On the Construction of Movement

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PREFACE

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habit.   Basic questions on the level of structure in normal movement. Characteristic signs of precision and variability. Levels-appearance of characteristic signs of precision.. Levels characteristics of de-automatization factors.

Chapter I

The Genesis of Motor Functions

Of all the domains of general physiology, none is as singularly human as is the physiology of motor functions. Although the presence of phylogenetic continuity in the development of motor functions is indisputable, it was more rapid and accelerating at a faster rate than the development of any other physiological function. An observer would be pressed to notice significant differences between any warm-blooded animal and man with regard to most other functional domains such as respiration, circulation or metabolism [Footnote 1]. The only functional domain which developed at a faster rate than motor functions is the domain of psychological phenomena. For contextual convenience we will refer to it as the domain of central processors. On methodological grounds they were singled out into a separate field of inquiry. The reasons which necessitated this separation reflects inherent difficulties in studying psychological phenomena. If we were to depict the evolutionary progress graphically, then, at least within the range of the warmblooded animals, respiratory and metabolic functions would be represented by lines scarcely rising from the abcissa. Psychological processes, on the other hand, would be depicted by a very steep curve. Unfortunately we would be in a position to plot only its right-hand (uppermost) portion, the part which refers to man. The rest of the curve would have to remain strictly hypothetical, due to the complete lack of objective evidence available with respect to animal "psychology, (notwithstanding the combined heroic efforts of animal psychologists, behaviorists and conditioned-reflex researchers). Motor functions would be the only domain depicted by a continuous evolutionary curve, steeply accelerating to the right, with all the components of the curve being plotted on real and objective grounds. Its rate of acceleration would far surpass that of the curve representing the evolution of the corresponding neurological structures; which in itself is anything but sluggish. This,, in addition to its potential role as a necessary "pendant" to psychophysiology of sensory processes, makes the physiology of motor function, interesting for both the psychologist and the neurologist.

The tremendous evolutionary importance of motor functions is accentuated by

the considerable length of time during which it occupied the dominant role in the phylogenesis of the entire somatic apparatus. The unprecedented rate of the development and evolution of the neuronal substrate of psychological functions can be explained by the fact that these systems had to undergo an even greater change than did motor functions in a comparable period of time. They started lower in importance than motor functions and finished higher. The substrates of psychological functions have gained their preeminent status in evolution only recently, since in early stages of development they served (and still serve in more primitive organisms) a considerably more modest and auxiliary role of providing an interface between sensory and motor processes. The contemporary range of animal forms—a living encyclopedia of phylogenetic history—makes available a record of the early stages of development of central processors. The beginning of what was to become a breathtaking career can be traced to their role as a humble signalman who had just introduced into the physiological repertoire (in Coelenterata and Echinodermata) a new, bioelectric ("telegraphic") type of communication to replace the more ancient humoral ("postal") type. However, the turning point in the history of the central nervous system was prompted by another factor—the emergence of elongated animal forms which replaced the more ancient radially-symmetric (stellate) ones. This ensured the dominant role of the anterior, oral part of the bodys which was the first to encounter both food and danger, and was therefore in a position to send messages to other segments of the body and initiate and coordinate their movements. The head end of the body thus became the dominant end. This signalled the beginnings of centralized nervous systems in place of the archaic, diffuse ones (Reflex - Republics Uexkull).

Furthermore, the head segments had all the prerequisites necessary for the emergence and development of telereceptors. These telereceptors evolved from more ancient contact receptors (olfaction from gustatory chemoreceptors, audition from mechano-receptors of vibration, and vision from skin chemophoto-receptors). Telereceptors proved to be a powerful centralizing factor because they enabled the animal to respond to stimuli arriving from distances which were considerably greater

than the actual linear dimensions of the animal. This led to the emergence of integrated locomotion as the most important type of motor behavior, overriding the local segmental responses which prevailed in the era of contact receptors, The biological importance of locomotor behavior led to the emergence of a powerful integrating synergistic apparatus: the thalamo—pallidar motor system, [or level5 as we will refer to it later (Chapter 4)]. This system can be considered the most ancient component of the true central nervous apparatus throughout the evolutionary history of the vertebrae which remained unsurpassed, in its capacity for vast motor integrations and muscular synergies until the development of man.

Sherrington had every reason to suggest that "telereceptors created the brain," or more specifically, what we referred to as the central processors. They also left an imprint on the spinal cord, which was originally organized in a strictly segmental fashion, but in the latter part of phylogenesis acquired properties of integral organization. The fact remains, however, that sensory systems and telereceptors above all, themselves were secondary, derivative devices. To understand that, we will have to advance the train of thought started by Sherrington.

Motor functions were the critical component in the entire evolution of the somatic system, with the possible exception of the latest phylogenetic stage. The survival of an individual specimen is determined by the adequacy of its act ionss in the progressively complex adaptive process. In this process the sensory functions play an auxiliary and subordinate role. Nowhere in phylogenesis was contemplation of the environment an end in itself. Sensory systems either serve the function of signalization per se, in which case no matter how sophisticated, they cannot by themselves ensure a biological advantage for the species if the motor systems are faulty; or they serve as necessary prerequisites for motor coordination, in which case the subordinate nature of their role is self-evident. With respect to both signalization and feedback, sensory systems serve as instruments for the motor system, affecting the biological destiny of the specimen or the species through the latter. In this sense, the central processors emerged as "auxiliary to auxiliary" devices. We will attempt to reconstruct how the emergence and evolution of telereceptors ands even more

important, the mechanism of sensory synthesis were determined by progressively increasing demands imposed by the motor system.

The increase in the complexity of motor tasks and the parallel development of more sophisticated coordination in a species follows two routes. On the one hand, the repertoire of motor responses becomes more diverse. These responses must become more differentiated and precise; the goals that govern the movements and actions of the animal become more complex. The aerodynamic properties of a bird's flight are immeasurably more complex than the locomotion of a fish which is almost entirely hydrostatic; and the kinetic repertoire of a hunting carnivorous mammal is immeasurably richer than that of a hunting shark. The younger breed of agile warm-blooded mammals prevailed over the clumsy Jurassic reptiles precisely due to their more sophisticated motor systems [Footnote 2]. On the other hand, among the motor tasks facing an organism, the role and scope of extemporaneous and unrehearsed motor behaviors increases at the expense of more archaic, stereotypic ones. Numerous studies of "the plasticity of the nervous system" demonstrated that the evolutionary progression is characterized by an increase in the adaptability of the central nervous system to unexpected changes in the environment and in the rapidity of adjustments to the most fantastic conditions. This is illustrated by the phylogenetic growth in the ability to accumulate individual experience and form new conditioned reflexes, that is, the animal's increasing ability to overcome the limitations of species-specific stereotypes.

Although slightly oversimplified, it can be said that the first of the two routes of motor development serves itself predominantly through the evolution of receptor systems, whereas the second route is related to the evolution of the central processors. On the one hand, receptor systems are systematically perfected. This can be traced back to the earliest phylogenetic stages: the overlaying of the archaic (paleokinetic, see Chapter III) protopathic tactile mode of sensation by a newer process, the more refined epicritic sensation, which is achieved through neokinetic neuronal processes. It is further manifested by the emergence of the youngest (also neokinetic) form of proprioceptions the geometric ones capable of analyzing postures and velocities.

This system is based on the semicircular canals (neolabrinth) and constitutes a clear modification of the ancient proprioception of tropisms, which is based on the otolitic apparatus (paleolabyrinth). It is sensitive to pressure, tension, orientation in the gravitational field, etc. On the other hand, central processors and the entire brain undergo profound qualitative changes in the course of evolution, as telereceptors become more elaborate and assume the dominant role. Among the most remarkable parallel structural changes are: (1) the shift from the monosynaptic thalamic organization of ascending neuronal pathways, to the circuits of cortical afferentation, consisting of two or more neurons, which signifies not merely the emergence of two more synaptic contacts on the path of a sensory impulse, but a profound qualitative change in the processing of sensory impulses in the intermediate ganglia, and (2) the shift from the system of insular sensory nuclei to the kind of continuous two-dimensional system of layers that characterizes cortical hemispheres (the importance of these changes for the evolution of coordinations will become apparent later in this discussion). (3) The adaptive evolution of the sensory system is manifested by the development and elaboration of synthetic sensory fields. This will be further discussed in Chapters IV and V. These sensory syntheses, in which raw sensations provided by separate sensory systems become integrated with memory traces of the animal's individual experiences into deeply transformed and generalized directions for coordinated movements and actions, stimulate and direct the emergence and development of central processors no less than do telereceptors. The phylogenetic course of the formation of these gradually elaborating fields is associated with the increasing role of memory traces--in other words Individual memory [Footnote 3].

