys the nature of the expected danger. And this would have been a first step in the formation of a language' (Darwin, 1871, p. 57).

Persistent use of such signs for the purposes of communication would have made the vocal cords stronger and capable of articulating a wider range of sounds. However, Darwin maintained that: 'the relation between the continued use of language and the development of the brain has no doubt been far more important' (Darwin, 1871, p. 57). The brain in effect developed a special apparatus to subserve the new linguistic activities in which primitive humans were beginning to engage.

The 'intimate connection' between the brain of modern humans and the faculty of speech was evinced by 'those curious cases of brain-disease, in which speech is specially affected, as when the power to remember substantives is lost, whilst other words can be correctly used' (Darwin, 1871, p. 58). For examples of such cases, Darwin referred the reader to the 1838 edition of John Abercrombie's Inquiries Concerning the Intellectual Powers and the Investigation of Truth. Darwin had read this book around the time of its publication—an instance of how the seeds of many of his later insights were sown at the time he was composing his notebooks.

This resort to clinical evidence to corroborate a claim was, as we have seen, a characteristic ploy. Darwin's choice of a source to demonstrate the point that damage to the parts of the brain could affect specific aspects of language is, however, a somewhat curious one. By 1871, a substantial literature existed on the phenomena of aphasia, which would have given greater weight to Darwin's contention; but he seemed unaware of these more recent developments in medical science. Thus, although he does cite his work on craniometry, Darwin makes no reference to Paul Broca's 1861 localization of the faculty of articulate language in the third frontal convolution of the cerebral cortex.

This lacuna gives an indication of the extent of Darwin's engagement with contemporary medical science. He used the various pieces of information about language he gathered from his reading and his numerous contacts in an eclectic fashion to make a particular point or in order to strengthen an argument. Given the breadth of his interests, it is perhaps no surprise that he made no systematic attempt to engage with the field. When news of major developments in neurology did reach him, Darwin's interest and enthusiasm was, however, genuine. Thus, Darwin was fascinated when he heard of David Ferrier's (1843–928) research on the electro-excitability of the cerebral cortex, from Crichton–Browne, and asked for more information (James Crichton–Browne–Darwin, 16 April 1873, Letter 8861; Darwin–Crichton–Browne, 17 April, 1873, Letter 8865).

**The impact of Darwin's ideas on neurology**

Darwin's Origin of Species is widely recognized as a seminal work that had profound implications for all branches of biology, including the sciences devoted to the study of the nervous system. An early exponent of an evolutionary approach to understanding the workings of the human nervous system was the English physician, John Hughlings Jackson (1835–911).

Jackson maintained that the functions of the human nervous system were only intelligible when it was recognized that the brain and its appendages were the product of a lengthy
evolutionary process. In the course of phylogenetic time, new structures had been superadded to older forms of nervous organization. These more recent accretions profoundly modified the operation of the pre-existing parts of the brain by inhibiting their functions (Smith, 1992, p. 164–66). Although a theorist, Jackson was above all a clinician who sought to apply these insights to the elucidation of the phenomena of nervous disease (Critchley and Critchley, 1998). He maintained that the symptoms of neurological disorders such as epilepsy and aphasia were to be understood as the signs of a dissolution of the complex hierarchical relations that had emerged in the human nervous system in the course of evolution. In crude terms, neurological disease put the evolutionary process into reverse.

Jackson was scrupulous in acknowledging the sources of his ideas. Thus, he credited his erstwhile teacher, Thomas Laycock, with the crucial insight of a continuity of function along the entire length of the cerebro-spinal axis. But Jackson insisted that by far the most important influence upon his thought had been the Victorian polymath, Herbert Spencer (1820–1903). Indeed, in 1881 he declared that ‘the main part of what I may be able to show in this work consists in illustrating Spencer’s doctrines of nervous evolution, by the reverse process of nervous dissolution …’ (Jackson, 1881, p. 6). Indeed at the outset of his most extended discussion of the implications of the theory of nervous evolution for neurology, Jackson declared that ‘the doctrine of evolution’ was ‘not simply synonymous with Darwinism. Herbert Spencer applies it to all orders of phenomena’ (Jackson, 1884, p. 45). In contrast to the many references to Spencer in Jackson’s writings, there is scarcely a nod to Darwin.

