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ON THE CURRENT PROBLEM CONCERNING THE LOCALIZATION OF BRAIN PROCESSES: A CRITICAL REVIEW

For almost two hundred years the problem of localization of the brain processes has been provoking discussion in the fields of medicine, philosophy, and in general critical reflection that at times is expressed in acute polemic terms—phrenology, the disputes over aphasia between 1861 and 1865, the Bergsonian interpretation of P. Marie's works, and so on—and at times dies down and seems to disappear. In the past quarter of a century, this discussion has not lost any of its fascination, but it cannot possibly be tackled without at least a minimum of historical background. We therefore propose, first of all, to review the main elements highlighting the development of the problem, since its present state becomes meaningful only in relation to the recent past. Since we cannot permit ourselves to recapitulate all aspects of its history in the course of this article, we shall give examples in the four fields we feel to be the most pertinent: human and animal neuropsychology, neurophysiology

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and neurochemistry. Finally, we shall set forth our reflections on the heuristic meaning of these examples, and endeavor to draw conclusions, some of which may answer problems that have never been raised before.

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To try seriously to put a date on the beginning of this logical impasse is a risky endeavor and requires considerable caution. The more distant the past, the more adventurous the undertaking, and the more esoteric the terms in which it is expressed. Concerning the period before the 18th century, all information must necessarily be taken with cautious reservations—reservations regarding a deceptively familiar vocabulary, and regarding previous stages of medicine's history, that we cannot be content to consider a forest of shadows occasionally illuminated by the capricious games of our presumed forerunners.

Without having to go back to anti-deluvian times we can recall an interpretation by Breasted in 1930 of the Edwin Smith papyrus, dated approximately 3500 years before our time, which seems to show that Egyptian doctors recognized that the brain played a certain role in the body's movements. Less far back in time, in ancient Greece, we know that Alcmeon De Crotone considered the human brain the seat of feeling. Despite Aristotle's hostility, this tradition, universally accepted by doctors and philosophers of Greek and Roman times, was backed up by Galen, and was therefore transmitted to the body of Medieval knowledge. Anatomic work of the Renaissance proves this truth. A few rare authors went even further, maintaining that different parts of the brain could sustain different functions; we can find indications of this in what is commonly called the Hyppocratic corpus, and what remains of the writings of Straton De Lampsaque or Erasistrate De Chios. Galen attributes to each of the four ventricles a particular function, and this opinion is adopted in the classical era, after a period of Medieval scholasticism that considered it a certainty. Descartes seemed to sustain quite another theory, endeavoring to isolate the essential organ of the spirit. We know that he considered it to be in the epiphysis. A while later Vieussens considered it to be in the radiant corona, and La Peyronie, in the *corpo calloso.* Some anatomical, clinical and physiological observations did exist at the time, but they all remained isolated from one another, not easily comparable, being based on prejudices that we no longer understand.

For the reasons mentioned above we find it misleading to begin discussing localization of the brain processes before F.S. Gall (1758-1828), the first to sustain the hypothesis concerning the major role of the cerebral cortex, that had been ignored by everyone until then, including Vico D'Azyr. He attributed to each of the parts of the cortex one of the 27 different functions that he felt he could single out. The proofs upon which he based his affirmations may appear quite fantastic to us, but nevertheless his keenest adversaries recognized his worth as an anatomist, and his most faithful disciples were the greatest Parisian doctors of the time (Broussais, Bouillaud, and many others), not to speak of the debt A. Comte and Littré owe him.

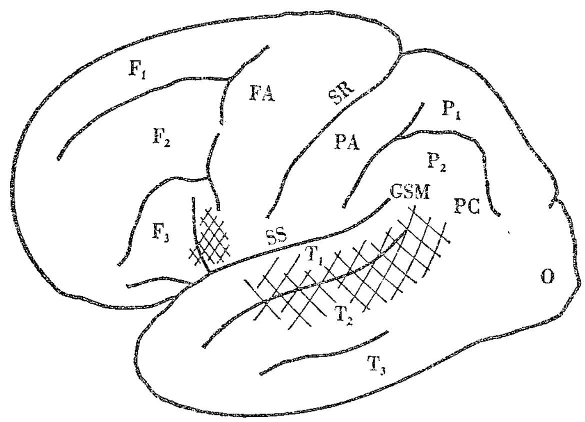

Fig. 1

LEFT CORTEX, SIDE VIEW

In crosshatching, the zones described by Broca (near F_3) and Wernicke (T_1, T)$_2$)

(SR: Rolandian fissure; SS: fissure of Sylvius; F_1, F_2, F_3: first, second, and third frontal convolutions; FA: ascending frontal convolution; PA: ascending parietal convolution; P_1: first parietal convolution; P_2: second parietal convolution; G.S.M.: Gyrus supra marginalis; PC: curved groove; T_1, T_2, T_3: first, second, and third temporal convolutions; O: occipital lobe.)

