THEORIES OF BRAIN LOCALIZATION FROM FLOURENS TO LASHLEY

by

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Introduction

A history of theories of localization of function in the brain can be found more or less briefly outlined in Boring (1929 and 1950) and Lashley (1929). Both writers point out that all such theories can be broadly divided into two types—localization theories, which hold that specific functions are controlled by specific parts of the brain, and field theories, which hold that the brain acts as a single functional unit. It is said that, historically, a swing of the pendulum tends to occur between these two positions. At one period the majority of informed opinion holds a localization theory, but a generation later this tends to be considered distinctly unorthodox.

Too much can be made of this distinction. Localization and field theories, as defined above, have not been held since the time of Gall. The first achievement of Flourens, usually regarded as the founder of field theory, was to show that the different parts of the brain have specific functions: he claimed that only the hemispheres act as a single functional unit. Later field theorists further restricted this claim. Nevertheless, the distinction between localization theorists and field theorists is broadly valid. The purpose of this article is to examine the factors responsible for the 'swing of the pendulum', that is, for the development and general acceptance of successive theories.

Two factors are shown to be important. The development of a new theory of localization depends partly on the development of new and more refined techniques of investigation, and partly on the nature of current psychological preconceptions. This is because such a theory must involve assumptions about psychological processes and brain function, and the models of brain function are themselves determined by psychological preconceptions. In the past these assumptions have been explicit. It is argued that the implicit assumptions of contemporary localization theory could usefully be examined, and brought into line with contemporary psychology.

I. Flourens' Field Theory

Theories of localization of function can be traced back as far as Aristotle, but the work of Pierre Flourens (1794–1867) was the first to be based on experiment, and Flourens is today recognized as the founder of the modern field theory of brain function.

He was undoubtedly a great physiologist. His experiments were systematic, his observations were always repeated, and they were made on a number of subjects. Using the methods of extirpation and stimulation he was the first

https://doi.org/10.1017/S0025727300024418 Published online by Cambridge University Press

to show experimentally that different parts of the nervous system have different functions. He concluded that the function of the spinal cord is conduction, that movement is controlled by the cerebellum, the vital functions by the medulla, and perception, memory, and will by the hemispheres.

In 1824 he put forward the first scientifically based theory of equipotentiality within the hemispheres.

> All sensations, all perceptions, and all volition occupy concurrently the same seat in these organs. The faculty of sensation, perception, and volition is then essentially one faculty.

He was the first to state the principles of equivalence of structure and of mass action.

> As long as not too much of the lobes is removed, they may in due time regain the exercise of their functions. Passing certain limits, however, the animal regains them only imperfectly, and passing these new limits it does not regain them at all. Finally, if one sensation comes back, all come back. If one faculty reappears, they all reappear. . . . This shows that each of these organs is only a single organ.

Again, like later field theorists, he emphasized the integration of the nervous system.

> In the last analysis . . . all the essential and various parts of the nervous system have specific properties, proper functions, distinct effects, and in spite of this marvellous diversity they constitute nevertheless a unified system. When one point in the nervous system becomes excited, it excites all others; one point irritated, irritates all. There is community of reaction. Unity is the great reigning principle (Flourens, 1824).

All this, of course, constitutes a field theory of brain function more thoroughgoing than any held since. No one today would be prepared to support the proposition that there is no localization of sensory function in the cortex, and that 'if one (sense) comes back, all come back'. Indeed, as will be shown, there was a good deal of evidence to the contrary available at the time. Nevertheless, Flourens' theories were at once generally accepted and remained orthodox doctrine for over forty years. There were two important reasons for this. Firstly, the techniques of stimulation and extirpation were too crudely developed to reveal much localization of function, and the knowledge of neuroanatomy then available too limited. The only parts of the brain distinguished were medulla, corpora quadrigemina, cerebellum, and the hemispheres; it was not known in what way, if any, grey and white matter differed in function. In the following experiment, for example, on which Flourens based his principle of equipotentiality, it is certain that he must have extirpated more than the hemispheres, and that septic and oedematous processes must have resulted in generalized damage of an unknown extent. He removed, 'layer by layer', different parts of both cerebral lobes of a pigeon, and found that the animal's sight weakened with each new extirpation until it was totally lost, and that 'from the moment that sight was gone, hearing was gone too; and with it went all intellectual and sensory faculties'.

