Synthesis of Contraries: Hughlings Jackson on Sensory-Motor Representation in the Brain

Final version:
2019 *Studies in History and Philosophy of Biology and Biomedical Science.* 75:34-44

ABSTRACT
This paper examines the concept of representation of the brain which occurs in the writings of the neurologist John Hughlings Jackson (1835-1911). Jackson was immersed in Victorian physiological psychology, a hybrid of British associationism and a reflex theory of the operation of the nervous system. Furthermore, Jackson was deeply influenced by Herbert Spencer, and I argue that Spencer's progressivist evolutionary ideas are in tension with the more mechanistic approach of the reflex theory. I also discuss Jackson's legacy in the 20th century and the longstanding debate about localisation of function in the brain.

"The nervous system is a representing system, and even the centres 'for mind' represent parts of the body." (Hughlings Jackson 1932/1985, p.41)

"Of what 'substance' can the organ of mind be composed unless of processes representing movements and impressions?"
(Hughlings Jackson 1931/1985, p.26)

1. INTRODUCTION: DELINEATING THEORETICAL TRADITIONS IN THE HISTORY OF NEUROBIOLOGY

John Hughlings Jackson (1835-1911) has a significant but ambiguous place in the history of the neurosciences. While the inference from the "Jacksonian march" to the representation of the body in the cortex is celebrated in accounts of the discovery of cerebral localisation (Kerr et al. 2005), Hughlings Jackson has also been an inspirational

figure for those opposed to the strict theory of localisation of functions in the brain such as Constantin von Monakow, Kurt Goldstein and Francis Walshe.[1] One purpose of this paper is to account for this puzzling state of affairs by examining Jackson's complex notion of representation in the brain and nervous system. I aim to show that representation, on his conception, is a synthesis of ideas derived from views of the mind and nervous system that are often taken to be mutually incompatible. These contrary traditions can be variously described as mechanistic as opposed to organicist, atomistic as opposed to holist, localising and not universalist, physicalistic rather than teleological. Thus, Jackson's nuanced vision of the nervous system has held an attraction for an ideologically diverse set of neurologists and neurophysiologists in the twentieth century, even when most of his specific doctrines regarding brain function and neuropathology were discarded.

While this paper is structured around a contrast between what I characterise as two alternative perspectives on the nervous system (and living organisms more generally), I must state at the outset that such binaries should only be employed with caution, and that the terms contrasted deserve serious analysis and qualification. This is not least because distinctions and categorisations which seem clear and intuitive in the light of contemporary science frequently fail to map onto historical examples.[2] In order to show that some qualified demarcations of opposing traditions are relevant to my study of Jackson, I will now discuss some of the existing debates around these terms amongst historians of neurobiology and related disciplines.

The development of the theory of cortical localisation is probably the most studied topic in the history of the neurosciences.[3] The 1860's and 1870's were key decades, beginning with Paul Broca's discovery of a cortical language area via a famous case study of aphasia

[1] See Harrington (1987, p.234; 1996, p.81). For example, Goldstein (1934/1995, p.40) writes, "no phenomenon should be considered without reference to the organism concerned and to the situation in which it appears….. Many an error would have been avoided in psychopathology if this postulate, quite deliberately stated by Hughlings Jackson decades ago, had not been so completely neglected."

[2] Discussions with Paolo Palmieri have made me appreciate this point more deeply.

[3] E.g. Tizard 1959; Hécaen & Lanteri-Laura 1977; Young 1990; Harrington 1987; Star 1989.

("aphémie"),[4] followed by the cortical stimulation experiments of Fritsch and Hitzig and of Ferrier (1876).[5] Jackson has been credited with being the first physician to offer an explanation of epileptic symptoms in terms of specific, localised pathologies of the central nervous system.[6] He hypothesised that seizures occur because of an excess of disorganised activity in brain areas involved in the control of movement. Through post mortem examination, Jackson discovered epileptic foci in both subcortical and cortical areas and proposed that those regions housed *representations* of movements involving particular body parts. Thus Jackson's concept of representation is bound up with his empirical findings relating to localisation, as will be discussed below in Section 4. In order to contextualise this discussion, it is necessary to attend to the neurobiological theories against which localisation is usually contrasted.

In *Localization and its Discontents* Katja Guenther examines the uneasy coexistence of *localising* and *connective* principles in neuropsychiatry and neurology from 1860 onwards, with a focus on the German tradition including Meynert, Wernicke and Foerster. In its purest form, research employing the localisation principle seeks one-to-one mappings between brain centres and mental faculties. Guenther characterises the reflex theory, which seeks to explain the workings of the nervous system in terms of arcs in which a sensory and motor nerve are joined at a spinal ganglion or cerebral centre to form an integrated unit, as a *connective* approach – one that sits in productive tension with localisation (2015, p.4 and p.26-31). As we will see in Section 2, Jackson's account of representation and localisation cannot be understood in isolation from the reflex theory, but in his case the notion of reflex is an off-shoot of British physiological-psychology and presupposes, rather

[4] For comparisons of Jackson's and Broca's accounts of aphasia, see Greenblatt (1969) and Lorch (2008).

[5] The interaction between Jackson and David Ferrier (1843-1928) is worth noting here. Both were professionally active at the National Hospital at Queen's Square in London, and each man endorsed the other's findings at key points in his published works, with Hughlings Jackson (1931/1985 p.38) reporting that concordance with Ferrier's results is a "matter of extreme satisfaction" to him and Ferrier dedicating his 1876 monograph, *The Functions of the Brain* to Jackson. Lorch (2004), Caspar (2014a) and Lekka (2015) provide some relevant history on the National Hospital.

[6] Critchley and Critchley (1998 chap. 8); and see Greenblatt (1977) and Bassiri (2016) on the conceptual development of Jackson's approach to pathology.

than undermines, quite a strict conception of localisation. Thus in Jackson's work, the reflex theory should not be thought of as excluding a localisation theory.

This difference is indicative of the fact that the notion of the reflex has its own complex history and has been employed by physiologists with radically different theoretical allegiances. George Canguilhem's *La Formation du Concept de Réflexe*, is especially relevant here.[7] The purpose of the work is to correct the account promulgated by "mechanist" physiologists, such as Emil du Bois-Reymond and Frank Fearing (1930/1964),[8] who have claimed that the reflex was discovered by figures acknowledged by them as intellectual predecessors in a lineage of mechanists, with credit given largely to René Descartes. Canguilhem's thesis is that the concept of the reflex emerges from work by anatomists and physiologists in a "vitalist" tradition which includes Thomas Willis in the seventeenth century, and John Augustus Unzer and George Procháska in the eighteenth.

This of course raises the question of whether we should accept the terms "mechanist" and "vitalist" as applicable to research spanning such a sweep of history. It bears emphasis that for Canguilhem "vitalism" does not entail any mysticism regarding the natural world, or even any metaphysical commitment to vital forces. Instead it can be characterised as positivistic approach in which biological phenomena are taken on their own terms and explanations referring to physical or chemical processes are not demanded.[9] One might call this a "biocentrism". In Section 3 I will dwell on the "biocentrism" in Jackson's work, which stands in contrast to the mechanistic dimensions of his theorising which I examine elsewhere (AUTHOR). I argue that Herbert Spencer's *Principles of Biology* is an important source for Jackson's biocentrism.

[7] See Schmidgen (2014) for a summary of Canguilhem's work on this subject. See also Roger Smith (1992, 2016) and Stanley (2015, chapter 6) on the social and political context of debates of reflexes and free will in Victorian Britain.
[8] T. H. Huxley is natural company here, but strangely he is absent from Canguilhem's narrative. Smith (2016, p.23) discusses Huxley's uptake of the reflex theory.
[9] Canguilhem (1955/2015, p.113); Lenoir (1994, p.9) makes the same point; see Allen (2005) on the distinctions between "mechanism" and "vitalism" or "organicism".

The contrast made by Ann Harrington in *Reenchanted Science*, between *holistic* approaches in biology and those that are atomistic, mechanistic, and reductive, is particularly useful to my investigation because it is broad enough to cover a range of interrelated tendencies within 19th and early 20th century science.[10] Harrington's focus is on the movement in Germany between the wars that includes Gestalt psychology, the ecology of von Uexküll, and the neurology of Kurt Goldstein (1878-1965), and is itself understood as a reaction against the arch-mechanism of the previous generation. That generation is represented by the "organic physicists" whose careers began around 1850: Hermann von Helmholtz, Emil du Bois-Reymond, Ernst Brücke and Karl Ludwig. They collectively sought to establish a "science which had extended the causal-mechanistic mode of understanding to include living phenomena" (Harrington 1996, p.7) and launched polemics against any notions that smacked of vitalism in the work of their forebears, including their teacher Johannes Müller (Finkelstein 2013, p.64-65).