The fashion of phrenology, challenged by experimenters like Flourens and clinicists like Leuret or Lélut expanded until, between 1861 and 1865 P. Broca, in a still memorable statement of principle, followed by numerous reports presented at the anthropological society of Paris, that he founded, established on precise and anatomical-clinical grounds the constant relationship between the loss of the faculty of articulated language and the destruction of a precisely circumscribed unilateral cortical region—at the foot of the third left frontal convolution (in a right-handed person). Thus, for the first time, the localization of a brain process was established on a definitely demonstrable basis: it was the localization of the highest function, and it had been proven in the human species. Moreover, although localizers and unitarians, whether accepting or denying them, could only conceive of bilateral and symmetrical localizations; the first well-proven localization was found to be unilateral.

During the last quarter of the 19th century, one fundamental discovery succeeded the next. Meynert (1864), Fritsch and Hitzig (1870), and H. Jackson (1870), after P. Broca, are considered the founders of the doctrine of localization of the brain processes. During the next thirty years the basic precepts of the break-down of the cerebral cortex into lobes and convolutions, the effects of ablations and stimulations, the balance of human clinical work, and cytology were definitively set down—Wernicke, D. Ferrier, Munk, Luciani, Seppelli, Charcot, Flechsig, K. Brodmann... The results are so numerous and confirm each other so well that the critical spirit now begins to wane before their richness. Certainty and ingenuity go hand-in-hand, both for those who summarize the working of the brain into the association of cortical centers of sensory perception, with cortical centers of motor projections, as well as for those who imagine that it works by means of a mosaic of tiny territories that can be precisely localized.

The reaction starts with Bergson, followed by P. Marie, and comes to a peak with Von Monakow and H. Head; in the field of anatomy with A. Gelb and K. Goldstein, and in the field of experimental physiology with Lashley. According to Goldstein, the brain always works as a whole (*im ganzheit*). Unprejudiced observation shows deficiencies in all areas of performance no matter where lies the origin of the lesion. According to Lashley, experiments with rats prove the equipotentiality of the brain, and any observed deficiencies can be explained by mass effects.

During the period between the two wars, it was agreed that focal lesions provoke specific symptoms, but negative examples were more frequently emphasized, whereby a sure lesion of known origin does not provoke predictable symptoms, anatomical-clinical correlations were minimized, and it was claimed that general disorders had been ignored because of prejudice, or that both persistent and temporary symptoms can be explained by an initial but temporary inhibition. Efforts were then made to distinguish the localization of a lesion from that of a capacity, the latter being rather unlikely, since a capacity belongs to a temporal order, more than to a spatial one.

More recently, the problem has gradually become modified, due to changes in research methods. Experimentation is carried out on species of animals on higher levels of phylogeny. Conditioning methods and large quantitative series are used; the potentials that are stimulated establish, by means of neurophysiological procedures, the functional heterogeneity of the cortex, and its somatology: the plurality of the various projection zones, even the principle of localization is renovated—it is now understood as much more complex, with multiple interactions and a network of stimuli and inhibitions. Cytological studies (P. Bailey, G. Von Bonin) no longer multiply distinctions between areas—instead they sustain the principle of division of the cortex—the idea of sectors of thalamo-cortical projections (E. Walker), each sector of the cortex corresponding to the thalamic level that sends it afferents: the result is a conception of the make-up of the cortex that no longer appears as a mosaic, and only retains greater differentiations of extent, of both histological and experimental value (Rose, Woolsey): from then on, the cortex appeared to be more and more closely associated with its thalamic afferents.