https://doi.org/10.1017/S0025727300024418 Published online by Cambridge University Press

The same criticism must be made of another ingenious experiment, designed to show that memory is a function of the whole hemispheres. He placed an obstacle immediately in front of the blind eye of a frog with one cerebral lobe removed, and noted that

it would at first hit the object when it jumped, but, reminded by the shock, it would later remember its position and did not fail to avoid it, even though I had blindfolded its other eye, I removed the second lobe. The frog immediately lost sight and memory. It threw itself twenty times against the same obstacle, something which no frog does either in the intact state or with one lobe removed nor even if both eyes are extirpated.

It is known now, however, that the frog is hardly incapacitated by loss of its hemispheres under aseptic conditions; and Flourens' frog must have suffered much more extensive damage.

II. Flourens' concept of mind

Secondly, Flourens' theories were accepted because they were perfectly compatible with contemporary philosophical assumptions. The theory that the brain is a homogeneous organ was not new, but had been current since the sixteenth century. It was believed that the brain is the organ where the mind, an immaterial *unitary* substance, operates on the body. Flourens' doctrine of the unity of the nervous system, 'action commune', was an expression in physiological terms of this concept. It was generally held that psychological processes could not be localized, since they are only aspects of a unitary spirit. Flourens' contemporary, the great physiologist Johannes Müller, discussing localization, argued:

the mind is a substance independent of the brain and hence . . . a change in the structure of the brain cannot produce a change in the mental principle itself, but can only modify its actions. . . . The loss of portions of the cerebral substance . . . cannot deprive the mind of certain masses of ideas, but diminishes the brightness and clearness of conceptions generally (Muller, 1838).

Earlier anatomists, such as Willis (1621–75), who had shown by dissection that the pons and medulla are subsidiary parts of the cerebellum, and that from them arise the nerves supplying the lungs, heart, and stomach, had concluded that the cerebellum and cerebrum have distinct functions. These conclusions were not accepted because of the prevailing doctrine that the whole brain is a common 'sensorium', where impressions are received from the nerves and presented to the mind, and where the mind sends out its mandates to the moving parts. Flourens provided an experimental basis for the revision of this doctrine, confining the sensorium to the cerebrum. But he was primarily concerned to refute the phrenological theory of Gall (1758–1828). Gall described the location of thirty-seven different mental faculties, from cautiousness to amativeness, in different parts of the brain. Although he was a considerable anatomist, phrenology was as speculative a doctrine as the orthodox theory of the sensorium. It had tremendous popular appeal but it was bitterly attacked by most scientists and philosophers as irreverent and materialistic because incompatible with the concept of brain as a sensorium. Flourens' work was hailed as a convincing experimental refutation of this heresy, and a validation of orthodox concepts.

Consequently the observations that were incompatible with equipotentiality of the cortex were disregarded. Bell (1774–1842) had argued that the fact that separate nerve tracts lead to separate parts of the cortex indicates that these have distinct functions. It was pointed out by some that the insane are not usually blind and deaf. The experiments of François Pourfour de Petit were forgotten. This eighteenth-century French surgeon had adduced strong evidence that the control of movements of one side of the body is localized in the hemisphere of the other side. Contralateral hemiplegia was at the time ascribed to loss of fluid from the contralateral ventricle, which moved into the wounded ventricle to replace its lost fluid, with a resultant loss of power on the contralateral side. Petit opened the skull of an officer who had died from a rapier thrust beneath his right orbit, and who before death had sustained a complete left hemiplegia; he found pus pouring from a right anterior abscess, but nothing amiss in either ventricle. After a number of similar post-mortem observations he decided to operate on dogs, destroying various parts of their brain through a trephine hole, noting their loss of power, and then examining their brains. He observed that paralysis of the opposite side always ensued, and dissection led him to the discovery of the decussation of the pyramids (Rawson, 1927).