It is useful to compare the German cohort with their contemporary in England, the comparative biologist Thomas Henry Huxley (1825-1895). Matthew Stanley (2015) characterises his public lectures and other forms of activism as aimed primarily at institutionalising a "naturalistic" approach in science, which is contrasted with the British tradition of research continuous with natural theology. Like his German counterparts, Huxley was fond of drawing analogies between living organisms and man-made devices employed for similar functions – such as the horse and the steam engine – buttressing the comparison with reference to the recently discovered law of conservation of Energy.[11] For both Huxley and du Bois-Reymond, the epitome of scientific explanation is both reductive (explanation via decomposition into microscopic component parts) and mechanistic (demonstrating how the local causal interaction between such parts brings about the macroscopic phenomenon) (AUTHOR forthcoming).

[10] Note that the terminology of "holistic" as opposed to "atomistic" or "dissective" figures heavily in Goldstein's *The Organism* (1934/1995).

[11] "A living body is a machine by which energy is transformed in the same sense as a steam-engine is so, and all its movements, molar and molecular, are to be accounted for by the energy which is supplied to it." (Huxley "The Progress of Science", quoted in Stanley 2015:200); cf. Helmholtz (1861).

It is an important point for my study that teleological explanation is excluded by this approach. For one thing, reference to long-range goals or purposes in nature is eschewed in favour of description of local causal interactions of the sort described in classical physics and chemistry. Huxley's conversion to Darwinism was, argues Stanley (2015, pp. 52-61), most strongly motivated by its potential to render teleology, and hence natural theology, obsolete, a strategy comparable to that of du Bois-Reymond in his lecture on Darwin (1879). The central claim of this paper, presented at length in Section 4, is that Jackson's notion of representation is distinctive in its synthesis of seemingly irreconcilable teleological and mechanist strands of thought. This might strike the reader as amounting to the claim that Hughlings Jackson was a "teleomechanist" as characterised by Timothy Lenoir in *The Strategy of Life.* I should here pre-empt this interpretation by pointing out the differences between my account of Jackson and Lenoir's account of the post-Kantian tradition of German biology.

Firstly, I do not claim to have found vestiges of Kant's *Critique of Judgement* in Jackson's writing on the nervous system. The terms most associated with Kant's writing on biology, like "natural purpose" (*Naturzweck*), are not employed by Jackson. While it could be argued that Jackson is indirectly connected with this tradition, via the mediation of Herbert Spencer, it is left for scholars of Spencer to settle the question of whether he should be thought of as a teleomechanist.[12] Secondly, Lenoir relies heavily on Lakotos' theory of scientific research programmes to describe teleomechanism. I do not find this useful when approaching Jackson, especially because Jackson's corpus of writings forms an irregular structure of interrelated theories and observations which do not arrange themselves neatly into Lakatosian constructs such as the "hard core" and "protective belt." Thirdly, Lenoir sets up "reductionism" and "vitalism" as two ends of a spectrum in which "teleology" occupies the middle ground (1982, p. 9). This way of arranging terms is problematic as it blends together differences over methodology, ontology, and preferred accounts of explanation.

[12] Taylor (2007, p.69) does employ this classification.

To summarise, I have found it beneficial to frame my analysis of Jackson's account of brain representation in terms of a contrast between two rather loose constellations of ideas and approaches in physiological psychology and biology which I will place under the general headings of "reductive" and "holistic". In the next Section I describe the reductionistic influences on Jackson's thought, with emphasis on British associationist psychology and the reflex theory of the nervous system, in particular the anatomist Charles Bell. Section 3 presents the holistic side of the picture, with particular attention to Spencer's theory of the role of the nervous system in arranging progressively more elaborate "correspondences" between external environment and the inner domain of the organism. Section 4 makes the case that Jackson's notion of representation is best understood as a synthesis of these contrary tendencies. Thus there is a tension in Jackson between the idea of representations as the states of the sensory-motor system which constitute the elements of reductive explanations of behaviour and mental life, and a holistic picture in which representations serve to co-ordinate the actions of all parts of the organism, an "integrative action" (to borrow Sherrington's phrase) which cannot be understood unless the goals of the animal are taken into account. Jackson was himself a highly influential figure, and I offer a brief discussion of his twentieth century legacy in Section 5, noting that the holistic aspect of the concept of neurological representation is erased in at least one important instance – Penfield's "homunculus."

2. REDUCTIVE TENDENCIES IN BRITISH PHYSIOLOGICAL PSYCHOLOGY

Here I examine two significant influences on Jackson's concept of brain representation: the "ideas" or "impressions" of British empiricist psychology and the reflex theory of the nervous system as presented by Thomas Laycock. As many have noted British empiricist "ideas" are ancestors of contemporary notion of brain "representations" (e.g. Rorty 1979). The proposal that complex mental states are compounded from atomic ideas or impressions, according to laws of association, has been highly significant in the history of psychology, and British psychology in the 19th century was dominated by associationist theory. Furthermore, as Harrington (1996, p. 14-15) argues, associationism is an atomistic

vision of the mind in which simple ideas are the elements via which complex thought processes can be reductively explained. For this reason, associationist psychology was a target of criticism for those such as William James (1890) who advanced a more holistic picture of the mind.

Hughlings Jackson was particularly influenced by the sensory-motor version of associationist psychology, one that melded psychology with recent discoveries in neuroanatomy and neurophysiology. In his "Study of Convulsions" of 1870 Jackson asks,

> "What can an 'idea,' say of a ball, be, except a process representing certain impressions of surface and particular muscular adjustments? What is recollection, but a revivification of such processes which, in the past, have become part of the organism itself?" (Hughlings Jackson 1985/1931, p.26)

These two rhetorical questions suggest that there is indeed an empiricist imprint on his thought. But whereas the British empiricists of the 17th and 18th centuries claimed that the "idea" of a ball came about with the association of relevant experiences received via the five senses (sensory "ideas" in Locke or "impressions" in Hume), by the nineteenth century equal weight is placed on motor experiences – intentions to move and experiences of the "muscular sense", such as feeling of strain or tension in particular muscles.[13] Jackson even claims that motor representations are part of the substrate of "visual ideas" (1931/1985 p.53). Here he cites arguments from the psychological works of Alexander Bain (1818-1903) and Herbert Spencer (1820-1903). But in order to give an account of this distinctive version of British empiricism it is worth going back to the work of the surgeon and anatomist, Sir Charles Bell.

Charles Bell (1774-1842) is best known for his discovery of the dedicated sensory and motor functions of the posterior and anterior branches of the spinal nerve roots,

[13] As Jackson elsewhere states, "there must be a motor, as well as a sensory, element in the nervous arrangement in the 'organ of mind' which is faintly discharged when we 'think of' an object." (Hughlings Jackson 1931/1985 p.54); see Smith (2016, chapter 5) for a detailed discussion of the version of British empiricism that posits a "muscular sense", attending movement and agency.

respectively, and his conception of the sensory-motor nervous system.[14] In contrast to earlier opinion which posited that a single nerve fibre could play a role both in sensation and motor control, and that the cerebral cortex had a uniform function, Bell reports that there is specialisation of function in both the central and peripheral nervous system (Bell, 1833a, p.6).

It might be imagined that in his forthright assertion of the principle of localisation of function in the brain and nervous system Bell was giving expression to the phrenology that was fashionable in the Edinburgh of his youth. However one historian, Carin Berkowitz, takes his ideas about the brain to be relatively untouched by phrenology, though deeply affected by the philosophical atmosphere of the late Scottish Enlightenment, in which the thought of David Hume and Thomas Reid continued to resonate.[15]

Bell's exposure to British empiricist philosophy, and in particular Reid's theory of perception, is evident in his Bridgewater Treatise on natural theology of 1833, *The Hand its Mechanism and Vital Endowments, as Evincing Design.* Here is a telling excerpt from a chapter on the senses:

> The impression on the nerve can have no resemblance to the ideas suggested in the mind. All that we can say is, that the agitations of the nerves of the outward senses are the signals, which the Author of nature has made the means of correspondence with the realities. There is no more resemblance between the impressions on the senses and the ideas excited by them, than there between the sound and the conception raised in the mind of that man who, looking out on a dark and stormy sea,

[14] The priority of Bell's report of dedicated sensory and motor nerves was, of course, disputed by the French physiologist, François Magendie and this principle of separation of functions is now known as the Bell-Magendie Law (Berkowitz 2015 chapter 5).
[15] See Berkowitz (2015:7). One of Bell's teachers was William Cullen, an associate of David Hume; another was the philosopher Dugald Stewart, who had himself been a student of Thomas Reid. Bell's correspondence with his brother George, following his move to London, indicates that found it worthwhile to read Locke's *Essay Concerning Human Understanding*, and that he valued the opinion of Dugald Stewart on his new manuscript on the brain (Bell 1870).

> hears the report of cannon, which conveys to him the idea of despair and shipwreck. (Bell, 1833b, p.170).