Animal neuropsychology, particularly from 1951 onwards, shows, through the work of Lashley's students, such as Pribram, Chow, Semmes, that destruction of associated areas results in specific sensorial deficiencies, very different from those resulting from the lesion of areas of corresponding projections. Due to their increasing precision, anatomical-clinical and neurosurgical studies are revealing the lack of comprehensive views of cerebral functioning, and are establishing that the functional assymetry of the hemispheres is not limited to the faculty of language, but is also present in the praxis and gnostic faculties. It would seem that the study of human cortical functions can no longer be carried out without recourse to methods borrowed from other disciplines, some of which are neighboring, such as experimental psychology (H.L. Teuber), and others more distant, such as structural linguistics (Luria).

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To provide some suitable information concerning the present status of the problem, it would be superfluous to summarize all the results of this research; rather, we shall choose a few examples that seem illustrative, to help us show the empiric background of current concepts regarding the problem of localization of brain processes. We will borrow our examples from human and animal neuropsychology, neurophysiology, and neurochemistry respectively.

Both clinical and experimental research in neuropsychology have established that in man the minor hemisphere—the right hemisphere in a right-handed person—plays a determinant role in spatial functions, the identification of complex perceptive groups and human faces, as well as the awareness of half of the body or of space, opposite the side receiving a hemispheric lesion. They have also established the initial factors concerning the localization and side of the damage in cases of aphasia: the left hemisphere with an anterior, frontal pole is essential to oral or writtten expression of messages. A posterior, temporal pole is essential to the reception and comprehension of verbal sounds; at the level of the temporo-parieto-occipital crossing is an area that enables the categorizing of sensorial factors. The role of the occipital lobe, on the dominant side, regards the recognition, on sight, of the meaning of objects, colors, and graphic symbols. The subjects, having undergone a division of the corpus callosum, thus resulting in the isolation of each hemisphere, proved the results of unilateral lesions. It is true that these studies only give indications concerning the distinctive role of each hemisphere, its way of dealing with information, while they are unable to show whether either hemisphere is totally involved or whether a particular area of it is involved. The results of research in split-brain subjects (or animals) reinstated the value of the role that the interruption of connections between the two cortical areas had. Since 1874, Wernicke had provided a model by means of which he challenged the concept of the division of cortico-cortical connections. Division of the corpus callosum provokes damage to the faculty of reading, without injuring the faculty of writing except for some alteration of print. This is pure alexia, and can be explained as follows: the only visual information that reaches the cortex arrives at the right occipital lobe (because of damage to optical radiations on the left side), but, unable to pass through the corpus callosum, it does not reach the language centers on the left side, and therefore is not deciphered. The result is the inability to read.

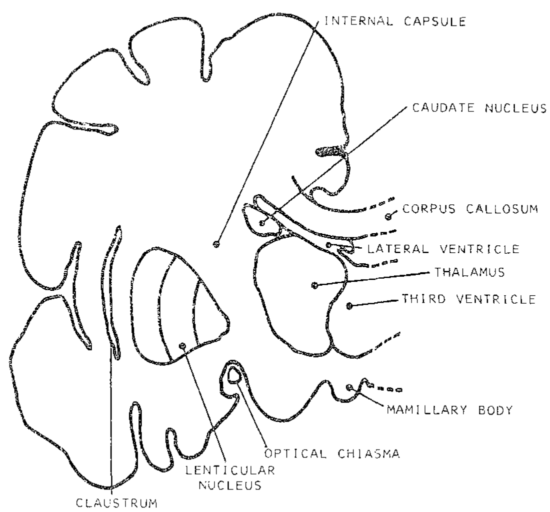

Fig. 2

FRONTAL SECTION OF LEFT HEMISPHERE

Neurosurgery, corroborated by pathological anatomy, enables us to establish a connection between anterograde amnesia—gradual forgetfulness—and lesion of the Papez circuit, that joins the mammilary body to the anterior nucleus of the thalamus, from there to the gyrus of the hippocampus, and then returning to the mammilary body by way of the posterior column of the trigone. Any kind of interruption, even assymetrical, causes an important amnesiac syndrome. In the case of unilateral lesions of the hippocampic formations, the mnemonic deficiency varies according to the side damaged: in the case of lesions to the right side, non-verbal faculties are affected (position, images, the ability to learn labyrinths); in the case of lesions to the left side, only verbal faculties are affected (B. Milner, Corsi).