III. A new concept of brain

It has been argued above that, for an empirically based theory of specificity to develop, more refined techniques would be needed than were available to Flourens, and, for such a theory to be generally accepted, the orthodox concept of brain would have to be abandoned. The latter change occurred first. The essential preliminary to the more detailed assumptions of localization theory was an attempt to account for the workings of the nervous system in purely physical terms. The earlier semi-scholastic conception of the brain as a sensorium where mind interacted with body, the nerves being passive conductors of animal spirits, was replaced by an explicit determination to 'constitute physiology on a chemico-physical foundation' (Helmholtz, 1847, quoted in Boring). In 1848 du Bois Reymond demonstrated the electrical nature of the nervous impulse and in 1850 Helmholtz measured its speed. During the next decade reaction times began to be measured. No wonder that Müller hesitated to accept these discoveries with their implication that the nervous system is wholly orderly and physical.

During this period, too, it was discovered that the grey matter of the brain is cellular, that the white matter is fibrous, and that the fibres begin and end in the grey cells. The contemporary model of the brain, based on these observations and the new preconceptions, is described by the psychologist, Alexander Bain (1818–1903), in his book, *The Senses and the Intellect*, 1855. He states in his preface:

> Conceiving that the time has now come when many of the startling discoveries of Physiologists relative to the nervous system should find a recognised place in the Science of Mind, I have devoted a separate chapter to the Physiology of the Brain and Nerves.

In this chapter he compares the nervous system to a telegraph system, with a general terminus, the brain, from which wires proceed to substations, from which further wires proceed. The function of the nerves is solely to transmit impulses. The brain is also compared to a voltaic battery.

> The brain is not a sensorium where impressions are poured in and stored up. A stimulus or sensation acting on the brain exhausts itself in the production of a number of transmitted currents or influences. . . . The revival of the impression is the setting of the currents anew. . . . No currents, no mind (Bain, 1855).

Later, he expounds Flourens' doctrine of equipotentiality, combining this with the concept of the brain as a voltaic cell. Nevertheless, the change in attitude to cerebral functioning which was essential for a revision of Flourens' doctrine had occurred. 'No currents, no mind' is an assumption of startlingly materialist implications, compared with Müller's theory of twenty years earlier.

IV. The era of localization theory

The first outright opponent of the principle of homogeneity was Broca (1824–80). It is interesting that Broca was a pupil of Bouillaud, Professor of Clinical Medicine at La Charité, one of the few academic champions of phrenology. Bouillant had offered a sum of money to anyone who could produce the brain of an individual who had lost his speech, and in whom the anterior lobes presented no lesions. Broca found at the autopsy of a man whom he had recently examined and discovered to have no defect except inability to speak, a lesion at the base of the third frontal convolution of the left hemisphere. He announced in 1861 that this was the centre for speech, and drew broader conclusions.

> I believe in the principle of localisation . . . the totality of the convolutions does not constitute a single organ, but many organs or many groups of organs, and there are in the cerebrum large discrete regions corresponding to large discrete mental functions (Broca, 1861).

This generalization was based on rather inadequate evidence, since, as Marie showed later, of Broca's two original patients one had further lesions involving Wernicke's zone, and the second had a generalized cerebral wasting. He does not seem to have developed a theory significantly different from Gall's, and he would probably have attracted little attention had the opposition to Flourens not then become general.

It was pointed out above that Flourens had neither sufficiently refined techniques nor adequate knowledge of neuro-anatomy to develop an empirically based localization theory, even if he had wished. Forty years later there was an immensely increased understanding of the gross and microscopic structure of the brain, and its fibrous connexions. In the 1860's Hughlings Jackson was able to point out the relationship between convulsions on one side of the body and disease of the opposite hemisphere, and to conclude that the convolutions round the corpus striatum were directly concerned with contralateral movement. In 1870 Fritsch and Hitzig published their findings on the electrical excitability of the cortex, which had formerly not been considered irritable. They took special precautions to prevent haemorrhage and laceration, which abolish excitability, and showed that with a weak current different movements could be elicited from different parts of the anterior cortex of the dog. They further showed that excitation of similar points in different animals, and upon opposite sides of the brain in the same animal, produce similar results, and the removal of the excitable areas of one side of the brain interferes with the voluntary movements of the other side. Ferrier confirmed these facts by experiments with dogs and monkeys, and for the next thirty years physiologists were busy mapping out the cortex into areas according to function, using Flourens' methods of stimulation and extirpation—but with very different results.