According to this slightly schematized model, the second constituent of motor development is provided by the increasing role of extemporaneous reactions, based on the animal's individual experience, and is related predominantly to the evolution of the cortical central processors. The latter provide the prerequisite for further elaboration of the purposive structure of the organism's actions and its memory capabilities. At a certain evolutionary stage, the role of central processors is advanced from that of subordination to that of predominance in directing the further

development of the entire neuro-somatic system.

The phylogenesis of the central nervous system, unlike that of all the other somatic organs and systems is not limited to mere quantitative growth but involves the emergence of qualitatively new structures which had no homologs in preceding evolutionary stages. The emergence of these structures leads to an increase in the number of neuronal levels of processing. Due to the discrete nature of the neuronal scheme, this predictably results in quantum leaps in the development of the central nervous system, since the elaboration of the reflex arc (or a neural path in general) becomes possible only if new relay neurons are built in. This quantum aspect of the evolution of the central nervous system is exemplified by the development of the visual system from amphibia to birds, from the unineuronal, "retinotectal" scheme to the two-neuronal,, "retino-lateral geniculate visual cortex" scheme. For a period of time, the two systems worked side by side after which the old one underwent an involution (as in the case of mesencephalic visual centers) or, more often, underwent a modification in order to form a functional synthesis with the newer system. This is precisely what characterized the gradual development of the central substrate of motor control. An interactive structure which included several coordinated neuronal levels gradually evolved.

Throughout phylogenesis the dominant force in the evolution of the brain was passed from motor to sensory to central processing systems. Such gradual change in the leading determinant constitutes a very general biological principle, which was manifested in the following, more fundamental transition. Initially, the nervous system was not organized according to the neuronal principle, nor did this transformation occur instantaneously. Nervous systems of the "prevertebrata" are not neuronal, and even in the vertebrata, the highest mammals included, autonomic systems in their post-ganglion portions are neuropilic rather than neuronal. Furthermore, even the most central components of the nervous system in higher vertebrata operate, in certain respects, according to a continuous and diffuse neuropilic principle. It cannot be

entirely excluded that the morphology of the first cortical layer is also neuropilic, and so most probably are numerous cortical clusters of small cells.

Many of the aforementioned neuronal structures which emerged throughout evolution dominated the entire central nervous system at certain phylogenetic stages. They were overridden by newer structures at later stages. Progressive "encephalization" of functions, pointed out by Monakow and von Economo, constituted another important development, which caused the change of the roles, qualities and the very nature of the functions of the central nervous system. By "encephalization" two, (probably interrelated), developments are implied; (1) the progressive loss of autonomy and functional impoverishment of the caudal portions of the central nervous system i.e., the spinal cord; and (2) a gradual shift of a number of physiological "centers" towards more orally located nuclei. This unrelenting process is directly related to the aforementioned changing role and ever increasing dominance of the brain. Beginning at a certain evolutionary point, cerebral ganglia turn from the role of sensory auxiliaries and integrators into a dominant organ which will reign over the whole of subsequent development. At the present evolutionary stage, the primacy of the central nervous system both for the narrowly defined behavioral sphere and for autonomic, trophic, metabolic and immunobiological functions, is beyond doubt.

The increasing complexity of motor tasks facing an animal is not in itself a smooth and gradual process. To the contrary, changes in life history (zoological, ecological, environmental, etc.), lead to the accumulation of nev problems of coordination which are characterized by new purposes, motor patterns and new type of sensory control. For a period of time the animal copes with these new tasks relying on its existing repertoire. Eventually, however, the contradictions between the new purposes and sensory demands of the new tasks, and the inadequate means of coordination available to the animal leads by way of natural selection, to the prevalence of animals that can meet the new environmental demands. They come to possess a whole new class of movements that are homogeneous with respect to their

type and complexity, and similar with respect to the required sensory control. Had evolution unfolded according to the theory of Lamarck, through gradual exercising of organs, one could have expected some hypertrophic, quantitative, and gradual adaptive changes in the brain. Conversely, the principle of natural selection^ presupposes that the development of the central nervous system in response to new types of motor requirements can occur only through the increasing prevalence of specimens with qualitatively different, mutated brains. The emergence of a new structure in the central nervous system represents a biological response to a new quality or types of motor tasks. It will be further argued that this process is inevitably associated with the emergence of a new synthetic sensory field, and similarly with the emegence of a new class of motor acts, which are qualitatively new with respect to sensory control and execution. We will refer to the combination of the aforementioned morphological and functional properties implicit in the new type of motor acts, as a new structural level of motor programming and motor coordination.

It is now possible to formulate the trends which characterize the new structural levels of motor programming. The more recent these levels are phylogenetically, the higher is their position in the motor hierarchy. This in turn means that they are:

(1) more closely associated with telereceptors and based on cortical integrative systems,

(2) more extemporaneous, i.e. capable of executing ad hoc tasks of coordination and plastic shifts of behavior,

(3) more synthetic, i.e. drawing on synthetic sensory fields with complex psychological organization, and

(4) more dependent on rich memory elements accumulated from individual experience.

These trends characterize every specific motor act and action controlled by a corresponding structural level.

Every new level introduces a news hitherto unavailable, repertoire of motor acts. We must discount the old notion that phylogenetically younger components provide new aspects of coordination, and therefore each phylogenetic

morphological layer of the brain is equatable with a particular single aspect of coordination which enters every composite motor act. Instead, each new morphological stage, each new functional level of structure introduces a new spectrum of motor acts. Given that the central nervous system of an advanced vertebrate can be characterized by N structural stages and corresponding N levels, its motor repertoire consists not of N properties of motor coordination, but rather of N different lists or sets of composite motor acts, each being a complete entity specific to the execution of a distinct set of tasks. It would be difficult to understand the biological meaning of and justification for the existence of motor actss which over long periods of phylogenesis are void of any salient aspect of coordination, or conversely, the existence of secondary, auxiliary aspects of coordination unrelated to any major adaptive determinant, thus constituting a background without a figure. At every evolutionary stage a particular level of motor programming which is discernable in man played a distinctly dominant role, (this statement will be qualified in Chapter III), and set the "upper limit" for the motor repertoire of the organism. Every such stage, on the other hand, was characterized, within the limits of modest motor tasks that faced the organism, by fully shaped and well coordinated movement.

That whole repertoire of motor acts are associated with each specific level of motor programming is most clearly supported by studies of distinctly focal or distinctly systemic lesions of the central nervous system. Such lesions, as clinical neurologists know, lead to the disintegration of specific lists or classes of motor acts, or their basic components, rather than of particular aspects of every motor act. The degree of selectivity of such disintegration is quite amazing. Spared motor acts are sometimes extremely similar to the ones impaired in terms of appearance but are invariably quite different with regard to their behavioral purposes. A patient is unable to raise his hand in response to the verbal command, "Raise your hand," but can easily do so if asked to take off his hat. Another patient suffers from disintegration of facial automatismss and his condition can be mistaken for total facial paresis. And yet he can easily, and with high degree of precision, assume a wide range of facial postures by deliberate imitation or by following verbal instructions. A third patient

(hemiplegic) is unable to perform voluntary movements of his shoulder, but is perfectly capable (especially in the states of affect, seminarcosis, or drowsiness) of executing the same motor acts when they are components of synergistic involuntary acts. Yet another patient is unable to draw a circle or a diagonal cross when asked to do so, while at the same time has no problems in printing letters "0" and "X." Similarly, an inability to walk on a plain surface may coexist with a perfect ability to do so if marks are put on the surface at equal distances. Numerous and varied examples of this kind can be offered. In order to achieve a virtually complete restitution of a motor skill, it often suffices to switch it on to another, intact level3 by re-formulating the motor task.