The taxonomy of inner states which includes both "impressions" and "ideas" is of course most commonly associated with Hume. Bell's twist is that he denotes with the word "impression" not a kind of mental state but an "agitation" of the nerve belonging to a sense organ. "Ideas", in contrast, are those *mental* states elicited by nervous activity, where the sensory modality of the idea is specific to type of nerve stimulated.[16]

Bell departs from the empiricism of Locke and Hume in emphasising that perception is an active bodily process, not just the passive reception of sensory nerve irritations (Cf. Berkowitz 2014:380-1). More precisely, Bell presents the case that in infancy all the other senses are reliant on the sense of touch for their correct development[17], and that the sense of touch requires both movement of the hand and awareness of this action:

> When treating of the senses, and showing how one organ profits by the exercise of the other, and how each is indebted to that of touch, I was led to observe that the sensibility of the skin is the most dependant of all on the exercise of another quality. Without a sense of muscular action or a consciousness of the degree of effort made, the proper sense of touch could hardly be an inlet to knowledge at all. I am now to show that the motion of the hand and fingers, and the sense or consciousness of their action, must be combined with the sense of touch, properly so called, before we can ascribe to it the influence which it possesses over the other organs. (Bell 1833b:192-3)

[16] Bell (1833b:172): "Every impression on the nerve of the eye, or of the ear, or on the nerve of smelling, or of taste, excites only ideas of vision, of hearing, of smelling, or of tasting; not solely because the extremities of these nerves, individually, are suited to external impressions, but because the nerves are, through their whole course and wherever they are irritated, capable of exciting in the mind the idea to which they are appropriate and no other."

[17] Reminiscent of Berkeley's contention that tactile experience is needed in order for the infant to associate visual sensations with the correct perception of distance. Smith (1973:89-91) credits Berkeley for inspiring a sustained interest during the 19th century in the role of touch and the motion sense in the acquisition of knowledge, and the view of the primacy of touch was widespread in that era.

We arrive at what Roger Smith (1973:83) calls the "sensory-motor model of nervous function". So when Hughlings Jackson (1931/1985 p.41) states that, "the *substrata* of mentation are sensori-*motor* processes"[18] (emphasis original), he should be understood as standing very much within this tradition.

In essence, the idea is that complex mental states are concatenations of the simple sensory and motor impressions which are sent to and from the brain via the dedicated nerves. The study of neural anatomy and physiology is the examination of the biological underpinnings of our psychological states. Moreover, the sensory-motor theory does not claim that there are no mental functions beyond sensation and motor control, but instead it asserts that sensory-motor processes are what underlies them:

> This does not….. exclude the other so-called 'function' of the cerebral hemisphere, 'ideation, 'consciousness,' etc. Sensori-*motor* processes are the physical side of, or as I prefer to say, form the anatomical substrata of, mental states. It is with these substrata only that we, in our character as physicians and physiologist, are directly concerned. (Hughlings Jackson 1931/1985 p.49)[19]

Such ideas were widespread in Jackson's time and place -- an intellectual movement which Danziger (1982) and Smith (1973) refer to as British "physiological psychology". It is quite likely that the direct sources for Jackson's empiricist and associationist theorizing were the psychological works of Herbert Spencer and Alexander Bain. For instance, Jackson quotes Spencer's *Principles of Psychology* in a statement on the importance of touch reminiscent

[18] Given the context of the quotation, I take it that by "processes" Jackson means "activities" and not "nerve threads" as anatomists then used the word.

[19] Hughlings Jackson (1932/1985 p.64) tells us that this picture is also shared by Ferrier*:* "Ferrier agrees with me in thinking that the whole anterior part of the brain is motor, and that, to use his words, 'mental operations….must be merely the subjective side of sensory and motor substrata' (*Functions of the Brain*)". This raises the question of their position on the mind-body relationship, which I discuss in another paper (AUTHOR).

of the passage from Bell quoted above.[20] The following summary of Spencer's associationist psychology and physiology could equally well describe Jackson:

> the organism's interaction with its environment leads to it experiencing sensations. These sensations provide the basic building blocks of the mind, the subjective counterparts to …. reflex actions ….. Just as memory, reason and will are constructed from the compounding and re-compounding of reflexes, so, subjectively, the higher mental faculties are created from the compounding and re-compounding of basic atoms of experience according to the mechanism of the association of ideas. (Taylor 2010:80)

The passage just quoted brings our attention to the reflex theory which I will now discuss in relation to Thomas Laycock (1812-1876).[21] Jackson had been a student of Laycock at the medical school in York from 1852-1856, and he continued to give credit to Laycock's ideas in his writings on epilepsy and localisation. In a passage quoted at the very start of Jackson's pamphlet of 1875, "On the Anatomical and Physiological Localisation of Movements in the Brain", Laycock states:

> the brain, although the organ of consciousness, is subject to the laws of reflex action; and … in this respect it does not differ from the other ganglia of the nervous system. (Laycock, 1845:298; quoted in Hughlings Jackson 1931/1985 p.37)

It had been a matter of dispute in the mid 19th century whether the nervous tissue of the cerebral cortex had a different function and constitution from the rest of the nervous system.[22] Marshall Hall (1790-1857) and Johannes Müller had by then accumulated

[20] "as Spencer says (*Psychology*, Part 24, p.358), 'tactual impressions are those into which all other impressions have to be translated before their meanings can be known' " Hughlings Jackson (1931/1985 p.75).

[21] The connection between Jackson and Laycock is discussed extensively by Greenblatt (1965). Laycock himself has received surprisingly little scholarly attention. It is worth noting that Laycock received some of his medical education in Germany and translated texts by Unzer and Prochâska (Laycock 1851), physiologists whose studies of the reflex Canguilhem places in the "vitalist" tradition.

[22] As Greenwood (2010:283) relates, Pierre Flourens (1794–1867), François Magendie (1783–1855), Paul Broca, (1824–1880) and Johannes Müller (1801–1858) all posited that the there was an important distinction between the voluntary actions generated by the cortex and the reflexive functions of the lower brain and spinal cord.

detailed knowledge of the peripheral nerves supporting reflex responses: the sensory afferent which receives the stimulus (e.g. a prick to the toe) and sends an impulse to the spinal cord, from where it is relayed to a motor nerve, initiating the stereotyped movement (e.g. withdrawal of the toe). Laycock and Jackson asserted that the workings of the brain were reflexive at all levels, though differing in the predictability of the response given any sensory stimulation, and also in reaction times. As such the same kinds of sensory-motor response mechanisms, replicated innumerable times, comprise the cerebral cortex as well as the peripheral and spinal nerves and sub-cortical structures of the brain. In this view they were joined by T.H. Huxley and Herbert Spencer (Richards, 1987:283).

It is useful here to quote a passage from Laycock (1845:303), which argues that the brain, like the lower nervous structures, mediates sensory-motor reflexes, and at the same time generates and associates ideas:

> We must consider then each half of the encephalon as consisting of two tracts of cortical, and two of medullary substance; the medullary associating ideas and combining muscular movements; the cortical, conducting impressions to the gray matter, giving rise to sensation and perception, and thence to the muscles, exciting motion. That impressions received by the sensitive nerves excite trains of ideas is generally acknowledged… .

With the reflex picture in place, the word "representation" can be used just to indicate what kind of reflexive movement the neural tissue is involved with – whether it involves the hand, foot or cheek, flexion or relaxation of a muscle. While Laycock does not talk of movements being "represented", I believe this notion is conveyed instead by his use of the term "inscribed":

> an infinity of muscular acts are already inscribed within the structure of the anterior gray matter of the spinal ganglia, and require only the appropriate sensory impression to rouse them into action. (Laycock, 1845:303)

In a similar vein, Hughlings Jackson (1931/1985 p.61) describes the reflex as combining "processes representing sensation and those representing motion". We can say *what* any

nerve or brain structure represents if we know its causes (sensory stimuli) or observe its effects (motor responses).

This is what I refer to as the reductive and mechanistic notion of representation. For one thing, it rests on nothing more than a *causal relationship* between the representation and its external object. This should be contrasted with notions of an *intentional relationship* between representation and what it symbolises, one which cannot simply be identified with a causal chain connecting the two (Ramsey 2007). On the purely causal view, representations are amenable to mechanistic explanation because what it takes to explain how a representation arose is to describe the sequence of causes leading up to it, and the biological mechanism this casual chain is embedded in (e.g. walking, speaking). Furthermore, the amalgamation of associationist psychology with the reflex theory allows one to explain representations reductively, as constituted from mental or physiological atoms – for example, brain traces due to movements in individual muscles, or momentary sensory stimuli.[23]

3. HOLISTIC OUTLOOKS IN THE PHILOSOPHY OF HERBERT SPENCER

The topic of this section is the second strand of thought in Jackson's conception of representation – the holistic theme that stands in apparent tension to the reductive one presented above. This holism comes with a top-down, functional approach the explanation of living systems, and I will show how this can be gleaned from Spencer's evolutionary philosophy. While the reflex theory just sketched presents a vision of the nervous system as a sequence of physically determined operations that together give rise to intelligent behaviour – finding its most exaggerated form in T.H. Huxley's picture of "conscious automata"[24] – the central argument in favour of extending the application of reflex theory

[23] It is worth comparing this with the combination of associationist psychology and reflex theorising in Meynert's early work (Guenther 2015, p.26ff)
[24] Huxley (1875), and see critical responses from W. B. Carpenter (1875) and James (1879); discussed in Stanley (2015, chapter 6) and Smith (2016, chapter 3).

from the peripheral nervous system into all regions of the brain comes from comparative and evolutionary biology. This is as much true for Laycock (1845) writing fifteen years before the publication of the *Origin of Species* as it was for Huxley and Jackson in the 1870's and 80's. Thus, particular attention must be paid to Spencer's theory of evolution which at the time was as influential as Darwin's.