Damage to the frontal lobes, particularly of a tumorous kind, causes intellectual deterioration together with apathy, upsets in temper and instinctive feelings of liberation. On the other hand, lobectomies and the cronic consequences of cranial traumas cause little or no deficiency in every-day life and in standardized tests. This does not constitute a contradiction, but rather the necessity to recognize that the right and left frontal lobes perform different functions, and each lobe has its own sphere of different functions.

Animal neuropsychology, especially concerning primates nearer to the human species, provides us with similar results, that sometimes confirm the attainments of human neuropsychology, and sometimes serve as its model. Nevertheless, their similarities, despite their importance, should not let us forget the differences between the two species.

In 1936 Jacobsen described, in the case of the monkey, a deficiency in differentiated responses caused by frontal bilateral lesions: the animal was still capable of distinguishing the stimulus that produced a reward, if presentation was not delayed; he lost this capacity if the response was delayed. This deficiency is caused by a lesion that is becoming increasingly easier to individualize: that is the dorso-lateral frontal cortex, at the level of the region of the sulcus principalis, at the middle section of the two edges of this groove. Some sub-cortical formations play a small role in the outcome of this kind of behavior.

Jacobsen was of the opinion that this was a short-term memory deficiency. Later on, in 1969, alternating both the position of the stimulus producing the reward, and the object-reward, Mishkin

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demonstrated that dorso-lateral lesions produce a deficiency in spatial alternation, while orbital lesions disturbed differentiated alternation in a comprehensive manner, and that dorso lateral lesions farther back (arched grooves) produced a deficiency in spatial alternation, even without delays. At the level of the frontal region distinct zones could thus be dissociated, exhibiting behavior analogous in appearance, but affected by different mechanisms; the frontal lobe thus seems to be made up of a series of functional fields, extending in vertical and horizontal directions. Even though similar deficiencies are rarely found in other species, and do not seem to exist in man, they prove to be exempt from the sensorial dictates of stimulus presentation, and the topographical precision thus attained is precious confirmation of the general principle of localization of the brain processes.

On the other hand, lesions in the sub-temporal zone only produce a visual deficiency, that in addition only affects complex discernment, necessary for visual learning. Iwai and Mishkin were able to dissociate an anterior zone, corresponding to the memory of correct answers, and a posterior zone, near the pre-striated foveole region (Cowey and Gross) that sustain a purely perceptive function. Comparisons have been drawn between this deficiency of mnemonic retention and the mnemonic difficulty observed in man in the case of damage to the bilateral hippocampic zone. The relationship between this sub-temporal zone and the occipital striated cortex are still under discussion: some experimenters are under the impression that information travels from the striated area to the infero-temporal area, there to undergo a complex process of discrimination, categorization and memorization; others admit that the infero-temporal area influences the striated area, but by a partly sub-cortical path.

In the field of hearing, in front of the primary auditive area, an associated area has been isolated, that performs the same function for auditive information as the infero-temporal area performs for visual information.

This body of research among the primates thus enables us to isolate distinct cortical zones, whose removal causes the loss of various kinds of complex behavior. Such particularized functional zones are not known in man, but this may only be due to the considerable length of normally observed lesions. Animals must also be distinguished from man for another reason. In the former case deficiencies are clearly observable only when the lesions symmetrically touch the two hemispheres, while in the latter case each hemisphere possesses functional specializations in relation to the other.

In the past thirty years neurophysiology has undergone considerable changes, due to a refinement of technical methods and a much wider gamut of models. Stimulations and provoked capabilities had, for a long time, enabled us to trace cortical maps of motor and sensory performance, and to establish a strict somatology, demonstrating the correspondence between each point on the opposite half of the body, if not exactly to a point, at least to a small area of the cortex (Woolsey), and to complete the primary areas, by way of the secondary areas coming from a different center, that sometimes exhibits bilateral performance. The practice of pre-operatory stimulation in man gives similar results (W. Penfield). The registration and stimulation of isolated cells by means of micro-electrodes, the histology of the columnar arrangement of sensory cells, the relationship of cortical areas to one another and to sub-cortical centers have clearly established the extreme precision of cortical localization, at the same time emphasizing the intricate and complex nature of interaction between primary, secondary and associative areas.