The aforementioned morphogenetic principle of the emergence of new levels accounts for the fact that the central nervous system of an advanced vertebrate, i.e. anthropoid or man, represents in a sense a geological cross-section. In this cross-section the whole evolution of the central nervous system is reflected, beginning with the diffuse neuropils of lower invertebrates and primitive spinal reflex arcs characteristic of the early chor-dates. All this is recapitulated in a highly advanced central nervous system, in the sequence of its layers, stages, and structures, with as much precision as the history of a tree is recorded in its annual rings.

In a similar fashion, the coordinated sets of movements available to man provide simultaneous recapitulation of the whole phylogenetic history of motor functions, beginning with the archaic peristaltic-like movements of Annelida and swallowing-vomiting movements of Holothurians. Such recapitulation gives advantages over neuromorphology. It captures phylogenesis in its dynamics, through the motor acts themselves, thus enabling their comparison with the motor behaviors of modern representatives of every phylogenetic stage with respect to their content, purpose and structure. At the very bottom of the geological cross-section, deep within the layers of motor behaviors found in man, archaic paleokinetic coordinations are found, which in advanced vertebrates are relegated to visceral functions: peristalsis of the intestinal system, constricto-dilating properties of the vascular system, gastric sphincters, gallbladder, colon, etc. At higher levels, elementary with

respect to structure and afferentiation, neokinetic coordinations are found--spinal reflexes, which were studied in detail by Sherrington and his followers. Continuing higher we enter the domain of movements characterized by more complex biological motivation and the kind of synthetic afferentation that includes telereceptors and individual memory components— the domain of true psychophysiology. Still further up, the youngest phylogenetically, singularly human coordinations are found. They are predominantly cortical, their origins cannot be reduced simply to biological causality. These coordinations are related to speech, writing, and object-oriented activities which constitute components of labor activity and have social-psychological determination. Each of these subsequent layers is associated with a particular morphological substrate, and none of them negates underlying relatively more ancient layers of coordination. Instead, all these layers become integrated into unique and elaborate syntheses.

In subsequent chapters, beginning with Chapter III, general characteristics of various hierarchic levels of motor organization will be discussed as well as important general facts related to the theory of coordination functions. Before we enter this discussion, however, certain clarifications will have to be made.

Footnotes:

Footnote 1 : We do not mention here physiology of work, which is a singularly human domain of physiology. When the physiology of work (we imply predominantly physical labor) studies the actual process of work, i.e., work-related motor acts, it becomes the physiology of motor functions. Alternatively, when it addresses itself to visceral functions, then the physiology of work is concerned with functions which in man are embedded in a new context, although they remain superficially identical (if considered by themselves) to functions found in the animal world. Motor acts, on the other hand, both work-related and numerous others, are intrinsically different in man and in the animal world.

Footnote 2 : This was due to the evolutionary victory of cortically-controlled adaptive motorics over archaic extrapyramidal motor stereotypes (see Chapter 7) .

: The increasing role of telereceptors in determining the evolution of motor functions can also be explained by the fact that it promoted the emergence of complex forms of motor integration (e.g. locomotions) which necessitated sensory feedback (Chapter II). Movement became dependent on the sensory apparatus, whereas in most archaic species sensation was dependent on movement (e.g. tactile exploration in worms and caterpillars).

Footnote 4 : We are in no position to predict the outcome of the debate between the "neuronists" and "antineuronists" with regard to morphology. It may turn out that the chances of observing a synaptic contact under the microscope are as low as that of tripping on a meridian while walking in a field. Even now it is indisputable, however, that: (1) functionally synaptic contacts are the points of discontinuity between different excitable elements, and (2) the neuropil type of organization coexists with the neuronal type in highly advanced nervous systems and is as closely related to paleostructures and functions as the neuronal type is related to new structures.

Captions

Picture 1;   Sagittal sections of vertebrate brains:

a-brain of a shark

b-brain of a lizard

c-brain of a rabbit

d-brain of a man

Phylogenetically "new brain" is depicted in dark color, "old brain" in light grey, cerebral ventricles in dark grey.

1-olfactory lobes; 2-"pallidum"; 3-diencephalon; 4-thalamus; 5-cerebellum; 6-brain stem.

Picture 2; Graded "layerization" of the motor systems in the brain. Sensory nuclei are depicted by circular contours, motor nuclei by angular contours. A-spinal level: peripheral sensory and motor neurons with a synaptic contact between them. B-thalamo-pallidar level. Th-Thalamus, P-"Pallidum," CC-cerebellar cortex. C-the

emergence of motor cortex (MC) and pyramidal tract. S-striatum (the phylogenetically youngest and dominant nucleus of the extra-pyramidal system).

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<center>CHAPTER VI</center>

Cortical levels of regulation of movement

<center>Parieto-premotor level of actions (C)</center>

All the coordinations and many of the movements described in the previous chapters are available to animals no less than they are to man. Moreover, at various stages of mammalian evolution species are found with higher development of certain aspects and manifestations of the spatial-field level than in men, e.g. they are of more rapid and more sustained running, better equipped for climbing or swimming; higher developed correctional visual aquity; more refined visual- and olfactory-based spatial orientation; more precise aiming of attack. Such instances indicate that the evolution of this level has already reached its point of culmination. It is true that the variety of movements of the spatial-field level is greater in man than in any other species. Hox\rever, more detailed analysis, in part developed in this chapter, reveals that many of those human movements which superficially appear to be related to the spatial-field level, are, in fact, controlled at a higher level of regulation. This is seen if one employs as a criterion the leading type of afferentation. With respect to this lack of parallelism between the general evolution of the CNS and the development of the spatial-field level, one can point out that the spatial-field level is not yet really cortical. The spatial-field level is no less developed in those species which have neither the cortex nor the pyramidal tract. Although it is associated in man and higher mammalians with the cortical hemispheres5 this association is limited to cortical periphery. It has been astutely suggested, comparing the cortex to the spinal cord, that the pyramidal field is the "anterior horns of the brain."

The level to be discussed in this chapter is entirely cortical although it does have extensive connections which extend in major ways into subcortical structures,

and it is almost uniquely human. The distinct evolutionary difference of this level from the lower levels underscores the tremendous, not yet fully appreciated fundamental difference between cortex and the more ancient nuclear type of neural organization. It was pointed out in Chapter I that throughout a very long period of phylogenesis, the head brain served only auxiliary functions with respect to efferent and higher sensory systems, its whole development being determined by them. The head brain gained its dominant role only recently in vertebrate evolution. Evidently the cortical princip of organization opened up entirely new possibilities for the brain. Judging by many indices an intensive growth of neural function continues to take place even now in the primates, whereby the head brain dominates and leads, in the evolutionary sense, not only the entire somatic system but all the life processes both in normal operation and in pathology. This process is difficult to discern directly, just as the unequipped eye is incapable of discerning the motion of the hands of a clock. It is tempting to think that all these opportunities were made available to the brain by the cortex with its singular organization. Who knows where this process will lead in the remote future!

The theory of coordination presented in this book is based on the principle that qualitatively different types of afferentation associated with anatomically distinct CNS structures control the coordinations of different groups of movements. These groups of movements may be quite dissimilar with respect to a variety of features. With respect to the brain stem and sub-cortical structures this principle provided convenient and easily applicable criteria of systematization, since sharply distinct systems of afferentation could be found there which corresponded to equally distinct anatomical structures .

As one attempts to carry such distinctions into cortex, they become complicated and vague with respect to both anatomy and types of afferentation Already at the spatial-field level whose afferentation includes a number of lower level, ancient cortical areas of the hemispheres, we encountered an extremely complex afferent synthesis which was very generalized and quite removed from the primary sensory elements. The higher order level of coordination of movement

involves even more generalized afferentation, which is even further removed from primary sensory reception and which is based on memory engrams of previous experience to an even greater extent. At this level the task of separating the levels of afferentation let alone attributing them to distinct cortical field and systems, becomes extremely complicated.