What were the reasons for the general development and acceptance of theories of localization at this time? The obvious explanation, that areas of functional localization were found because in fact they existed and could be detected with the improved techniques, is inadequate. Most of the early localizations were wide of the mark—Ferrier insisted that the visual centre lay in the angular gyrus, and that the occipital lobes were the centre for visceral sensation. Extirpation of the frontal lobes was variously reported to produce paralysis of the trunk (Munk) or of the head and eye muscles (Ferrier), inattentiveness (Ferrier), and no detectable symptoms (Schafer). Tactile sensibility was localized in the cingular gyrus by Ferrier and Schafer, but Hitzig and Munk localized it coextensively with the motor area. Physiological techniques were still, in fact, very crude. Strong electric currents applied to the frontal lobes tended to excite the motor area. Although antiseptic measures were usually taken, septic processes must have confused many of the results. There was little understanding of the stages of recovery, so that the numerous symptoms occurring immediately after extirpation were referred to the site of lesion. Since the relation of cortex and subcortex was ill understood, any function remaining after a cortical extirpation seemed to prove that the function must be localized elsewhere in the cortex. Anatomical studies were very incomplete—Ferrier's mistaken localization of the visual cortex was probably caused by an unwitting severing of the optic radiation, and an incomplete removal of the occipital lobes. No wonder that the announcement of each new cortical centre provoked violent controversy from other physiologists, who claimed to have located the same function elsewhere. A detached observer, faced with the conflicting data, might well have agreed with Goltz (1882) that the hypothesis of circumscribed centres for special functions is untenable, and that there is no area of the cortex exclusively concerned with sight, hearing, smell, taste, touch . . . or the higher functions.

V. The assumptions of nineteenth-century localization theory

Goltz, however, was in an unpopular minority, and it seems reasonable to conclude that the physiologists of the last quarter of the nineteenth century interpreted their results as indicating the existence of local centres because of a prior conviction about the nature of the brain. An analytic trend was general in scientific thought at that time. The cell theory, originated by Schleiden, was developed by Virchow, Professor of Anatomy in Berlin. In 1858 he suggested that a disease originates within a single cell, and is propagated by malignant cell formation.

> Every animal [he wrote] is a sum of vital units, each of which possesses the full characteristics of life. . . . The composition of the major organism, the so-called individual, must be likened to a kind of social arrangement or society, in which a number of separate existences are dependent upon one another, in such a way, however, that each individual possesses its own peculiar activity and carries out its own powers (Virchow, 1858).

This emphasis on the discrete and diverse functions of the cells was echoed by the contemporary stress in psychology on the elementary particles of thought-ideas. Mental processes were almost universally understood at this time in terms of more and more complex associations of elementary ideas. The aim of Associationism, in fact, was

> to construct a psychology without a soul, by taking discrete ideas, and showing how, by their cohesions, such things as reminiscences, perceptions, emotions, volitions, passions, theories, and all the other furnishings of an individual's mind can be engendered (James, 1891).

Hence the assumption by physiologists that they should look for the elementary structures of the brain corresponding to its elementary functions.

The hypothesis generally held in the 'seventies, then, long before there was much evidence to substantiate it, was that the cortex is the surface of projection for every muscle and every sensitive point in the body. These different cortical cells were held to represent the elementary ideas of sensation and motion of which all mental processes are composed. The fibres between the cells represent the association between ideas, hence there was thought to be a complete and neat parallelism between brain processes and mental processes.

It is important to note the difference between the localization theory held by physiologists of this period and the older phrenologists. The difference depends on the development in the assumptions about mind and brain described above. The later localizers held that elementary motor and sensory functions were localized, but not the higher mental functions, still less traits such as 'hopefulness'. Some, for example, Ferrier, argued on mainly deductive grounds that intelligence is dependent on the frontal lobes. Psychology, the argument ran, has shown that all the higher thought processes can be explained in terms of the association of ideas, together with the power of attention. Intellectual attention involves implicit head and eye movements, and hence depends on the frontal lobes, which Ferrier had shown to be the centre for these movements (1886).

Other physiologists, unable to confirm Ferrier's experimental findings, adapted different theories. Munk, for example, argued that

> intelligence has its seat everywhere in the cortex of the brain and in no part in particular. Any lesion of the cerebral cortex whatsoever alters intelligence, all the more severely the more extensive the lesion, and this is always due to the loss of its groups of images or representations, simple or complex, which had their foundations in the perceptions that belong to the injured cortical area (Munk, 1890).