David Ferrier was one of Jackson’s colleagues at Queen’s Square. Ferrier was inspired by Jackson’s clinical writings to launch a programme of experimental research designed to cast further light on the localization of sensori-motor functions in the cerebral cortex. Ferrier felt no special need to insist upon the veracity of the theory of evolution; he simply took it as an established truth from which important corollaries were to be drawn. For instance, when trying to rebut the claims of those critics who questioned his claims about the existence of motor centres in the cerebral cortex, Ferrier asserted that ‘such conclusions only indicate a grave misconception of the constitution and evolution of the nerve centres’ (Ferrier, 1876, p. 137).

The theory of evolution implied that there must be a homology of structure and function in the brains of organisms that were descended from common ancestors. But Ferrier was also aware that ‘the degree of evolution of the central nervous system, from the simplest reflex mechanism up to the highest encephalic centres, and the differences as regards the relative independence or subordination of the lower to the higher centres, according as we ascend or descend the animal scale, introduce other complications, and render the application of the results of experiment on the brain of a frog, or a pigeon, or a rabbit, without due qualification, to the physiology of the human brain, very questionable …’ (Ferrier, 1876, p. xiv). Because of this caveat, it was only safe to draw inferences about the workings of the human brain from experiments on those animals that were genealogically closest to man. Thus Ferrier explained that he had concentrated his investigations on monkeys because ‘the brain of these animals is constructed on the same type as the human brain, and their habits are such as to afford the most reliable data for inferences applicable to the physiology of the brain of man’ (Ferrier, 1876, p. 163).

Queen Square was thus one centre in which evolutionary—although not necessarily Darwinian—ideas were entrenched. The newly established Cambridge school of physiology was to be another important site at which the implications for neurology of the theory of evolution were to be developed (Geison, 1978, p. 220–1). It was there, for example, that Walter Gaskell (1847–1914) elaborated his hypotheses on the evolution of the vertebrate nervous system (Gaskell, 1889).

A notable alumnus of the Cambridge school was Henry Head (1861–1940). Although he had trained as an experimental physiologist, Head spent most of his career as a clinician with a special interest in diseases of the nervous system. Head, however, retained the evolutionary preconceptions he had derived from his time in Cambridge. Thus, Head regarded his early research into herpes zoster as a corroboration of Gaskell’s views on the phylogenetic origins of the human nervous system (Jacyna, 2008, p. 114–5).

Perhaps, the most famous of Head’s later research were the experiments on sensation that he conducted on his own arm in collaboration with William Halse Rivers Rivers (1864–1922). The main conclusion of these protracted investigations was that in humans peripheral sensation was dependent on the cooperation of two distinct nervous mechanisms. ‘Protopathic’ sensation was crude and amorphous in nature and represented a primitive mode of feeling. ‘Epicritic’ sensation, on the other hand, was a more recent acquisition that made available a far more refined and discriminate range of feelings. In the healthy individual, the epicritic nervous system served to limit and moderate protopathic sensation. Disease or injury might, however, not only abolish epicritic feeling but also unleash untrammelled protopathic sensation (Rivers and Head, 1908).

Head and Rivers’ understanding of sensation owed clear debts to Jackson’s version of the theory of evolution. This is above all evident in its use of the notion of different levels of nervous organization, corresponding to different points in evolutionary history, between which hierarchical relations obtained. As in so much of late 19th and early 20th century evolutionary speculation, there is little that is distinctly Darwinian. In particular, there was little if any reference to the doctrine of natural selection in this literature.

Another graduate of the Cambridge school of physiology was Charles Sherrington (1857–1952). Head and Sherrington were friends and collaborators, and shared many fundamental assumptions about the functional organization of the vertebrate nervous system. On the first page of his monumental The Integrative Action of the Nervous System (1906), Sherrington alluded to the ‘Darwinian doctrine of evolution’. He was making the point that, whereas the theory of evolution—in common with that other great early 19th century innovation, the cell theory—had initially had its chief impact in morphological studies, its applications in the field of ‘energetics’ were in the early 20th century becoming ever more evident (Sherrington, 1906, p. 1–2).