From a strictly morphological point of views the organization of the cortical hemispheres is in perfect agreement with a picture of functional continuity and generality. Whereas lower-order systems are composed of distinct cellular nuclei interconnected by fiber bundles which allow relatively clear analysis with respect to their neural composition and hierarchic interrelationships, cerebral cortex consists of a continuous cortical layer permeated in all directions by an equally continuous layer of fibers of white matter. With the exception of the primary fields and layers of the cortex ("entrance and exit gates of the cortex") and their closely adjacent secondary areas (e.g., area parastriata and premotor zone) all the other cytoarchitectonic subdivisions of cortical hemispheres do not reveal discernable hierarchic relationships, and possibly do not even have them in any permanent fashion. The problem of cortical localization is one of the most difficult fundamental problems of contemporary neurology, in large measure because of the extreme complexity and functional plasticity of connections and relationships between its anatomical components.

The cortex-based levels of movement coordination reflect such synthetic quality of function, continuity of morphological organization and complicated hierarchical relationships; they are less obvious, merge into one another and do not lend themselves easily to description, and specification. In some instances, the analysis of certain types of movements clearly reveals the exi; tence of a whole class of hierarchically interrelated levels, each associated with a particular type of coding or a particular type of pathology. In other instances, even the separation of two distinctly different levels cannot be achieved with certainty.

Physiological analysis of cortically controlled movements is still in the

embryonic stage. The material for such analysis has been provided thus far mostly by focal brain lesions in humans and to a limited degree by experiments involving partial cortical extirpation in primates. We will have drawn our conclusions largely from this material, despite all the shortcomings of clinical observations.

For the above-discussed reasons, we are in no position to attribute to the cortical levels of coordination an anatomical and functional distinctness comparable to the one naturally established for the lower levels. This was foreshadowed already with respect to level C where we had to consider two sublevels which merged. Until further clarifying experiments are conducted, it may be appropriate to consider levels D and E, which will be discussed below, as multilayered complex levels consisting of unseparable or flexible subdivisions. Any attempt at further subdivision would require guesses that lack an adequate factual base.

Level D to be described in .this chapter is almost singularly human (it is no accident that speech and writing are controlled at this level) and is clearly still far from its culmination. It is barely represented in isolated manifestations in higher order mammalians~-horses, dogs, elephants (a number of more or less plausible accounts to this effect can be found in writing by Brehm). Even in primates the relative role of this level is very small, as it is in humans at early ontogenetic stages, during the second year of life, and it is resorted to only after the failure to solve a motor task on more habitual lower levels. The singularly human nature of this "level of actions" is precisely why it was not discovered until clinicians described its disintegration following focal lesions in particular cortical locations. One must admit that physiological experiments with humans employing cortical stimulation or recording of bioelectric potentials has failed thus far to add anything of substance to the clinically obtained data. Although we must also begin with a negative definition as our point of departure, we will set ourselves the task of achieving, as clearly as possible, a positive characterization of this level.

The various and disparate clinical pictures of motor deficits on the level of action (generically referred to as apraxia, although it would be more appropriate to use the term dispraxia) are difficult to characterize. There are no persistent motor

losses, such as paralysis or pareses and not even any persistent deficits of coordination in the common usage of this word.

It is not coordination of motor acts that suffers in apraxia, but its very execution. While the understanding of the essence and the objective of a motor task is perfectly intact (this is how an apraxic patient differs from an agnostic patient in whom the very understanding of the task is impaired), the bridge that leads from the understanding of the task to its motor solution is lost. An apraxic patient is not armless—he is merely helpless. Unlike an ataxic patient in whom the spatial-field level is affected and who is not in control of his own arms, an apraxic patient (provided that the case is not complicated by background deficits) is in full control of all of his organs, yet he cannot apply them to achieve any product beyond the elementary motor combinations available already to higher mammalians.

The apraxic patient also loses the ability to acquire or recover motor skills and habits which are more than elementary. Able to understand the task correctlyj such a patient has no illusions regarding his ability to solve it and is usually unhappy with himself. This is different from certain other types of patients in whom a similar failure is associated with the lack of critical judgment with respect to their actions. The loss of vast contingents of motor acts and of the ability to acquire new ones is observed against a background of intact active mobility, elementary motor control over motor periphery and the absence of any major losses of strength, velocity, or precision of movements.

Detailed clinical observations of apraxic patients initiated by Nothnagel and H. Jackson in the 1800's and first analyzed in depth by Liepman in the 1900s enable us to single out the class of actions (in other words, object-oriented actions, goal-directed chains, etc.) as a separate level of coordinations. This is fully justified by the fact that there is a distinctly selective disintegration of the motor acts of this category following focal brain lesions in various, but very distinct, locations. By analyzing that which is lost and that which remains intact with regard to motor coordination we can distinguish the level of actions from previously described levels and outline its main positive characteristics.

It is not possible to discuss the question of cortical localization at this level without reopening the whole complex problem of cortical localization in general. We will limit ourselves at this time, however, to outlining the cortical fields which are critical for the normal functioning of the level of actions, and whose lesions cause the aforementioned apraxic deficit; As a general rule,, the fact that distinct focal cortical lesions are associated with distinct syndromes of function disintegration proves only that the corresponding loci constitute the obligatory points of passage of the given type of neural process, critical way-stations without which the given type of neural process cannot be realized.

Two groups of cortical fields, presumably corresponding to such obligatory points of transit, and probably corresponding to the "entrance" and "exit" gates for the neural process of the given level, can be specified at this time with respect to localization of the level of action. In a characteristic way these fields are grouped in two areas of both hemispheres, relatively far removed from each other. The first group is located in the inferior portions of the parietal lobes of the hemispheres, occupying a middle ground between the visual, auditory and synthetic tactile-receptor sensory fields (respectively, occipital lobe, temporal lobe and the post-central gyrus), as well as the intermediary zones adjacent to them. The second group of fields included in this system is found immediately anterior of the motor pyramidal field 4 and is usually referred to as the premotor zone (Brodmann fields 6a and 6,). The inferior border of this area is immediately adjacent to the Broca's "motor speech center" (Figures 47, 70, 71 and 72) .

The first group of fields in the parietal area is intimately connected, both anatomically and functionally, with the tactile, auditory and visual sensory fields, both primary and secondary, between which it resides, while the second group in the premotor area are more connected to effector systems. The functional proximity of the premotor fields to effector systems can be demonstrated by the fact that electric stimulation of these areas elicits movements of separate body parts, something that electrical stimulation of the parietal area does not elicit. The effects of stimulation of

the premotor fields can be distinguished from those of direct stimulation of the pyramidal zone by their higher thresholds, more pronounced summation effects, facilitation and residual after-discharge, considerable latency of the onset of the motor reaction in response to stimulation; and finally by the fact that the elicited motor responses are not limited to isolated muscles or narrow muscle groups (as is the case with stimulation of the pyramidal system), but rather constitute greater fragments of integral movements; whole synergies are elicited which embrace both antagonistic and protag-onistic muscle groups. O.Vogt found that cortical incision along the border between the premotor and the pyramidal fields leads to the immediate elimination of these effects, thus demonstrating that motor responses elicited by premotor field stimulation involve passage from the premotor field on to the pyramidal system and the pyramidal efferent route. Myeloarchitectural studies of cerebral fiber pathways have demonstrated, however, that premotor fields are connected not only with the pyramidal fields of the cortex, but also with pallidum and even with the lower-order nuclear group of the extra-pyramidal efferent system (Figure 72). The issue of the connections between premotor zones and striatum has not been adequately clarified. It can be concluded that premotor field are efferent in nature both in terms of their location, connections and the affects of experimental stimulation; yet their efferent nature is not nearly as direct and clear-cut as is that of giganto-cellular layer V of the pyramidal field, or the hierarchically complex striatum. The behavioral deficits caused by parietal lesions definitely signify impairment of afferent functions sui generis; whereas the deficits caused by premotor lesions point to the impairment of processes which are very close to efferent functions but reveal in them some new and peculiar content. From the functional point of view, the position of premotor fields is similar to that of fields 18 and 19 of the visual cortex; they may be considered as secondary efferent fields.