The 1875 pamphlet that begins with a statement of Laycock's reflex theory states subsequently that,

> the cerebral hemisphere is made up of processes representing impressions and movements. It seems to me to be a necessary implication of the doctrine of nervous evolution as this is stated by Spencer. (Hughlings Jackson 1931/1985 p.42)

Similarly, at the start of his third Croonian Lectures Jackson argues, on the basis of evolutionary continuity, for the sensory-motor theory and for the uniformity of function in all areas of the nervous system (peripheral, spinal and cerebral). He declares, "[i]f the doctrine of evolution be true, all nervous centres must be of sensori-motor constitution" (Hughlings Jackson 1932/1985 p.63).

Various commentators have discussed the extensive influence of the systematic philosopher, Herbert Spencer, on Jackson.[25] According to Spencer's Lamarkian and progressivist theory, evolution is the advance from "lower" (less complex and specialised) to "higher" (more complex and specialised) forms. The same process is as much in play in the development of an individual animal from the homogeneous mass of an egg white to the differentiated form of the chick, as it is in the evolution of a sophisticated vertebrate species from its simple, wormy ancestors.[26] The structures within an organism, like the nervous system, make manifest this homogeneous-to-heterogeneous trajectory, and so the directed process of evolution serves as a key to understanding the arrangement of the resulting forms.

[25] Greenblatt (1965); Critchely & Critchley (1998, chapter 7); Smith (1982b); Feuerwerker et al. (1985). It is worth also noting the influence of phrenology on the young Spencer (Richards 1987, p.251).

[26] For discussion see Gould (1977:31); Smith (1982a); Richards (1987:282-294); Taylor (2010, chapter 4).

Jackson employs the notion of *dissolution* – Spencer's term for the reverse of the process of evolution – to account for neurological disease. In the dissolution of the nervous system, the highest, most evolved structures are lost and the resulting neurological symptoms are the result both of the loss of the highest functions and the loss of the control of the lower centres that used to be enacted by the highest centres:

> The doctrine of evolution implies the passage from the most organised to the least organised, or, in other terms, from the most general to the most special. Roughly, we say that there is a gradual 'adding on' of the more and more special, a continual adding on of new organisations. But this 'adding on' is at the same time a 'keeping down.' The higher nervous arrangements evolved out of the lower keep down those lower, just as a government evolved out of a nation controls as well as directs that nation. If this be the process of evolution, then the reverse process of dissolution is not only 'a taking off' of the higher, but is at the very same time a 'letting go' of the lower. If the governing body of this country were destroyed suddenly, we should have two causes for lamentation: (1) the loss of services of eminent men; and (2) the anarchy of the now uncontrolled people. (Hughlings Jackson 1932/1985 p.58)[27]

In his "Croonian Lectures on Evolution and Dissolution of the Nervous System" of 1884, Jackson states that the motor nervous system consists of a three-level hierarchy: at the bottom, the anterior horn cells of the spinal cord and nuclei of the motor cranial nerves; in the middle is "Ferrier's motor region" (primary motor cortex); the highest level is to be found in the most anterior region of the cortex. In the following passage from the second Croonian Lecture, each level of the hierarchy is said to represent the body (not movements) in a distinctive way, differing from the other levels with respect to complexity and "directness" of the representation:

> The lowest centres are the most simple and most organised centres; each represents some limited region of the body indirectly, but yet most nearly directly; they are representative. The middle motor centres are the convolutions making up Ferrier's

[27] Such political analogies, common in Victorian Britain, are discussed extensively by Roger Smith in *Inhibition* (1992).

> motor region. These are more complex and less organised, and represent wider regions of the body doubly indirectly; they are re-representative. The highest motor centres are convolutions in front of the so-called motor region…… The highest motor centres are the most complex and least organised centres, and represent widest regions (movements of all parts of the body) triply indirectly; they are re-re-representative. (Hughlings Jackson 1932/1985 p.53) [28]

This passage, of course, raises the question of what is meant by these structures being "representative", "re-representative", etc.. In the light of Laycock's reflex theory, it is plausible to interpret these passages as claiming that the lowest motor centres are part of the mechanism for simple, predictable, stimulus-response reflexes, such as blinking when a projectile approaches the eye. They represent a body part "most nearly directly" in the sense that activity here is the proximal cause for movement in that part. These centres are most "organised" in that they are inflexible and stereotyped and cannot be incorporated into complex, planned actions. In contrast, the highest centres are part of the mechanism for the complex, skilful actions over which we apparently have conscious control. Even though skilful actions are on a continuum with the simplest reflexive movements, because of their complexity they do not occur unless a higher centre is there to co-ordinate the appropriate sequence of muscle operations. The highest centre is least "organised" in the sense that the movements it orchestrates are flexible, not always predictable from observation of sensory stimuli, and can be combined with other movements into novel and complex sequences. The highest centres are an indirect cause of muscle contractions and so are said to represent those movements only indirectly.

An implication of the reflex theory is that all bodily actions are produced by reflexes of greater or lesser complexity, and none are attributed to a supra-physiological mind or Will. Reflexes, however elaborate, are still just physical cause and effect chains – complex organic mechanisms. However, there is reason to think that Jackson means more by

[28] Elsewhere Jackson states that it is *movements* that are represented, not simply body parts. E.g. "The higher the centre the more numerous, different, and more complex, and more special movements it represents" (Hughlings Jackson 1932/1985 p.30).

"representation" of bodily movements in neural tissue than just shorthand for the downstream causal effects of activation in that tissue. In the 1875 pamphlet, Jackson also discusses representation as a matter of the organism's adjustment to its environment:

> What peripheral parts of the organism do their nervous arrangements of cells and fibres represent or re-represent? Or in still other words, What particular adjustment of the organism to the environment, or of parts of the organism to one another, do they represent? (Hughlings Jackson 1931/1985 p.49 fn1)

Herbert Spencer defines *life* as, "the continuous adjustment of internal relations to external relations" (Spencer 1870, p.293). The above quoted passage obviously echoes Spencer's definition, and later in the pamphlet Jackson relates this concept to the reflex theory. In the "lower centres" there is "a direct adjustment of few and simple movements to few and simple peripheral impressions" (Hughlings Jackson 1931/1985 p.60). These are the simple reflexes. The "higher centres" can likewise be understood as housing sensory-motor reflex mechanisms but ones where the motor response is not inevitable and occurs with some delay. We are told that,

> In the very highest centres there is a similar adjustment, but then it is of exceedingly special movements (representing movements of the whole organism) to the most special impressions from the environment. (Hughlings Jackson 1931/1985 p.60)

In other words, the reflexes mediated by both the higher and lower centres facilitate the organism's adjustment to its environment. But the most "evolved", higher centres are responsible for adjustments in which both the sensory stimuli and movements elicited are "special" – by which, I presume, he means that such stimuli cannot be reduced to very simple patterns (e.g. presence or absence of light) and the movements are elicited are skilful ones. Furthermore, Jackson's notion of centres which re-represent movements has a parallel in Spencer's idea that the cerebellum and cerebrum are centres of "doubly-compound coordination" (Smith 1982a p.77, Smith 1982b p.251). Here the contrast is between centres which co-ordinate adjustments to stimuli currently present in the environment, and the higher centres which ensure that behaviour is well-adjusted to objects far off in space and time.

It is important that Jackson, in describing the highest centres, emphasizes their representation of "movements of the whole organism" rather than select parts. This bears on the point to be discussed in Section 4, that Jackson is not a strict "localiser". The assumption here is that the most complex learned actions, from sword fighting to writing, require the motor control centres to have a sense of the comportment of the whole body and its changing configuration in space. Therefore an extremely localized representation of movements in body parts is not sufficient to govern these – the highest centres must integrate "information" (to use an anachronistic term) about the state of the whole organism. This is in fact what Hughlings Jackson states in his "Remarks on Evolution and Dissolution":

> The highest centres are, we repeat, nothing else than centres of universal and most complex, etc., representation, or what is equivalent of universal and most complex, etc., co-ordination. There is nothing else for them to represent than impressions and movements. ….. They are the unifying centres of the whole organism, and thus the centres whereby the organism *as a whole* is adjusted to the environment. (Hughlings Jackson 1932/1985 p.81-82)

It is important to appreciate that such claims are buttressed by a Spencerian notion of evolutionary progress occurring along *multiple dimensions*, where increasing specialization occurs in tandem with increasing "integration" and "co-operation" (Hughlings Jackson 1885, p.945). Along with the tendency towards more complex and specialised movements and centres controlling them, those higher centres also become more integrated with one another, meaning that they become more mutually inter-dependent and also better able to co-ordinate their actions for the benefit of the organism as a whole (Taylor 2010:62-63; Feuerwerker et al. 1985:208-9). So while Spencer explicitly rejects teleological agency, divine operation, and vitalistic forces in his account of evolution, he does, arguably, embrace the teleological thinking of the German embryologist von Baer (Taylor 2010:69-70; Gould 1977:30-32), who put it that biology requires a set of explanatory principles beyond physics and chemistry to account for

organism level co-ordination in such processes as metamorphosis and embryogenesis (Caneva 1990; Richards 2009:38).