Thus, experimental observations similar to Flourens'—that intelligence does not depend on any one part of the brain, and that the greater the lesion, the greater the mental loss—were differently interpreted because of Munk's different preconceptions about the brain and mental functioning. Instead of concluding, like Flourens, that 'the faculties of perceiving, understanding, and willing constitute a single function', he claimed that intelligence results from co-ordination of a great many differently located elementary functions. Here is a particularly clear illustration of the way in which assumptions about mental processes have influenced the interpretation of findings in this field.

Later, however, it came to be generally accepted that the frontal lobes and certain posterior parts of the brain were 'silent', and not projection areas. In these areas the higher mental processes were said to be localized. Flechsig, the originator of this theory, considered that the function of these areas was to associate together the impressions received from the adjacent sensory and motor areas. The frontal lobes, for example, lying between the olfactory and tactile areas, combined the perceptions and memory traces of these areas. Flechsig was primarily an anatomist, and the experimental investigation of the theory was mainly the work of Bianchi, the last of this great school of physiologists. He argued that

> intelligence emanates from the play of sensory images . . . and of infinite combinations of these and other images not sensory in character. I believe it is permissible to suppose that this vast co-ordination . . . has its seat in an organ distinct from the organs of perception (Bianchi, 1922).

This organ he located in the frontal lobes, which until very recently have continued to hold this distinction. There was no question at any time during this period, however, of a specific localization of traits akin to phrenology. Such a doctrine was quite inconsistent with Associationist psychology, which held that any complex function was the result of an interaction between many simple functions, localized in various parts of the brain.

The influence of psychology on physiology at this period was remarkable. Observations were scanty, and the main emphasis in discussing residual defect after lesion was always on a theoretical and *a priori* analysis of the psychic mechanisms involved. Problems of brain function were either overlooked, or considered to be already solved by analogy with psychological laws. It was implicitly assumed that the laws of association adequately described the integration of the cortex, and text-books on the brain devoted much space to expositions of psychology. The sum of cortical cells was held to correspond to the sum of elementary ideas, and the way in which these combine was considered to be firmly established. A more sophisticated and later writer, William James, pointed out:

> If we make a symbolic diagram on the blackboard of the laws of association between ideas, we are inevitably led to draw circles, or closed figures of some kind, and to connect them by lines. When we hear that the nerve centres contain cells which send off fibres, we say that Nature has realised our diagram for us, and that the mechanical substratum of thought is plain. In some way, it is true our diagram must be realised in the brain, but surely in no such visible and palpable way as we at first suppose (James, 1891).

The physiologists, however, worked with this rather crude Associationism, untroubled by the problems of unity and connation which were already leading to the downfall of the doctrine.

VI. Lashley's Field Theory

Classical localization theory met with no important challenge until the publication in 1929 of Lashley's *Brain Mechanisms and Intelligence*. It has been argued above that the development of a new theory of localization depends both on the development of new techniques and on the nature of current psychological preconceptions. Lashley made use of new techniques in order to investigate the effect of brain lesion on intelligence, and interpreted his results in the light of a field theory of brain function and psychological processes. Nineteenth-century physiologists had no adequate techniques with which to assess the effects of cortical extirpation, and their descriptions were vague and impressionistic, for example, that the animal was 'reduced to idiocy'. Since cage behaviour may be almost unchanged after a clean-cut restricted extirpation, and special tests are needed to reveal the altered functions, it is not surprising that earlier physiologists concluded that mental changes result only from the most extensive ablations. The positive results of Ferrier and Bianchi were probably due to an operation that was more extensive than they supposed. However, none of the earlier experimental work can be adequately assessed since the details of numbers of animals used, the exact extent of operation, the period of time between operation and observation, and how the changed behaviour was assessed, were in most cases not recorded.

The first great contribution of psychologists to this field was the provision of objective techniques. Franz, in 1907, used methods evolved by Thorndike for the study of intact animals, to assess the effects of ablation. After bifrontal ablation of ten monkeys and cats, he found that the recently acquired ability to escape from a puzzle box was lost, but could be relearned in about as many trials as the first learning. He performed control experiments, cutting the dura mater only, excising only one frontal lobe, and excising other lobes of the brain (Franz, 1907). The basic advances in methodology had been made—that is, the use of objective tests that could be quantitatively scored, the procedure of training, operating, then retraining, and the use of experimental control. To these Lashley (1929) added the use of enough animals to allow for statistical analysis of results, and the attempt to assess the extent of lesion by post-mortem examination.