A review of the cortical systems of the level of actions would be incomplete without mentioning yet another important characteristic: the integrity of the left infero-parietal area (associated, as is the rule for cortical organization, with the right side of the body) is also a necessary prerequisite for the functioning of the level of

actions. As a result of this there is a functional inequality of the two sides of the body, i.e. right (or left) dexterity, which is manifested for the first time at the level of actions. On the spatial-field level, let alone lower levels B and A, such inequality is not found [Footnote 1]. As was pointed out in the preceding chapter, vicarious substitution of one arm for the other can be easily achieved at the spatial-field level. At the level of actions, however, both general degree of skillfulness and the specific parochial acquired skills may be very different for the two hands, both in terms of their quality and composition. This feature may be used as an auxiliary criterion in deciding whether a particular motor act ought to be ascribed to level C or level D. Skills associated with level D, the level of actions, and based on the leading afferentiations that characterize this level do not allow as a rule easy transfers or substitutes between the hands.

We shall now turn to the functional analysis of level D. As in preceding chapters, we shall begin with the description of its afferentation and move on to the discussion of general characteristics of the motor acts associated with this level. Then a review of typical functional pathology will be offered followed by the review of normal composite motor acts executed on this level. This order of discussion seems most appropriate with respect to level D.

Objects constitute the leading afferentation of level D. Admittedly, treating objects as a type of afferentations presupposes a very broad interpretation of the latter term. The psychological image of an object is the result of considerably deeper generalization and more complex synthetic interaction between sensory and memory elements than the kind of synthesis which takes place with respect to the spatial field. It is not the object per se something with a geometric form, mass, or consistency, that constitutes the leading aspect at the level of actions (see p. 126), but rather it's the quality of purposefulness in the action involving the object, regardless of whether the action is directed at the object or whether the object is the instrument of the action. This quality is precisely what suffers in so-called agnostic (or ideatoric) apraxis which will be discussed later in more detail. The functional systems involved in the processing of sensory information about the object and determining exactly what 3

and in which orders can and should be done with the object, constitute the afferent systems corresponding to the level of action.

For further analysis it is useful here to introduce two neurological concepts of undisputable heuristic value; the concept of the purposeful structure of action and the concept of the motor composition of action. The purposeful structure of action is determined by the content of the problem at hand and it determines in its turn the task-relevant sensory or sensory-cognitive synthesis which can ensure the solution of the task. By so doing, it determines also the leading level of motor construction most appropriate for the task. The motor composition of action is already the outcome of the interaction between the motor task at hand and the kinetic options available to the organism. One might say that the motor composition is the outcome of introducing particular values into a general equation. The motor composition includes the ordered listing of the elements of the chain (providing that a sequentially organized action has to be accomplished), the determination of specific motor acts corresponding to these elements, and the background composition of simultaneous components of a complex motor act. The motor composition is determined by the biomechanical characteristics of the levers and kinematic linkages of the body, innervational resources; existing inventory of sensory corrections: and finally by the tool which can be used to accomplish the necessary action. The motor composition is therefore a function of both the task and its executor. The same task of rapid locomotion in space is solved by a man via running or bicycling; by a horse via galloping; by a bird via flying, etc. The determination and formation of the motor composition of movements and actions will be discussed in Chapter VII.

We shall now turn to the purposeful structure of the actions of this type, since it is as intricately associated with the afferent aspect of the given level as the motor composition of actions is with its efferent aspect.

Purposeful chains of level D are often termed "object-oriented actions," which is perfectly justified by the fact that most acts of this level essentially involve objects. This is a manifestation of a characteristic, gradual increase in the "objectivization" of the levels in the psychological hierarchy, as they are increasingly directed towards an

active, change-inducing interaction with the external world. This object-orientation as a characteristic of coordinated contingents of movements becomes increasing "encephalized" in the course of evolution. The role of lower levels becomes increasingly limited to auxiliary, background functions, that are related predominantly to "propriomotor" movements and components, which control and mobilize one's own body. This latter task becomes increasingly difficult as the mobility of the body and the demands for precision and complexity of its movements increase. It is also undisputable that the very contingents of movements become increasingly object-oriented throughout evolution; the role of the hand in this process has been adequately illuminated by philosophers. Objects enter motor acts of the level of actions both as passive objects of manipulations, as tools of actions, and also as symbols which facilitate and concretize abstract actions, e.g., a blueprint, a chess-piece, a written letter, or a hieroglyph. Many objectless actions undoubtedly belong to this level as well (providing that the notion of what constitutes an object is not totally inflated), e.g., athletic games, tactical military operations, etc.

It is a peculiar and thus far poorly understood quality of object-oriented actions that the leading role is assumed by the object in such actions and it reflects a very deep coordinational coding that is totally outside of the conscious domain. When an object is used as a tool in the context of a highly automated, habitual activity, it is directly experienced by the person as an organic part of his/her own body, to the point that one has the illusory feeling that the active, dominant regulation of movements originated in the tool itself.

The object itself exists in both space and time. Likewise, the purposeful aspect of the action with this object includes not only the purposeful perception and parsing of the space in which the action is organized, but also the synthetic experience of time in which the sequence and the functional connections among the elements of the action chain is organized. Afferentation at the level of actions includes both synthetic time and synthetic space which have totally different characteristics than of afferentation at lower levels. A review of the evolution and increased complexity of

these two psychophysiological categories as we ascend toward the level of actions may help clarify their peculiarities at this level.

In the preceding chapter we reviewed the evolution of "spatial" synthesis from the lowest levels up to the sub-level of the upper spatial field. The space of this sub-level, analyzed in detail, is completely metric (i.e., having a scale) and geometric (i.e., containing components of geometric form and geometric congruity), which makes it the most objectivized among all the "spaces" associated with various levels of coordination. Compared to lower levels, it relies on the most refined and phylogenetically youngest type of sensory reception; compared to higher levels which are more generalized and more removed from primary sensory input, it is based on the most peripheral cortical systems.

The space in which the organization of object-oriented actions takes place, has a number of features that affect not only the structure of the general leading afferent synthesis of this level but also the very coordina-tional composition of the movements controlled by this level. Already level C2 was characterized by the departure from a fixed system of coordinates (an ability to copy rather than to trace as in level Cl) and from a fixed scale (the emergence of homology instead of congruency as in level Cl). Such abstracting transformation of space goes even further on to the level of actions. A geometric form is replaced by a scheme; that is to say, metric, quantitative relations are replaced by topological, qualitative ones. Compared to the spatial field level, the space of the object-oriented level loses in concreteness but gains in systematization, conceptualization, extraction of that which is significant. Qualitative concepts like "open" and "closed" shape; relations like "above," "below," "outside," "inside," "between," etc., are extrapolated and organized at this level. The processes associated with this level are termed by psychologists as "categorical organization of space," and one refers to them as subordination of geometric form to a topological conceptual scheme.

Every geometric image can be described with respect to its topology and its metrics. The former implies the combination of qualitative features of the object, which do not depend on its size, shape, particular characteristic of the curvilinearity

of its contours etc. Topological characteristics of a contour includes for instance, those which describe the form as closed or open, as having intersecting lines or not (e.g., digit eight or zero), etc. In addition to such features, there are others that specify number but not metrics that must also be regarded as topological in our context. Four-angleness or five-pointedness of a form are examples of such features. All the shapes in the upper row of Figure 73 are members of the same topological class while being totally dissimilar in terms of their metrics. Indeed, each of them has five points; five intersections of constituent lines, etc. Item 6 of Figure 73 is similar to the first five in that it is also a closed form with intersections, yet it must be assigned to a different class on the basis of its having only one intersection. The alphabet offers a familiar example of topological features; each capital letter represents a separate topological class, so that the letter "A" class embraces capital "A"s of all sizes, styles or scripts, etc., providing that certain auxiliary and strictly calligraphic features are disregarded, The chalk-drawn layouts for the game of hopscotch which cover pavements in great numbers every spring are also members of the same class for each version of the game, regardless of the scale or drawing skills. The habitual scheme according to which a given child draws "a house" or "a man" can also be usually considered as a particular topological class—and nothing more.