This gives us a clue that "co-ordinations" and "representations" of Jackson's highest cortical centres are thought not to be explicable in the simple cause and effect terms of the lower reflex mechanisms, but instead call for analysis in terms of the actions of the whole organism. In short, while the operations the lower centres sit well in a reductive theory of the nervous system, the higher centres necessitate a theory which posits that the parts of the system are directed towards a goal defined by the whole organism. In the 1875 pamphlet, Hughlings Jackson makes a striking comparison between the body's representation in the brain and in reproductive cells. In arguing that it is indeed conceivable that there be a representation of the entire body, including the viscera, within the brain, Hughlings Jackson gives this as a proof of possibility:

> there is a case in which it is plain that a very small part of the body (the germ cell) represents the whole of the man it is detached from; so much so that it 'potentially contains' even the tone of his voice and tricks of manner. (Hughlings Jackson 1931/1985 p.48)

This comparison is clearly stated, but it raises its own questions about what "represents" would mean for Hughlings Jackson given the theories of development prevalent in his time. This could be an allusion to the epigenetic theory of von Baer who, as Richards (2009:59) relates, "understood individual development as a consequence of the essence (*Wesenheit*) or idea of organization present already in the just-fertilized egg".[29] However, in another

[29] Spencer (1864: §52) endorses von Baer's description of the stages of embryogenesis, and notes the similarity between his own theory of evolution and that of Schelling, a prominent figure in *Naturphilosophie*. In this passage we see Spencer (1864: p.376) invoking both bottom-up and top-down influences, from whole organism to component parts, and vice versa:

> "Various classes of phenomena compelled us to conclude, that each kind of organism is composed of physiological units, having certain peculiarities which force them to arrange themselves into the form of the species to which they are peculiar. And in the chapters on Genesis, Heredity, and Variation, we saw reason to believe, that while the polarities of the physiological units determine the structure of the organism as a whole; the organism as a whole, if its structure is changed by incident forces, reacts

puzzling passage Jackson (1932/1985 p.81-82) writes that, "[u]sing old-fashioned language they [i.e. the 'highest centres'] are potentially the whole organism; the whole organism is 'potentially present' in them." One might speculate that with the phrase "old fashioned language" Jackson is alluding to the preformationist theory of development which was out of favour by the 1830's (Gould 1977:29). On such accounts, the adult organism is present in the germ in a literal way.

4. INTEGRATIVE REPRESENTATIONS AND THE ISSUE OF LOCALISATION

With both strands in place – the mechanistic and reductive ones – it is now feasible to see how these apparent contraries are synthesised within Jackson's concept of representation. I introduce the term "integrative representation" to refer to this synthetic concept. Before examining this, it is worth briefly recapping the material presented above. The idea of the highest centres as having a holistic, integrating function – representing the whole organism by having it "potentially present" in those centres – would seem to be in tension with the pared down, mechanistic notion of representation as merely shorthand for the cause and effect relationships of sensory-motor reflexes, the notion which was derived from the empiricist tradition and from the reflex theory as presented by Laycock. From the most reductive, mechanistic perspective, the organism is governed by a causal chain of action and reaction, which can be explained just in terms of the states of the small component parts of the system and the local interactions between them. From the integrative one, the most evolved mental faculties, through their ability to co-ordinate and direct the operation of components throughout the whole body, ensure that the most successful adjustment between environment and organism will occur. Such a system can only be explained in a non-reductive, top-down fashion, with reference to the goals of the entire system and how these impact on the states of the parts.

Jackson was not unique in his positing of what I call "integrative representations" at the summit of the nervous hierarchy. In his 1887 "Remarks on Evolution and Dissolution of

> on the physiological units, and modifies them towards conformity with its new structure."

the Nervous System" Jackson notes his "great satisfaction" to find the psychiatrist Charles Mercier in agreement with his views, quoting from Mercier:

> Thus we arrive at this most important conclusion: that the highest nervous processes, which form the substrata of the most elaborate mental operations, represent at the same time not only the most elaborate forms of conduct and muscular movements, but also *every part of the organism* (italics in original) in some degree. (Hughlings Jackson 1932/1985, p.82)[30]

Jackson goes on to summarise his opinion in the following way:

> The assertion I make is that the *physical basis* of the ego represents – that is, that the highest centres represent – or co-ordinates the whole organism in most complex, etc., ways. Just as the consciousness of the moment is, or stands for, the whole person psychical, so the correlative activities are of nervous arrangements, representing the whole person physical. (Hughlings Jackson 1932/1985, p.82)

In spite of the fact that Jackson was not the only one of his contemporaries to present the idea of neural representation in a holistic light, this aspect of Jackson's views seems to have caused particular problems for subsequent interpreters. Questions have arisen over whether body parts, muscles or movements were represented in the cortex, whether or not Jackson endorsed localisation of function, and what in fact was meant by the term "representation". For example the neurologist William Gooddy (1956) complains at length that a major problem with Jackson's writings on the topic is that he never defines "representation". Francis Walshe (1961:128) disputes Gooddy's criticism, writing that Jackson often equates the term with "localization" and also with "coordination", and that he "makes it clear that a cortical region 'representing' movements is thereby to be understood to contain neural structures engaged in processes which initiate and determine movements." While various passages do support Walshe's reading[31], Jackson does occasionally write of representation of body parts rather than representation of movements.

[30] On the same page Jackson quotes Théodule Ribot, "Le moi est une co-ordination".
[31] In particular: "[m]ethod of representation and localization are only different names for one thing" (Hughlings Jackson 1932/1985 p. 33); "the two things – representation and co-ordination – are really one" (Hughlings Jackson 1932/1985 p. 41)

For example, in the "Study of Convulsions" paper of 1870 where, according to Gooddy (1956:171), Jackson first mentions the idea of representation in the central nervous system, it is parts of the body that are represented:

> "Parts which have the most varied uses will be represented in the central nervous system by most ganglion cells." (Hughlings Jackson 1870/1970 p.186)

When presenting his account of localisation and brain representation, Jackson took the condition of paralysis to be just as relevant as epilepsy (Hughlings Jackson 1931/1985 p.63), though his research on convulsive disease is more well known. He contrasted the "discharging lesions" which cause epilepsy via the erratic over-excitation of connected tissue, with the "destroying lesions" which cause paralysis. Jackson relates the "simplest case" of a hemiplegia which demonstrates a localised representation of movement in the corpus striatum, a subcortical brain structure involved in motor control:

> A blood clot which has destroyed part of the corpus striatum has made an experiment, which reveals to us that movements of the face, tongue, arm, and leg are represented in that centre. This is the localization of the movements anatomically stated. Hughlings Jackson (1931/1985 p.63)

However, Jackson did not subscribe to a strict theory of localisation, one which posits a one-to-one mapping between brain areas and specific functions. For instance, in the 1882 paper, "On some implications of dissolution of the nervous system", Hughlings Jackson (1985/1932, pp.33-344) contrasts his position both with that of the "universaliser" (denier of localisation) and the "localiser" who thinks that there is a "centre for… [e.g.] the movements of the face only, one for those of the arm only", and so on. Jackson tells us that the description of movements as if only happening in one specific body part is "artificial" and stated for convenience of exposition (p.35). In reality, different regions of the body must co-operate in order for successful movement to occur, and this is reflected, Jackson believes, in the organisation of the brain, such that the hand area is also, in part, an arm area. This is also known as the theory of *preponderant* representation. As Foerster (1936 p.141) explains,

> According to his [Jackson's] doctrines a single part of the body, let us say the thumb, is represented *preponderatingly* in one part of the cortex, but it is represented in other parts of the precentral convolution as well, although in a different degree and in different combinations with other parts of the body.

While Walshe (1961) informs us that Jackson uses "to represent" synonymously with "to co-ordinate", this again raises the question of what such "co-ordination" might mean for Jackson. Here it is worth examining a passage on the pathology of motor control in epilepsy from the second Croonian Lecture. Jackson uses an analogy with a naval command structure to explain how the "discharging lesions" of epilepsy can lead to more systemic disturbances than the local paralysis caused by non-epileptogenic lesions:

> the case analogous to the epileptic fit, is when one of the twenty-four highest navy officials becomes occasionally insane. Then by issuing foolish orders to lower officials, 'discharging downwards,' he produces widespread and yet slight disturbance in the navy. But, by wrongly advising his colleagues, 'discharging collaterally,' he leads them to issue foolish orders to lower officials; leads them to 'discharge downwards.' Thus, by a multiplication of foolish orders, the whole navy is severely and universally 'convulsed.' (Hughlings Jackson 1985/1932, p.55)

The commonplace metaphor of the brain as the control centre for the body is not often so richly illustrated as it is here. It is important to note that in the naval command analogy, the controllers, the highest officials, are the same kind of thing (i.e. human beings) as the entities controlled (the lower officials). This is different from the metaphor of the instrument and instrumentalist which Jackson elsewhere warns us against as an analogy for motor control (Hughlings Jackson 1931/1985 p.42), emphasising the continuity between the lower level motor system and highest mental faculties. An important point about Jackson's idea of representation is that, unlike the computational notions prevalent today, it has none of the connotation of representations being "disembodied" or abstracted from

their biological basis, as software is from hardware.[32] On the basis of the naval board analogy, it is tempting to read "represent" as meaning the same thing as "govern" or "command". However, Jackson disavows any association between brain "representation" and "representative government" (Hughlings Jackson 1985/1932 p. 99 fn).