In an entirely different field, neurophysiology of sight was demonstrating how the various characteristics of a stimulus are successively perceived by a hierarchy of cells: after the retina, from the periphery to the cells of the striated and peri-striated areas (which, in turn, are separated into simple, complex and hypercomplex categories, and then from a lower to a higher order) to the center, each of the characteristics of the stimulus are analyzed at a distinct level (Hubel and Wiesel); we have even been able to identify cells having specific receptive fields for height, direction, movement, orientation, and finally for shapes and colors. The columnar organization of the cells of the visual cortex corresponds to a repartition within the various layers according to their hierarchical order (simple, complex, hypercomplex). There is nevertheless a tendency to maintain that these visual cells, besides carrying out their function as trait detectors, can act as spatial analyzers: whatever its shape or orientation, the invariant of each stimulus would be determined by means of the cell's accomplishment of Fourier transformations of the sensory entryways. The cells of the infero-temporal area would play a role in the categorization of the characteristics extracted by the cells of the visual cortex, both because of a previous influence of the infero-temporal area on the striated cortex, and because of the reception of information in the infero-temporal area that has already been analyzed in the striated cortex. Cells of this infero-temporal area seem to produce a specific response to stimulation that seems natural to the animal. In addition to this kind of interaction we can observe an interaction between the retino-geniculo-striated system and the retino-tectorial system. The latter, more archaic, particularly influences the localization of the stimulus (a functional opposition that is presently being challenged). On each level that we have just described, many other influences act upon this hierarchy of visual cells.

Motor cells, also arranged in columns, are organized in such a way that each group corresponds, for example, to each precise movement of each articulation of the fingers (Asanuma and Rosen). Some pyramidal cells are activated during movement, others, while there is no movement (Evart). In addition, effector cells continuously receive information from the periphery according to their columnar arrangement. Cortical motor performance is not confined only to the fourth area; the precentral and supplementary areas also have a primary motor function, besides a sensory one, and the post-central and secondary sensory areas have a primarily sensory function, although also a partially motor one. The integration processes carried out on the level of these motor cells, and the large number of cortical areas in which they are located necessitate the total renovation of the previously simple principle of localization of the brain processes. The relationship between specific behavior and the activation of specific cells could be demonstrated; for example, recording by means of micro-electrodes shows that the cells of the frontal dorso-lateral cortex give off energy in a specific way, in relation to different performance times of differentiated alteration, and the direction of the choice to be made (Kuboda and Niki, Fuster).

Other experimental results have permitted us to envisage more subtle relationships between these areas. In the posterior paretal region, that is an associative area, there are cells (relating to motor and sensory functions of the opposite hemisphere) that are activated when a sensory stimulus, interesting to the animal, and coming from a specific sector of space, becomes an object within reach, within eyesight, or is touchable. Some of them are activated only when tactile and visual stimuli converge (for example, when the animal's glace can carry to the cutaneous receptive area), others only when the object is previously unknown to the animal. These experimental observations can be compared to certain kinds of spatial disorientation effects observed in man after posterior paretal lesions.

This kind of localization nevertheless does not lead us to postulate a functional mosaic of cortical areas, due to the continuous integration of other information coming from peripheral zones and from cerebral control mechanisms; the only true interpretation of any kind of behavior can be found in the interrelation of these focal elements.

Neurochemistry, a recent discipline that is acquiring essential importance, is threatening to modify considerably the whole problem of localization of the brain processes. Nevertheless, we must not forget that there is still a considerable gap in our knowledge of the effects of a cerebral lesion on behavior and the histochemistry of the nervous system. We must therefore be cautious in making generalizations. We can, however, take into account methods such as fluorescent photomicrography, or the selective destruction of cell bundles by a determinant neurotransmitter. Thus, in the cerebral trunk a dopaminergic bundle has been identified, that has its cell bodies in the locus niger and its cell endings in the caudal center. It plays a decisive role in the integration of movement. Knowledge of its neuro-chemical function has renovated the treatment of Parkinson's disease, and it is known that the caudal centers of persons suffering from this illness have a marked lack of dopamine.

Two noradrenalinergic bundles have also been isolated in the cerebral trunk, one dorsal, the other ventral; of which the cell bodies are to be found in the locus caeruleus of the 4th ventrical shelf. Their endings reach the cerebral cortex, the cerebellum, and the hypothalamus. They play an important part in waking up, attention, emotions, the regulation of visceral functions, and the "pleasure system" (masturbation). Although important for basic research and its applications, the extent of our knowledge of neurochemistry only covers a tiny part of the field yet to be elucidated.