A written letter in its spatial realization and a spoken phoneme in its acoustic realization are perfect examples of the primacy of the topological scheme over metrics at level D. Of the two examples, the first is more tangible and is more convenient for analysis. Such analysis reveals that not only is the symbolic meaning of a written letter conveyed exclusively by topological rather than geometric characteristics, but even the movements involved in writing it are equally topological, unrelated to the metrical characteristics of the scale, form, or geometric homology.

It has been argued earlier that throughout the evolution of afferent space, the style of this space at each level determines, via sensory corrections, the style of movements generated at this level. The following phenomenon is of interest in this context. It already has been pointed out that in order to make a movement automatic, a number of background components of coordination must be relegated to lower

levels and this implies their relegation to different systems of afferentation. For example, in order for a spatial field level movement to become automatic, whereby background components are relegated to the level of synergies, tactile-proproceptive afferentation must be substituted for visual afferentation, i.e. visual control over the corresponding component must be eliminated. If our general approach to automatization is valid, we should expect that in other cases involving relegation from the level of actions down to the spatial field level, the automatization should be associated with the introduction rather than elimination of visual corrections. Such situations can indeed be found. A normal adult, with his/her characteristic predominance of the object-oriented level, always draws a scheme rather than a form. In other words drawings reflect his conceptualizations and generalizations rather than his percepts. Therefore, a beginner artist must learn how to see the external world as it is actually represented in his retina, how to look at nature and reproduce it in correct illumination and perspective. This is different from laymen who conceptualize nature and replace it with ideograms, when they attempt to draw. Acquisition of skills and habits of drawing from nature offers an example of automatization of a levels-of-actions related process, in which there is introduction of visual control into the process. Needless to say, such control operates in experienced artists below the level of consciousness, which is to be expected from any well-automated act.

The characterization of spatial synthesis at the level of actions would not be complete without two more features.

First, the space of level D has topological rather than geometrical organization not only with respect to its afferentation but also with respect to its efferent processes. This does not necessarily mean that movements at this higher level cease to be metrically organized; it does mean, however, that the particular contributions of this level to such movements is topological rather than metrical. To the extent that metric movements are present at the level of actions, this indicates that there is participation in them of the spatial field level which provides a certain auxiliary background component. Level D movements are different from independent Level C movements in

that the latter can only be metric (otherwise, disintegration of level C, i.e., ataxia, would be observed)5 whereas the former are not metric as a rule unless level C is involved as well. It has already been mentioned that handwriting is not metric. Neither are taking off a hat; lighting a cigarette, or the depiction of a house or a man. By their very nature, tying and untying a knot, putting a rubber band around a box, or taking water with a cup from a pail are all topological rather than metrical. In all these instances the success of the movement is contingent upon its topological rather than metrical outcome. This is the reason why in ataxia a considerable number of the leve-of-action movements are preserved in spite of the disintegration of the spatial-field level; the only object-oriented actions which suffer are those that depend heavily on the C-level metric backgrounds.

Second, the previously described qualitative, meaningful transformation of space characteristic of the level of actions is intimately interrelated with the formation of the very concept of the object. This does not happen in abstraction and without a reason; rather it is part of the evolution from geometric (visual or tactile-proproceptive) image, which has color, weight, motion, etc., to a generalized, categorical and functional image of a thing or an affect. In the geometric image, form and metrics are significant; from the object point of view both are rather secondary. Undisputably, metric characteristics are significant in certain objects of particular designations, e.g., ruler, magnifying glass, blade, etc. But let us ask what is significant, for instance, in a cup, with regard to its functional manipulation as an object. Its width, its height, its being round as opposed to angular is inconsequential; on the other hand, its having a solid side, solid bottom and a handle are important— and these features are strictly topological. On this basis, any child can form the concept of a cup, recognize and appropriately use any particular cup, even if he had never before seen a cup with certain particular metric characteristics. What is significant in the metric characteristics of a bottle, a fork, a hammer, a button, a pencil? Admittedly, being outfitted in strictly topological, non-metric shoes would be no fun; but the importance of metric backgrounds in certain situations has already been mentioned.

Temporal synthesis undergoes an equally significant transformation from level to level, but its evolution has been studied to a lesser degree. At the level of synergies it is most clearly represented as a rhythm (i.e. temporal pattern) at the spatial field level—as distinct points in time (e.g. in aiming), synchrony, duration, velocity. At the level of actions it is represented as a purposeful and causal progression; as the linkage of successive elements of the chain of which the action is composed. Time is organized at the level of actions also not metrically but topologically, or categorically; elements like "before," "after," "post hoc," "propter hoc" are crystallized here.

The evolution of the interrelationships between spatial and temporal synthesis on the one hand and afferent and efferent systems of corresponding levels, on the other hand, comes about in substantially different ways. Spatial syntheses are closely connected with afferentation at all levels. At level C they form an objectivized external field for the structured extrojection of sensory elements. At the level of actions they offer prerequisites for categorical structuring of the external world, helping to single out distinct objects for active manipulations. Thus subjective space grows out of afferentationss objects grow out of space, and more generalized objective concepts grow out of the object. Conversely, temporal syntheses are more closely related to efferent systems at all levels. At the level of synergies they are incorporated into the very composition of the movements, embodying its rhythmic dynamics. At the level of the spatial field, they determine velocity, pace, appropriate moments in time for precise active responses. At the level of actions, subjective time is transformed into purposeful connections and linked chains of active behavior with objects. Thus subjective time grows out of the effector systems; purposeful actions grow out of time; at higher levels behavior grows out of purposeful actions; and finally the ultimate synthesis of behavior leads to the emergence of individual personality. It is of undeniable interest that, according to the (e.g. in aiming), synchrony, duration, velocity. At the level of actions it is represented as a purposeful and causal progression; as the linkage of successive elements of the chain of which the action is composed. Time is organized at the level of actions also not metrically

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disorganization that follow lesions in corresponding areas. We will further demonstrate that this peculiar development and extension of the Bell and Magendie law is also reflected in the localization of the working apparatus of the level of actions.

As is the case with space and time, the motor acts of the level of actions are not the first to provide the stage for the emergence of objects. To the contrary, interactions between a moving organ and an object takes place by necessity at all levels of coordination, although they are different at each of them. This should be noted so we do not erroneously attribute certain motor phenomena to the level of actions when we engage in the systematization of movements and the diagnosis of their impairments.

Grasping and holding of objects can be focused in man already at the lowest level of coordination—at the rubro-spinal level A, beginning with the tonic fixations which are observed in newborns from the first days of life (Chapter VII, page 162). Level A participates in the acts of grasping and holding an object also in adults, except that here, unlike in a child, it is a background rather than a leading level. It is level As which ensures the precise grasping and enveloping by fingers of an object regardless of its shape,, that inspired Bethe to invent the practically valuable idea of the design of a grasping hand prosthesis (Figures 74 and 75) although he made an erroneous theoretical generalization. Bethe was wrong in associating the mechanism by which the hand adapts to the shape of the object, not with the plastic or fluid tonus (which would be appropriate), but with the mechanisms of compensatory adaptation in locomotion, which (as we have seen) are executed at a much higher level, that of the spatial field. This error led Bethe to equate two mechanisms which have nothing in common anatomically or functionally; and it interfered with his progress in solving the problem.

The level of synergies participates as a background in a number of object-oriented actions, either indirectly by supporting locomotions which in their turn provide the background in an object-oriented action; or by providing direct background synergies. This level, however, has very little direct interaction with the

object per se and distinct object-related components can be found beginning only with the spatial-field level.

At the level of the spatial field the object is represented in a variety of ways.