In sum, Jackson presents a highly *integrative* notion of representation. Cerebral representations are not strictly associated with individual body parts or muscle movements, but somehow holographically represent the entire region of the body relevant to the movement, even the whole body, while at the same time co-ordinating or controlling more local parts. Furthermore, these representations do not pertain to a mental or computational domain that is dualistically separated or abstracted away from the corporeal nervous system. For Jackson, representations are neurological and not psychological, and the "controlling centres" in the brain are fully integrated into the body in its entirety.

5. THE AFTERLIFE OF JACKSON'S SYNTHESIS

The 20th century was the century of the brain. That is to say, it was the first era in which the various disciplines that had played a role in the discoveries of nervous structure and function -- medicine, physiology, anatomy, cell biology, etc. -- organised themselves into the interdisciplinary science which we now know as neuroscience. It is noteworthy that the major protagonists in this disciplinary formation, some of whom will be discussed below, very deliberately placed themselves in the lineage of the 19th century masters, and Jackson's name is often invoked in this context. However, as we will see, the uptake of his

[32] In the 1875 pamphlet Jackson cites contemporary authors who argued that mental function could not be understood without examining the brain in conjunction with the rest of the body:

> "Every psychical fact is a product of sense work, brain work, and muscle work" (Lewes, *Problems, etc.* quoted in Hughlings Jackson 1931/1985 p.42)
>
> "Bain writes that the organ of the mind 'is not the brain by itself; it is the brain, nerves, muscles, organs of sense and viscera.' " (Hughlings Jackson 1931/1985 p.47)

George Henry Lewes was the partner of Marian Evans (George Eliot) and an associate of Herbert Spencer.

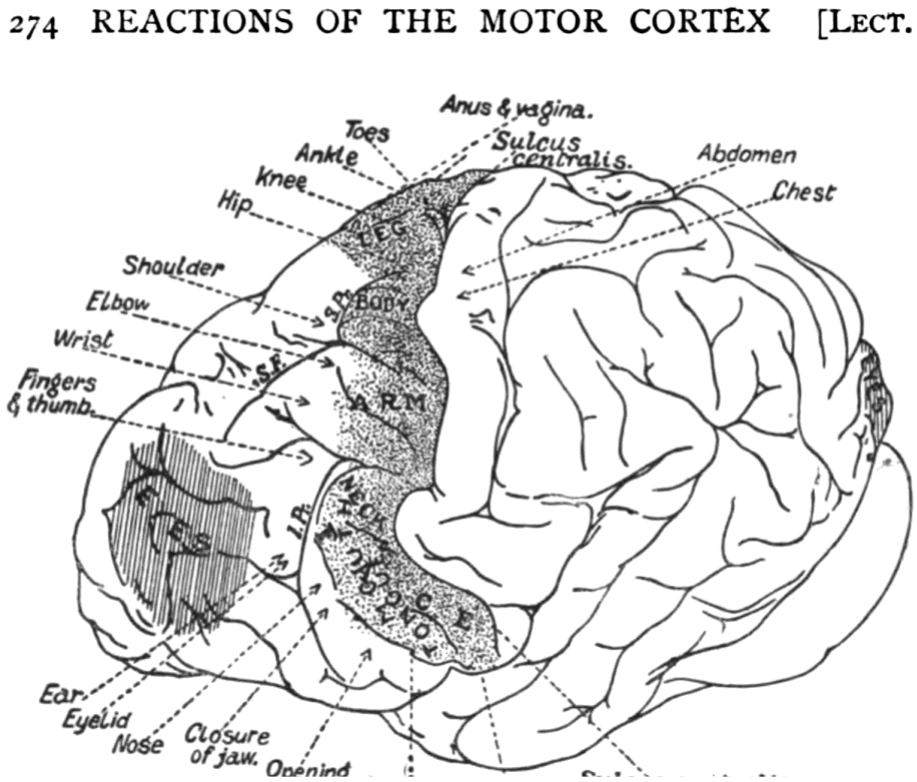
ideas was selective, and the more exotic and Spencerian of them do not make their way much into the next century.

Sir Charles Sherrington (1857-1852) played a leading role in the disciplinary formation just mentioned (Casper 2014, Smith 2000). Sherrington's Silliman lectures on "The Integrative Action of the Nervous System" set the stage for neurophysiology in the 20th century. The title ostensibly invokes the Spencerian concept of integration, and this idea is clearly in play in the following passage:

> The integrating power of the nervous system has in fact in the higher animal, more than in the lower, constructed from a mere collection of organs and segments a functional unity, an individual of more perfected solidarity. (Sherrington, 1906:353)

Feuerwerker et al. (1985) argue that Spencer's evolutionary philosophy looms large for Sherrington, via the influence of Hughlings Jackson. But in Sherrington the strongly progressivist elements, and those that remind us of the teleological thinking of von Baer, are now gone. We are no longer told that the representation of the entire body in the highest centres of the cortex is an evolutionary apex (Sherrington 1906:288).

FIGURE 1



Motor cortex map of chimpanzee brain from Sherrington (1906 p.274).
This reproduces work first published by Grünbaum and Sherrington in 1901.

In a passage reminiscent of Jackson, Sherrington writes of "preponderant" representation (1906 p.269) and warns us against overly simplistic interpretations of brain maps:

> The discovery of localization of function in parts of the cortex has given the knowledge which now supplies to the student charts of the functional topography of the brain much as maps of continents are supplied in a geographical atlas. The student looking over the political map of a continent may little realize the complexity of the populations and states so simply represented. We looking at the brain chart of the text-book may never forget the unspeakable complexity of the reactions thus rudely symbolized and spatially indicated. (Sherrington, 1906:270)

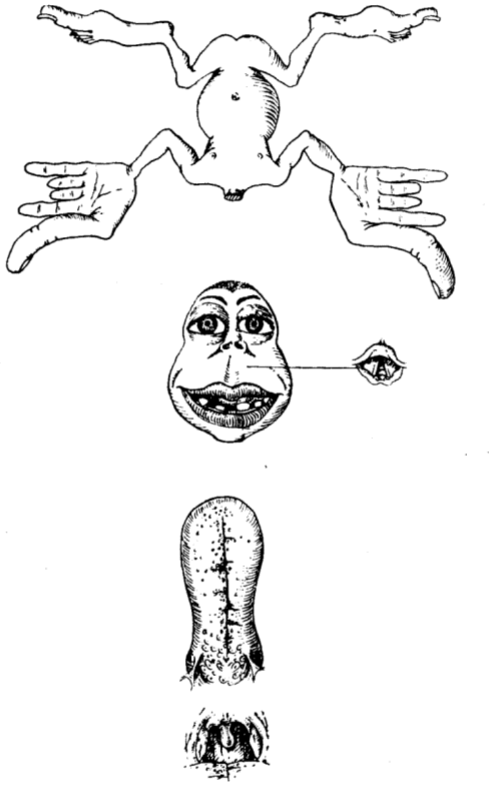
It is worth juxtaposing Sherrington's warnings against the simplistic interpretation of findings of functional localisation with that icon of strict localisation in the 20th century,

Penfield's homunculus. This controversial creature[33] was born in 1936 when the American born neurosurgeon, Wilder Penfield (1891-1976), enlisted the artist Hortense Douglas Cantile (1901-1979) to give a graphical rendering of the results of stimulation of the cortices of 163 epileptic patients. In these operations, points on both the motor and somatosensory cortex received electric current, and any resulting muscle twitches or local bodily sensations were noted. Although the mapping between the co-ordinates of the point of stimulation and the bodily area affected varied from patient to patient, and from one operation to another even for one patient, the homunculus aimed to capture some generalisations regarding the nature of the body's representation in the brain – for instance, that certain body parts, such as the thumb and tongue, always had a disproportionately large cortical representation.

[33] E.g. Walshe (1957:232) "Nor are the moderns content with maps, for *homunculi* and *simiusculi* have now made their horrid appearance, lineal descendants of Lewis Carroll's Jabberwock, purporting to depict the fair face of nature, but in fact achieving something quite unnatural." On the controversy, see Arminjon (2009), Pogliano (2012), Synder and Whitaker (2013) and Ward (2014).