Running fifty rats through mazes before and after cortical lesion, Lashley found that the amount of impairment was roughly proportional to the extent of cerebral lesion, and that the same amount of impairment in maze learning is produced by equal amounts of destruction in any of the principal regions of the cortex. From these observations he deduced first the Principle of Equipotentiality, that the rat's cortex functions as a unit in maze learning and no one part of it has special significance, and, secondly, the Law of Mass Action, that the more cortex is available, the more rapid and accurate the learning. The degree of deterioration after injury is closely related to the complexity of the maze. These principles closely resemble Flourens', but Lashley restricted their application. Not every habit in the rat is governed by these principles. Brightness discrimination was disturbed only by lesions of the visual cortex, and he concluded that it is only the more complex functions which are not localized. He rejected the suggestion that his results might be due to the statistical effects of different sensory losses, and insisted that 'the more complex functions . . . are largely carried out in independence of structural differentiation' (1929).

Lashley's findings met with a rather uncritical acceptance, at least among psychologists. Hunter and Pavlov, however, suggested a different interpretation of his results. There is, they pointed out, a good deal of evidence that maze learning is dependent on sensory cues. If one sensory centre were destroyed, the rat would utilize cues from another, so that, whilst no one lesion would destroy the habit, it would be diminished roughly in proportion to the amount of cerebral tissue destroyed, as fewer sensory cues were available (Hunter, 1930; Pavlov, 1941).

Lashley supported his conclusion that maze learning is dependent on some unitary function of the cortex rather than on sensory cues by control experiments. He showed that learning is unaffected by section of the kinaesthetic paths, by enucleation of the eyes, or by removal of the occipital cortex from rats already blinded before training. The evidence here is, however, conflicting. Other experiments have shown that lesions of the dorsal spinal tracts have little effect on behaviour cued to proprioceptive stimulation, which they argue are routed round the lesion (Ghiselli, 1936; Brown, 1942). Finley (1941) removed about 10 per cent of the rat's cortex, keeping within the striate area, and found that in the dark these rats learnt mazes as well as normal rats, presumably by other cues. Pickett (1942) trained blind rats in a kinaesthetic maze, and found that, whilst anterior lesions produced some loss of the habit, there was little deterioration following striate lesions. These conflicting results cannot be reconciled

https://doi.org/10.1017/S0025727300024418 Published online by Cambridge University Press

without further experiment, but it is clear that different hypotheses can be put forward to account for the findings on which Lashley based his principles of equipotentiality and mass action.

VII. Lashley's assumptions

There can be little doubt that Lashley, like his predecessors, was influenced both in designing and interpreting his experiments by his prior conception of brain action. He explicitly rejected the reflex, analytic model of the brain, built up in the last half of the nineteenth century. He denied that integration can be expressed in terms of connexions between specific neurones, and asserted that brain function is not a summation of diverse functions, but a non-specialized dynamic function of the tissue as a whole. He offered a tentative theory of brain action, based on potential differences. A given ratio of stimulus intensities at two peripheral points may, he suggested, establish a potential difference between two corresponding areas in the cortex, resulting in a polarization of the cortical field, essentially the same for different points within the areas. The excitability of the final motor path would depend on the relative excitability of the two areas (Lashley, 1929).

This was the first attempt to give a physiological content to the principle of 'action commune'. Lashley was the first psychologist working with problems of brain damage to interpret cortical dynamics in terms of field theory, and to abandon Associationism.

In this he was largely influenced by Gestalt psychology. Wertheimer, the founder of Gestalt psychology, had made an attack in 1912 on what he considered the fundamental scientific assumption of his day, that scientific method must be analytic. He argued that the scientists should not proceed by dividing a whole into its elements, and discovering the laws of the elements. Instead, he stated:

> There are wholes, the behaviour of which is not determined by that of their individual elements, but the part-processes are themselves determined by the intrinsic nature of the whole (Ellis, 1938).