First, the object serves in the spatial field as the point of application of force, as a physical entity, something with weight and resistance. A ball in an athletic game, a discus or a javelin in corresponding athletic exercises are not objects or tools of actions in the sense of level D, but they are entities of the spatial-field level that are characterized by certain shapes and consistencies, weights and resistances. In essence they can be regarded as material points, which is how they are often considered in biomechanics.

Second, an object at the spatial field level is something which can be taken, reached, put aside, fetched, thrown, pushed,, snatched, etc. In this respect, observations of those animals in which the level of actions is unavailable or barely available, are of considerable interest. When a hen sees food separated by a grid, it can only react to it at the spatial field level, i.e. fruitlessly rush toward it along the optic axis of the minimal distance. In a similar situation, a dog or a monkey can fairly easily switch over to the level of object-oriented (chain) actions; instead of going toward the object, it goes away from it, toward an opening in the grid, i.e. it incorporates into its behavior two sequential interdependent acts, the first of which is motivated by purposeful rather than spatial relations. Higher primates are capable in such a situation of rising to the use of tools by, for example, fetching a stick. The same primate, however, will for some time fruitlessly try to reach the food along a straight line at the field level by jumping and rushing to the food and only after that will it resort to the level of actions by, for example, building a tower of boxes.

Third, certain other types of object manipulations must also be assigned to the spatial-field level even though these cases superficially appear to be related to the level of actions. For instance, a 1.5 year old (the age is important) infant or a primate are capable of approaching a set of wooden eggs nested inside each other (a peasant toy) as something that can be opened. Their afferentations are therefore beginning to approximate the level of actions. But a child or a monkey approaches the problem

strictly geometrically: since the toy eggs can be opened into two halves, they begin to pull these halves forcefully in opposite directions. As a consequences both the two halves and the other toy eggs contained inside fly in all directions. The movements of the child or the monkey are determined by the geometric image of the openable egg, rather than by the object-related experience,, which could have suggested a much more effective way of opening the egg by twisting or shaking it gently. Only when the latter is mastered is it possible to say that the act of opening has switched over to the level of actions.

In sum, a certain type of object manipulation must be excluded from the list of movements governed by the level of actions. These are the grasping movements,, not only those which are simple plastic ones (e.g., holding an apple, the handle of a briefcase, etc.)5 but also those which are skilled, involving tools; all types of movements in which an object emerges as a material point in space or in which the movement is determined by the geometric image of an object. All such movements suffer following lesions of corresponding lower levels, whereas the level-of-action (D level) movements remain intact insofar as the spatial-field backgrounds are of secondary role in them (e.g., movements related to dressing, washing, opening up a box, etc.).

Before we list specific integral movements of the level of actions, let us summarize their common features in an intact CNS, and offer the general characteristics of the motor actions which can be collectively referred to as "praxias."

Movements at the level of actions constitute conscious acts; in other words, they are not so much movements as they are already elementary actions determined by the context of the task at hand. To put on and button a coat, to eat an egg in a civilized way, to put a letter into an envelope and paste it; to sharpen a pencil, to kick a football into the opposite team's goal—these are examples of elementary object-oriented actions. Each of them is a complex of movements which collectively lead to the solution of a certain meaningful task. In most cases these actions are organized as successive chains of varying degrees of compositional complexity, whose elements are interrelated not according to spatial (kinetic, geometric), but according to

purposeful motives which cannot be reduced to simple displacements of objects in space or to overcoming physical resistances.

When D-level actions consist of a chain of elements, it is usually possible to single out leading component movements which realize significant purposeful stages of the action, and auxiliary or background elements, which play a secondary but important subsidiary role. Examples of such auxiliary movement elements can be found in various reiterating cyclic movements (cutting, spading, sawing, etc.) and swinging movements (e.g., hammering), as well as in various autonomous successive auxiliary elements, e.g. picking up a tool and putting it aside after usage, pulling an object closer, holding it while working on it, wiping away waste products, etc.

Variability in the acts of this level is manifested in a new and very characteristic fashion. On Level B we encountered almost complete absence of variability of trajectories and postures, in other words, we observed a fixed relationship between the essence of a given movement and its spatial-kinematic characteristics, a relationship which in many cases was strengthened by the phenomenon of dynamic stability. On level C we already encountered wide ranges of interchangeable postures and trajectories, and even interchangeability of the part of the body being used; precise or invariant characteristics were maintained only with respect to final, goal-related parameters. On the level of actions an even greater degree of variability and interchangeability is found. This tremendous increase in adaptive variability at the level of actions is made possible by its localization in the cortex which introduced into neurophysiology its greatest degree of flexibility and spontaneity. Variability results from the leading role played at this level by the purposeful aspect of more or less complex object manipulations. Even in most overlearned, skilled, highly-automated actions the composition of successive elements of the chain, their order or the number of reiterations of separate elements is never exactly the same twice in a row. Not only trajectories and parts of the body used, but also whole elements of the chain are easily interchangeable. When a craftsman has to fold a narrow strip of tin along its length, the chain of his actions will collectively lead to the invariant, required outcome, even though elementary

movements in the chain may be varied infinitely. He may attempt to fold the strip with his bare hands with pliers, with or without a vice, with or without a hammer (first getting it out of the drawer with a spatial field level movement), while pressing or holding the object in a variety of habitual ways. This is in perfect agreement with the general rule that all the non-metric topological aspects of an object-oriented action presuppose by their very nature either variability or indifference to the locus of particular spatial coordinates. Only the main, resultant core of the movement is invariant and strictly followed and it is precisely to this end that all the auxiliary, background components are adapted and varied within very broad ranges.

Two important and characteristic constraints, however, are imposed on the variability and interchangeability of elements at the level of objects, and each of these constraints is related to a major physiological problem. We will dwell on them further, in the context of the analysis of the motor composition of actions.

One of the peculiarities of the level-of-object movements closely related to the aforementioned purposeful organization of space, provides an identifying feature for them. This peculiarity, although it is negative, is very characteristic and highly suitable for identifying controlled movements of the level-of-action and for discerning the time of ontogenetic maturation of this level when it begins to dominate the spatial-field level which is ontogenetically earlier. The point is that at the object-oriented level, actions are guided by purposeful rather than spatial image, and the motor component of the level-of-action chains are dictated and selected according to the purposeful essence of the object, in other words according to what has to be done with it.

This purposeful essence of level-of-object movements often does not coincide at all with the geometric form or the spatial-kinematic characteristics of the object; in many cases, the movement-elements of object-oriented chain actions lead in a direction other than that prompted by immediate spatial perception of the object. Earlier (page 127) while discussing object-oriented movements controlled by the spatial-field level, we offered several examples of motor acts guided by spatial image. For some of these movements the spatial field level of control was relevant

and adequate; in others it lead to complete or partial failure of the whole action. Rinsing a brush in a glass of water while painting on a sheet of paper; opening a box by pushing its top down so that it will pop up, by extracting a screw by rotating rather than pulling it; turning a boat to the right by turning its rudder to the left—all these acts are examples of successive components leading "in the wrong direction"; against the immediate geometric logic of the object manipulation. The designers' concern about ensuring the congruency between the geometric logic of control levers and the functional, technological logics in complex mechanisms is fully justified: control systems of a modern aircraft offer a perfect example. However, the degree of "automatizability" of object-oriented actions which often go "in the wrong direction" is considerable and the aforementioned illusion of the subject's own organs merging with the components of the engine or of the tool, is extremely compelling. This is best illustrated by an example from World War I (before the standardization of aircraft equipment) when pilots were amazed to learn from mechanics that the aircraft they had just flown for the first time had a control scheme which was radically different, in fact opposite, to the more conventional one which they had used throughout their whole flying careers [Footnote 1]. Similarly,

it is much easier than one might think to re-learn how to ride a bicycle with the arms crossed.

With respect to the object, the essence of D-level actions consists not of the relocation of the object in space, but of more diverse and complex forms of affecting the surrounding environment. Lighting a match, shaving,, cooking, etc., are examples of actions of relatively simple actions whose objective and result are beyond a simple relocation of objects in space. Skilled industrial actions like painting, electric wiring, polishing, etc., are particularly obvious in this respect. Tools, like other objects, may also be considered on levels below the object-oriented one (e.g., tennis racket, cricket hammer, etc.) instead of considering them in terms of the purposes for which they were invented. The new aspects which are introduced

into movements at the object-oriented level are related not so much to the fact that the tools are used but to the method and the purpose of such use.