Sherrington’s contention was that evolutionary assumptions were fundamental to understanding the function, as well as the
form, of the nervous system. Animal life had originated in simple unicellular organisms. As these had evolved into multicellular animals, specialized nerve cells had developed that assumed paramount importance in assuring the unity and integrity of an ever more complex body: ‘it is nervous reaction which par excellence integrates it, welds it together from its components, and constitutes it from a mere collection of organs an individual’ (Sherrington, 1906, p. 2). The essential mechanism whereby this integration had been achieved over the course of phylogenetic time consisted in the compounding of originally simple reflex arcs into a coherent although immensely complex functional system.

Sherrington was much more explicitly Darwinian in his understanding of evolutionary processes than such figures as Jackson and Head had been. On a number of occasions Sherrington referred to Darwin’s work on The Expression of the Emotions in Man and Animals (Darwin, 1872b). For instance, he noted that ‘the hypothesis of evolution afforded a new vantage point’ for the study of the question of the movements associated with the expression of feeling (Sherrington, 1906, p. 256–7; see also p. 10, 260, 306).

It was, however, the central mechanism that Darwin had posited to explain the dynamics of evolution that was of most importance. Sherrington asserted that ‘the impetus given to biology by the doctrine of adaptation under natural selection, felt so strongly by morphological studies, seems hardly as yet to have begun its course as a motive force in physiology’ (Sherrington, 1906, p. 236). Like Darwin, Sherrington saw animals as seeking to survive in a challenging and highly competitive environment. The—in evolutionary terms—‘highest’ organisms were those that became best fitted to dominate this environment. A genuine hierarchy, therefore, is obtained in the animal kingdom, at the pinnacle of which stood man; and the ‘grading of rank in the animal scale will be nowhere more apparent than in the nervous system in its office as integrator of the individual’ (Sherrington, 1906, p. 237).

One area in which the theory of natural selection was of particular importance to the new neurophysiology was in the explanation it gave to the seemingly purposive nature of many reflexes. Sherrington observed that ‘older writings on reflex action concerned themselves boldly with the purpose of the reflexes they described’. They had, however, couched this discussion in language that revealed ‘for them the interest of the phenomena centred in their being regarded as manifestations of an informing spirit resident in the organism, lowly or mutilated though that might be’ (Sherrington, 1906, p. 236). There had been, for example, as late as the mid-19th century, much debate as to whether a psychic entity had to be invoked to explain the seemingly intentional nature of spinal reflexes (Clarke and Jacyna, 1987, p. 132–3). Sherrington thought it significant that ‘the best-known controversy (Pflüger, Lotze) as to the psychical powers of the spinal cord, occurred prior to the advent of the Darwinian theory of evolution’. Darwin had, in effect, rendered such speculations obsolete because his theory suggested ‘how purposive neural mechanisms may arise. It furnishes a key to the genesis and development of adapted reactions and, among these latter, reflexes’ (Sherrington, 1906, p. 235).

The work of such figures as Jackson, Ferrier, and Head and Sherrington shows how the promulgation and eventual widespread acceptance of the theory of evolution effected a fundamental shift in the way that the sciences of the nervous system were conceived and prosecuted. Fundamental to this change was a recognition that the human nervous system had not appeared in the world in a finished form as the result of a single act of creation. On the contrary, it was the result of a lengthy process of development in which the ancestral organism’s need to adapt to the demands and challenges of an ever-changing environment had been the primary driver. There was in consequence something adventitious and makeshift about the infinitely complex but extremely vulnerable set of contrivances that humans had evolved in the course of their species history. Moreover, the origins of this complexity were to be found in the primitive forms of organization with which the first animals had sought to acquire knowledge of and a measure of control over their world.

Jackson’s example demonstrates that in the 19th century the theory of evolution was not synonymous with ‘Darwinism’. While once influential figures such as Herbert Spencer are now largely forgotten; however, Darwin’s name remains emblematic of this scientific revolution.

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