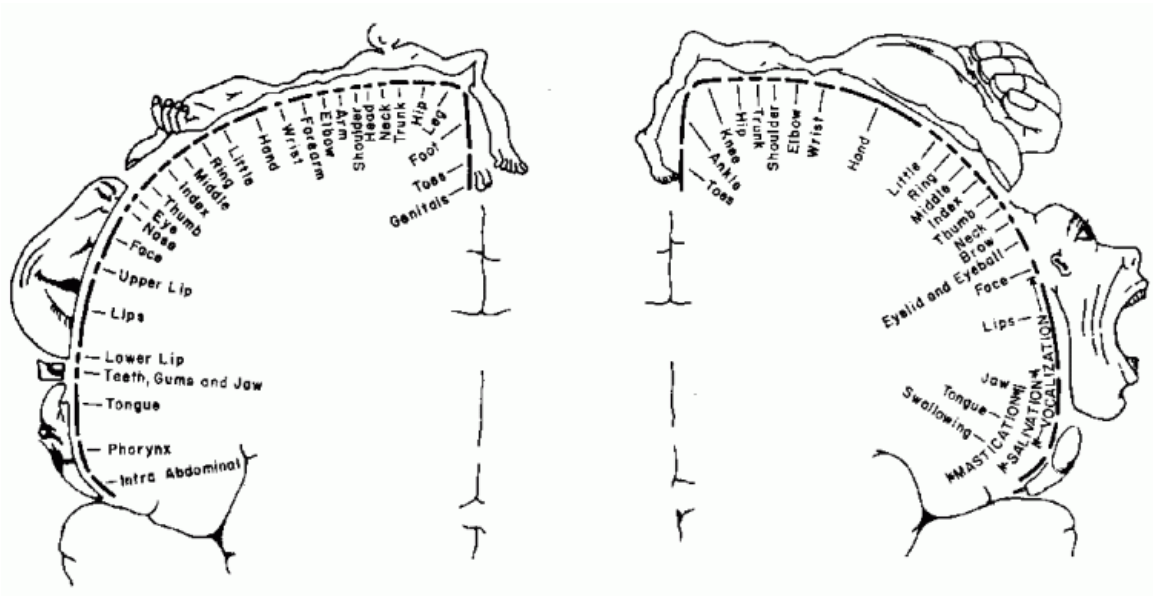
FIGURE 2

a) The homunculus of Penfield and Boldrey (1937). "The homunculus gives a visual image of the size and sequence of cortical areas, for the size of the parts of this grotesque creature were determined not so much by the number of responses ….. but by the apparent perpendicular extent of representation of each part when these responses were multiple for the same part" Penfield and Boldrey (1937:431-2). For example, the thumb and lips are exaggerated in size, indicating that a disproportionately large area of the cortex will yield responses in those parts when electrically stimulated.



b) The sensory (left) and motor (right) homunculus of Penfield and Rasmussen (1950, p44 and p.57), also drawn by Hortense Cantile. In the legend for the sensory version, Penfield and Rasmussen state that, "The right side of the figurine is laid upon a cross section of the hemisphere, drawn somewhat in proportion to the extent

of sensory cortex devoted to it. The length of the underlying block lines indicates more accurately the comparative extent of each representation."



c) The "Brainchildren" sculpture by Hortense Cantile, commemorating the opening of the McDonnell wing of the Montreal Neurological Institute -- a charming rendering of the idea of the body's representation in the cortex.

As with the more prosaic cortical atlas (Figure 1), the homunculus lends itself to conceptual service in the theory of strict localisation. This is particularly the case with the homunculus drawn draped over the cortex (Figure 2b). What it depicts on paper is a one-to-one correspondence between a location in the brain and a body part and either a movement (motor cortex homunculus) or a felt sensation in a specific part of the body (sensory homunculus). What it does not show, but is evident in the text and data tables printed along with it, is that movements can be elicited from stimulation of the cortex posterior to the Rolandic fissure (which has been classified by Penfield as a dedicated somatosensory region), and vice versa, stimulation to the motor area anterior to the Rolandic fissure often generates bodily sensations (Penfield and Rasmussen 1950, p.22 and p.46). So functions are not cleanly designated in these two regions.

One of the harshest critics of Penfield's work, and his homunculus, was Francis Walshe (1885-1973), a neurologist of the National Hospital in London. The themes of his criticisms are, firstly, that electrical stimulation experiments cannot reveal the true functional organisation of the cortex, and secondly, that the strict localisationist theory is a mistake which could be avoided if more attention were paid to the writings of Hughlings Jackson. For example he tells us that:

> The method of punctate electrical stimulation inevitably led to the evocation of small muscular movements, what Sarah Tower was later to call 'discrete movements,' and thus to a concept of what Jackson called 'abrupt geographical localizations' and to the 'cortical mosaic' of Fulton. Jackson maintained that no hypothesis of an integrative function for the cortex could be built on such foundations (Walshe 1961:120).

Walshe argues that the error of over-reliance on stimulation experiments and the neglect of careful clinical observation is compounded by the representation of the results of such experiments in graphical form, including the standard genre of brain cartography of the sort shown above in Figure 1 (Walshe 1953: 26). Yet already in the 1930's it had been argued by Foerster that stimulation experiments do not support the thesis of strict localisation, and that more subtle styles of graphical representation could better convey the

functional organisation of the cortex, with its anomalies and exceptions to strict localisation:

> The inconstancy of the effects and the variation of the responses of one and the same spot to repeated stimulations can be demonstrated in almost every focus of the precentral convolution. Each focus contains not only elements of the part of the body represented preponderatingly in that focus, but also elements of other parts of the body. The foci of the different parts of the body are not like the stones of the mosaic to which they were compared, but they overlap to a more or less considerable degree. The anterior central convolution does not resemble a painting of cubistic style, it reveals rather the intimate mixture of soft colours and smooth forms of a Raphaelitic Madonna (Foerster 1936 p.142-3).

We might fancy that in settling for the clearly delineated homunculus and recognisably human cartoon, Penfield missed an opportunity to have the strangeness of the brain's representation of the body in motion depicted artistically. This would be an alien creature indeed. Instead, Penfield settled for a depiction which was useful but limited. In a letter from 1946 which responds to some of Walshe's criticisms, Penfield gives a candid assessment of his homunculus:

> "it was", he tells us, "one of a number of illustrations which we used to try to illustrate the truth. Of course, there is nothing like the homunculus as far as cortical representation is concerned, but it seems to be the only sort of thing that people in general understand. I would gladly kill the damn thing if I could, but that is never possible."[34]

The idea that the brain houses a representation of both states of the body, and affairs in the external world, and that activity in sensory regions of the cortex are the bases of mental states which represent far-off stimuli, is as central to neuroscience now as it was to the physiological psychology and neurology of the 19th century. But of course the concept has "evolved". My examination of Jackson's concept of representation has seen us on a long

[34] Letter from Wilder Penfield to Francis Walshe, August 20th, 1946. Permission needed, Osler Library, McGill University

journey back to the British empiricists and ending with the homunculus of the mid 20th century. In current neuroscience, notions of representation are influenced by theories in cognitive science whereby mental representations, analogous to symbolic states of a computer, are the elements of the psyche. One aim of the integrative discipline of cognitive neuroscience is to explain neural responses in terms of mental representations, and vice versa. A question worth pondering is the extent to which the computational understanding of integration and co-ordination in the nervous systems, reliant as it is on the language of information processing and coding, is a replacement for or descendent of the evolutionary thinking of Spencer and Hughlings Jackson.

ACKNOWLEDGEMENTS

…….

BIBLIOGRAPHY

Allen, G. E. (2005) "Mechanism, vitalism and organicism in late nineteenth and twentieth-century biology: the importance of historical context". *Stud. Hist. Phil. Biol. & Biomed. Sci.* 36:261-283.

Arminjon, M. (2009) "L'homoncule de Penfield. Une icône neuropsychologique ?" *EspaceTemps.net,* Travaux, 20.07.2009 http://www.espacestemps.net/articles/homoncule-penfield/

Bassiri, N. (2016) "Epileptic insanity and personal identity: John Hughlings Jackson and the formations of the neuropathic self." In D. Bates and N. Bassiri (eds.) *Plasticity and Pathology: On the formation of the neural subject.* New York: Fordham University Press.

Bell, C. (1833a) *The Nervous System of the Human Body Embracing the Papers Delivered to the Royal Society on the Subject of the Nerves.* Washington: Stereotyped by Duff Green, for the Register and Library of Medical and Chirurgical Science.

Bell, C. (1833b) *The Hand, Its Mechanism and Vital Endowments as Evincing Design.* London: William Pickering.

Bell, C. (1870) *Letters of Sir Charles Bell Selected from his Correspondence with his Brother George Joseph Bell.* London: John Murray.

Berkowitz, C. (2014). "Charles Bell's seeing hand: Teaching anatomy to the senses in Britain, 1750–1840". *History of Science* 52(4):377–400

Berkowitz, C. (2015). *Charles Bell and the Anatomy of Reform.* Chicago: Chicago University Press.