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These examples have shown the precision with which nerve mechanisms necessary to certain functions can be localized. Sometimes they are isolated nerve centers, but more often they are systems of nerve centers, connected by multiple roads. Hierarchy and interaction are both basic and complementary principles. Projection zones receive specific messages, associative zones interpret the nature of these messages, enabling their categorization, discovering the invariants and memorizing them.

The extension of these operatory concepts to the working of the cerebral cortex in man, must nevertheless be made with caution. The less the specificity of the right and left hemispheres in man can be corroborated in the case of animals, the more we feel that globalist theories of cerebral equipotentiality are contradictory to experience, and the more we feel the necessity to take into account their empirical references.

Lashley contrasted localization with mass effects, the relationship between the quantity of nerve tissue destroyed and the magnitude of deficiency observed. In the case of animals as in that of man, the intensity of the deficiency depends on the extent of the lesions. To some extent, we can use the idea of foyer and field to understand this notion. By foyer, we mean a very limited area whose isolated destruction causes a serious deficiency in the performance of a given function. By field, we mean neighboring regions, whose destruction only causes a slight deficiency. The most severe deficiency can only be caused by the complete destruction of both the foyer and the field. Damage to the foyer, in spite of its limited extent, results in important and lasting deficiencies, while destruction of the field without damage to the foyer, results in a slight deficiency, despite the dimensions of the damage, and later recuperation.

Above all, Lashley was of the opinion that regardless of the kind of cerebral lesion, or of its location, the efficiency of all functions is decreased. Experimentation has not invalidated this idea, but has given it a less simple and generalizable meaning. An animal whose callous body and optical chiasma has been divided, and whose eye is obturated, only receives visual information on one side, and cannot transfer information from one hemisphere to the other. The ability to learn tasks requiring visual

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discrimination takes much more time than in the intact animal, and the aspect of curves is very different. At each session a lowering in retention can be observed since the previous session (Sechzer), the more so when complex tasks are involved, requiring cognitive activity (Voneida and Robinson).

In the case of man, all cerebral damage seems to lower the performance level, whatever is the exact seat of the lesion, and in proportion to its importance. This poses the problem of a basic function of the brain, and of its general functioning.

On the other hand, the effects of a lesion to the same point vary according to the nature of the lesion, the age of the patient when he is injured, the characteristics of the lesion, previously acquired experience, and eventual treatment and reeducation. In the case of animals, successively incurred lesions cause less deficiency than lesions incurred all at once. In the case of man, age is of predominant importance. Aphasia acquired in childhood regresses to a much greater extent than the same aphasia acquired as an adult. This aspect can also be found in the monkey; destruction of a zone in the young monkey only causes a temporary deficiency, that would be definitive in the adult. According to P. Goldman "functional saving" occurs to the extent that the tissues it needs have not yet reached a maturity that render them unfit for this vicariance, giving them specialized functions.

Functional recuperation in the child poses the problem of compensation ensured by the tissue that has remained intact. In the adult, it leads to two kinds of hypotheses; reorganization or reestablishment. Reorganization means that a function, previously accomplished by numerous centers at different levels, is now carried out by other centers of the system. Reestablishment means that a function is represented repeatedly at the level of a specialized area, and after a transitional phase of inhibition, the parts remaining intact recuperate their original functions. These processes do not mutually exclude one another, and can act differently in each particular case. True functional restoration certainly does not take place, but the organism is able to perform by different means and by making detours (K. Goldstein), at the cost of functions that it can more easily bypass. Only recourse to a new strategy can overcome the deficiency.

Finally we must point out the proven existence of regeneration of the divided axon, at the level of the central nervous system, even in the adult. It is true that such phenomena, because of their very general nature, are far from providing a precise and valid explanation of substitution phenomena.

To affirm that cerebral functioning is primarily organized on the basis of the principle of localization, and to deny that nerve tissues have any kind of elasticity, would mean to ignore a body of solid experience acquired among the young and adult, and to take for granted knowledge that is still missing. The body of empiric facts stemming from anatomical-clinical observation and from neurophysiology seems, in spite of all, to have too much in common to deny that the idea of localization represents one of the basic principles of the brain's working, certainly it is a very general principle, but not exclusive. The results acquired by following these guidelines, despite the undeniable progress over the last hundred years, and its recent acceleration, nevertheless reveals a still crude and approximate sketch of nerve organization.

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