Hence it is useless to study the elements, since the properties of the whole are 'emergent' and do not inhere in the parts. The organization of the whole was described by the Gestalt school in terms of field forces, by analogy with magnetic and electrical fields. The principle of Isomorphism was also enunciated, that the form of brain events is similar to the form of mental events, and should be studied by the same principles.

Gestalt psychology, therefore, implied not only a rejection of Associationist psychology, but also of the nineteenth-century theory of brain action. It is significant that Lashley advanced only psychological evidence against the doctrine of localization of function—his own experiments, Gestalt experiments on perception, and clinical data. Just as Ferrier and his contemporaries had quite consciously looked in the brain for the structural basis of association, so

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Lashley set out to show that the brain exemplified the principles of Gestalt psychology.

This fact probably accounted for a good deal of the impact which *Brain Mechanisms and Intelligence* made in general psychology. Moreover, it recorded the first experimental programme in the field which used the objective methods of animal psychology—and indeed much subsequent research has been methodically inferior. Nevertheless, Lashley has had curiously little influence on research into problems of localization and probably his main influence has been through the critical evaluation of localization studies made by his student, Hebb.

There appear to be two main reasons for this neglect. On the one hand, the new techniques developed by Lashley were capable of showing the effects of more and more restricted lesions. On the other hand, Lashley's work appeared just when developments in neurosurgery and psychological technique were making it possible to define the limits of *human* lesion with some degree of confidence, and objectively describe even minimal accompanying symptoms. During the nineteenth century, physiologists had been rightly mistrustful of clinical evidence, since anatomical control was so poor. It was supposed, however, to confirm the findings that mental changes occur only after very extensive ablation. Methods of psychological assessment were so poor that the less marked symptoms of brain damage were overlooked. Ferrier, for example, instanced the famous Phineas Gage, now considered a classical example of a frontal syndrome, as a man 'with little or no apparent symptoms during life' (1876). But since the 'thirties there has been a growing volume of clinical evidence of the precise effects of more and more limited lesions.

More important, subsequent workers in the field have shown a great lack of sympathy for Lashley's field theory. If one compares the general acceptance for forty years of Flourens' theory with the relative neglect of Lashley's (equally systematic, and empirically based), the importance of a generally acceptable approach becomes clear. It is true that modern clinical and experimental investigators have not explicitly rejected field theory. They do not as a rule make any explicit assumptions at all about psychological processes or brain action. This empiricism marks them off sharply from their predecessors, including Lashley. As has been shown, these earlier workers stated their assumptions about brain action and mental processes and then set out to find 'the anatomical basis of psychic processes' (Bianchi). Text-books of physiology no longer, however, base themselves on psychology, nor do modern accounts of intelligence discuss its relation with the brain.

Nevertheless, any attempt to relate psychological processes to brain structure must, in fact, involve such assumptions. Most modern workers argue as follows. A lesion at *X* produces symptom *Y*. This represents damage to the psychological trait *Z* which must be localized at *X*. This paradigm involves two basic assumptions, firstly that psychological processes can be resolved into discrete traits and aptitudes, and secondly that the brain is an organ composed of independent centres. That is, any part of the brain which appears to be a

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distinct structural unit, because of structural or axonographic characteristics, mediates a distinct function whose nature can be revealed by stimulation, or the effects of clinical or experimental ablation, or preferably both. The effect of these two sets of assumptions amounts to an implicit doctrine of psychic centres, the mapping out of psychological entities on the cortex. In other words, Associationism has been discarded in favour of trait-analysis, but the nineteenth-century model of the brain has been retained. Fulton, for example, has argued that the lessening of aggression after cingulectomy reveals the localization of 'emotional expression' in the 'visceral brain'. Neurosurgeons have attempted to alter personality in specific ways by lesions of specific parts of the frontal lobes.

This is, however, physiological and psychological evidence that the classical model of the brain as an organ of independent centres controlling different functions is inadequate. Large areas of the brain appear to be implicated in most psychological functions (Meyer, 1956; Tizard, 1958). The psychological entities which have been so readily localized (for example, ability to abstract, arithmetical ability) probably involve many complex processes which may be differentially impaired. These changing assumptions should be reflected in the field of brain physiology, where, as in the past, they can be expected to lead to new departures in research.

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https://doi.org/10.1017/S0025727300024418 Published online by Cambridge University Press