Caneva, K. L. (1990). "Teleology with Regrets". *Annals of Science* 47:291-300

Canguilhem, G. (1955/2015) *La Formation du Concept de Réflexe aux XVIIe et XVIIIe Siècles.* Paris: J. Vrin.

Casper, S. T. (2014a). *The Neurologists.* Manchester: Manchester University Press

Casper, S. T. (2014b). "History and Neuroscience, An Integrative Legacy". *Isis. 105:123–132*

Critchley, M and E. A. Critchley (1998) *John Hughlings Jackson: Father of English Neurology.* Oxford: Oxford University Press

Danziger, K. (1982). Mid-nineteenth century British psycho-physiology: A neglected chapter in the history of Psychology. In M. Ash and R.W. Woodward (Eds.), *Psychology in nineteenth century thought: International cross-disciplinary perspectives*. New York: Praeger

du Bois-Reymond, E. (1879) "Darwin versus Galiani". Translated by J. Fitzgerald. *Popular Science Monthly.* 14:409-425.

Fearing, F. (1930/1964) *Reflex Action.* New York: Hafner Publishing Company.

Ferrier, D. (1876/1984). *The Functions of the Brain.* Birmingham, Al: Gryphon Editions (The Classics of Neurology & Neurosurgery Library).

Feuerwerker, E., P. Couillard and Y. Gauthier (1985) "Herbert Spencer's Influence on the Genesis of Sherrington's Concept of the Integrative Action of the Nervous System." *Bull Can Hist Med.* 2(2):205-18.

Finkelstein, G. (2013) Emil du Bois-Reymond: neuroscience, self, and society in nineteenth-century Germany. Cambridge, MA: MIT Press.

Foerster, O. (1936) "The Motor Cortex in Man in Light of Hughlings Jackson's Doctrines" *Brain,* 59:136-159.

Goldstein, K. (1934/1995) *The Organism.* New York: Zone Books.

Gooddy, W. (1956) "Cerebral Representation" *Brain* 79:166-187.

Greenblatt, S. H. (1965) "The major influences on the early life and work of John Hughlings Jackson." *Bulletin of the History of Medicine*. 39:346-376.

Greenblatt, S. H. (1969) "Hughlings Jackson's first encounter with the work of Paul Broca: The physiological and philosophical background." *Bulletin of the History of Medicine* 44(6): 555-570.

Greenblatt, S. H. (1977) "The development of Hughlings Jackson's approach to diseases of the nervous system 1863-1866: Unilateral seizures, hemiplegia and aphasia." *Bulletin of the History of Medicine.* 51:412-430.

Greenwood, J. (2010) "Whistles, bells, and cogs in machines: Thomas Huxley and epiphenomenalism." *Journal of the History of the Behavioral Sciences,* 46(3), 276–299.

Gould, S. J. (1977). *Ontogeny and Phylogeny.* Cambridge, MA: Belknap/Harvard University Press.

Guenther, K. (2015). *Localization and its Discontents.* Chicago, IL: Chicago University Press.

Harrington, A. (1987). *Medicine, Mind, and the Double Brain.* Princeton, NJ: Princeton University Press.

Harrington, A. (1996). *Reenchanted Science.* Princeton, NJ: Princeton University Press.

Hécaen, H and G. Lanteri-Laura (1977) *Evolution des connaissances et des doctrines sur les localisations cérébrales.* Desclée De Brouwer.

Helmholtz, H. v. (1861) "Application of the laws of conservation of force to organic nature." *Railway Times* 13(23):222 and 233.

Hughlings Jackson, J. (1870/1970) "A Study of Convulsions" *Archives of Neurology* 22:184-188

Hughlings Jackson J. (1885, Nov. 21) "The Bowman Lecture on Ophthalmology and Diseases of the Nervous System." *British Medical Journal.* Pp.945-949.

Hughlings Jackson, J. (1931/1985) *Selected Writings of John Hughlings Jackson: Volume 1, On epilepsy and epileptiform convulsions.* J. Taylor (ed.) Birmingham, Al: Gryphon Editions (The Classics of Neurology & Neurosurgery Library).

Hughlings Jackson, J. (1932/1985) *Selected Writings of John Hughlings Jackson: Volume 2, Evolution and dissolution of the nervous system; speech; various papers, addresses, and lectures.* J. Taylor (ed.) Birmingham, Al: Gryphon Editions (The Classics of Neurology & Neurosurgery Library).

Huxley, T. H. (1875) "On the hypothesis that animals are automata, and its history". *The Eclectic Magazine of Foreign Literature (1844-1898);* Jan 1875; 21, 1;

Kerr, P. B., A. J. Caputy, N. H. Horwitz (2005) "A history of cerebral localization". *Neurosurg. Focus* 18(4):E1-3

Laycock, T. (1845) "On the Reflex Function of the Brain" *The British and Foreign Medical Review* 19(January-April):298-311.

Laycock, T. (1851) Trans and ed. *The principles of physiology, by John Augustus Unzer; and a dissertation on the functions of the nervous system, by George Procháska.* London: Printed for the Sydenham society.

Lekka, V. (2015) *Neurological Emergence of Epilepsy.* Berlin: Springer.

Lenoir, T. (1982) *The Strategy of Life.* Dordrecht: D. Reidel Pub. Co.

Lorch, M. P. (2004) "The Unknown Source of John Hughlings Jackson's Early Interest in Aphasia and Epilepsy". *Cog. Behav. Neurol.* 17(3): 124-132.

Lorch, M. P. (2008) "The merest *Logomachy*: The 1868 Norwich discussion of aphasia by Hughlings Jackson and Broca". *Brain* 131: 1658-1670

Penfield W and Boldrey E (1937): Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain* 60: 389–443.

Penfield W, Rasmussen T (1950): *The Cerebral Cortex of Man: A Clinical Study of Localization of Function*. New York, The Macmillan Company. Pogliano C (2012): Penfield's homunculus and other grotesque creatures from the Land of If. *Nuncius* 27(1): 141–162.

Ramsey, W. R. (2007) *Representation Reconsidered.* Oxford: Oxford University Press.

Richards, R. J. (1987). *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior.* Chicago: Chicago University Press.

Richards, R. J. (2009) *The Meaning of Evolution: The Morphological Construction and Ideological Reconstruction of Darwin's Theory*. Chicago: Chicago University Press.

Rorty, R. 1979. *Philosophy and the Mirror of Nature*. Princeton: Princeton University Press.

Schmidgen, H. (2014) "The life of concepts: Georges Canguilhem and the history of science." *Hist. Phil. Life Sciences* 36(2):232-253.

Sherrington, C. S. 1906 *The Integrative Action of the Nervous System*, New York: Charles Scribner's Sons

Smith, C. U. M. (1982a) "Evolution and the Problem of Mind: Part I. Herbert Spencer" *Journal of the History of Biology,* 15(1):55-88

Smith, C. U. M. (1982b) "Evolution and the Problem of Mind: Part II. John Hughlings Jackson " *Journal of the History of Biology,* 15(2): 241-262

Smith, R. (1973) "The Background of Physiological Psychology in Natural Philosophy". *Hist. Sci.* 11: 75-123

Smith, R. (1992) *Inhibition: History and Meaning in the Sciences of Mind and Brain.* Berkeley, CA: University of California Press.

Smith, R. (2000) "The embodiment of value: C. S. Sherrington and the cultivation of science". *British Journal for the History of Science* 33(3):283 - 311

Smith, R. (2016) *Free Will & the Human Sciences in Britain 1870-1910.* Pittsburgh: University of Pittsburgh Press.

Snyder PJ, Whitaker HA (2013): Neurologic heuristics and artistic whimsy: The cerebral cartography of Wilder Penfield. *Journal of the History of the Neurosciences* 22(3): 277–291.

Spencer, H. (1864) *Principles of Biology, vol 1,* First edition. London: Williams and Norgate.

Spencer, H. (1870) *Principles of Psychology, vol 1,* Second edition. London: Williams and Norgate.

Stanley, M. (2015) *Huxley's Church & Maxwell's Demon.* Chicago: Chicago University Press.

Star, S. L. (1989) *Regions of the Mind.* Stanford, CA: Stanford University Press.

Taylor, M. (2007) *The Philosophy of Herbert Spencer*. London: Continuum.

Tizard, B. (1959) "Theories of brain localization from Flourens to Lashley." *Med. Hist.* 3(2):132-145.

Walshe, FMR (1953) Some problems of method in neurology. *Canadian Medical Association Journal* 68(1): 21–29

Walshe, F. M. R. (1957) "Some reflections upon the opening phase of the physiology of the cerebral cortex, 1850-1900." In *The Brain and its Functions.* Springfield, IL: Charles C. Thomas.

Walshe, F. M. R. (1961) "Contributions of John Hughlings Jackson to Neurology: A Brief Introduction to His Teachings" *Archives of Neurology* 5:119-131

Ward, Z. (2014) "Letter to the Editor: Reexamining Penfield's Homunculus" *Journal of the History of the Neurosciences*, 23:198–203

Young, R. M. (1990) *Mind, brain, and adaptation in the nineteenth century : cerebral localization and its biological context from Gall to Ferrier.* Oxford: Oxford University Press.