Motor acts of the object-related level also can be characterized with respect to their motor composition, which is, first and foremost, to a great degree, specifically learnable and automatizable. These movements can be characterized as higher automatisms, object-related habits, skilled movements, Handfertigkeiten etc. These skilled movements are so numerous, so omnipresent both in everyday and in professional activities, and so qualitatively peculiar, that one is tempted to conceptualize them as representing a particular level of coordination, providing the background for the super-ordinate level of purposeful chain-actions, yet occupying hierarchically superior position with respect to all the other, previously introduced levels of coordination. Obviously, these skilled movements are not in themselves object-oriented actions, i.e., they do not contain the critical purposeful components. This is illustrated by the observations that in agnostic and ideatonic apraxias (see p. 136) they may remain perfectly intact yet lead to absurd outcomes once deprived of purposeful control. This also applies to dementias (a senile geriatric patient might knit a technically perfect sock with twelve toes in it) and to schizophrenia (a patient might produce meaningless perseverations of letters in elegant handwriting) etc. In the object-oriented action, automatisms furnish technical means rather than purposeful elements, which proves that such automatisms are organized below the object-oriented level.

It might be suggested that higher automatisms constitute a separate level, below the level of objects. This would appear to find support in the fact that they have their own separate cortical localization in the limited sense that localized lesions lead to their disintegration. It is precisely the higher automatisms that suffer following lesions of so-called premotor cortical fields (this will be further discussed below); and it is precisely the disintegration of higher automatisms which is referred to as "the pre-motor syndrome/" Nevertheless, this suggestion is entirely wrong, and all of the higher automatisms of the type discussed here are of a totally different nature.

In response, it is worth mentioning that we had encountered the phenomenon of automatization already earlier while discussing the spatial-field level. It has been established that this phenomenon consists of gradual relegation of a number of background components of a complex motor act to lower levels, where the most adequate sensory correction syntheses reside. There are no compelling reasons to dismiss the possibility of a similar mechanism behind the formation of higher, object-related automatisms.

Furthermore,, a detailed analysis of various higher automatisms conducted by us for a great many objects through the use of the cyclographic method,, in many contexts, everyday, professional, athletic, military, graphic, etc., has demonstrated that none of them contains anything that could not be accounted for by already known and previously described levels, either with respect to the coordinational corrections or the motor composition involved. None of these automatisms reveals a special type of sensory synthesis, which is what largely defines the presence and the composition of a separate level of coordination. None of these higher automatisms reveals any new features of the character or style of the process of coordination, or any new peculiarities of variability, interchangeability, transfer, vulnerability—in other words, any of those features and characteristics which are mandatory for declaring a certain contingent of movements a separate "level."

Once we move from negative to positive arguments, we become further convinced that every higher automatism invariably includes clearly discernable characteristics of one of the previously described levels of coordination, either level C or below. All of the coordinations involved may be seen under close analysis to have features of the spatial-field level (e.g. hammering automatisms of a blacksmith, or filing or cutting by a sheet-metal worker), or of the level of synergies (e.g. movements of a knitting needle or a violin bow), or even of the rubro-spinal level (e.g., grasping the handle of an instrument, or machine tool, rolling a pill, etc,). According to all the criteria used for hierarchic attribution (the criterion of the main sensory synthesis being first and foremost among them) these motor components of object-oriented actions invariably belong to one or the other of the lower, pre-object

levels. In the more complex automatisms, it is possible to discern a whole hierarchy of the levels of realization with an actual background structure that may be considered as a second order.

As a rule, the object-oriented level does not find such skills and automatisms ready-made, pre-existing in the repertoire of lower levels; instead they have to be formed in the context of action as they are being acquired. The peculiar feature of automatisms of this type is that they are acquired. The process by which they are acquired has a number of characteristics which also shed light on their central nervous structure. The initial stage of acquisition of a motor element of an object-related chain action is comprised solely of separate conscious, voluntary components which are usually realized through the pyramidal efferent system. At this stage (in a total novice) the precursor of the future automatism closely resembles the damaged remnants of that automatism in a premotor apraxic patient; the movement is disjointed, helpless, can progress only with the help of active, conscious attention, and is often accompanied by an overflow of efferent excitation,, useless syn-kinesias, etc. Providing that the efferent systems of the level of action function correctly, their cortical afferentations gradually become replaced by lower-level afferentations: the role of extrapyramidal components gradually increases; unconscious, non-voluntary and progressively adequate components emerge in the movement. The load on active attention decreases, as well as the load on the leading level. The latter retains control only over those details of the movement which depend substantially on the particular afferent features of the leading level. The automatization of the movement has taken place.

This process of active acquisition of automatisms during ontogenesis indicates that although the automatism does not contain in itself anything beyond components of the spatial-field level and lower levels, still the motives necessary for the formation or elicitation [Footnote 2] of the motor and coordinational combinations known as higher automatisms cannot be found on these levels or in their corresponding leading afferentations. All the technical, coordinational control over these automatisms takes place entirely at some lower level, yet their emergence,

acquisition and perfection, as well as their elicitation as the need emerges, are necessarily dependent upon the goals and motives originated on the level of actions This may be compared to the type of interrelationship we described earlier between the striate sublevel and the level of synergies during the act of walking. What could possibly motivate precise and highly coordinated manipulations with a needle, a carpenter's plane, a chisel, a microscope, a micromanipulator/or calligraphic pen had these movements become at some point self-contained not only with respect to their motor composition but also with respect to their purposeful structure and meaning? Thus, for instance, hammering a nail constitutes a typical ballistic aiming movement at the spatial-field level, supported by the auxiliary backgrounds from the level of synergies (coordination among joints, resistance to reactive forces, etc.), and the main characteristics of this movement, its force and spatial precision, rely on the afferent corrections of the spatial field. At the same time, the main coordinational control over such movements is executed at the level of object-oriented action, whereby the whole process is integrated in order to solve the main problem, that of driving in the nail. It is on this level that the decisions are made, whether the hammering ought to be forceful or restrained, vertical or angled, whether the hammering ought to be continued or should be stopped once the nail had been driven a certain depth into the surface. This level alone contains the motivation behind learning the swinging movements of hammering that are meaningful only in the context of a given task.

With respect to such higher automatisms it was suggested in the beginning of this chapter that the movement contingents of the spatial field level are incomparably richer in humans than in any other species, owing to the fact that the latter lack the motivations necessary for forming such contingents. This is in spite of the fact that animals possess many actual motor coordinational prerequisites for it as demonstrated by their ability to be trained. Elberfeld's horses and talking parrots are good examples. "If you beat a rabbit long enough,, he will light matches for you," one of the characters by Checkov pointed out. The point is that the man lights matches for totally different motivational reasons.

Analysis of higher automatisms reveals the physiological role of the premotor

cortex system where damage leads to general loss of automatization of D-level movements. This includes both the loss of the ability to retrieve overlearned automatisms and loss of the ability to acquire new ones. Evidently; under normal circumstances the premotor cortex systems operate as mediators of sorts which establish and maintain the interaction between the cortical constellations of the level of actions and lower levels of coordination. This conclusion is supported by the existence of abundant and well-studied pathways from the premotor cortical areas to the pyramidal fields and the pallidum, as well as to the frontal lobes which connect the premotor systems with the massive fronto-pontine-cerebellar tact. Premotor cortex systems exert their influence not simply upon lower-level efferents but upon entire levels as integral entities including their afferent and central integrative aspects as well as their narrowly defined efferent systems. The precise nature of the premotor control is not well understood at this time, yet it is clear that premotor areas play the role of an efferent system of a special kind at the level of actions. When this system is destroyed, the level of actions loses its access to the efferent periphery in all respects, except for a few and very abstract corrections of its own which were previously discussed.

It is now appropriate to turn again to the issue of the variability of the motor composition of actions and discuss it from a new vantage point. Earlier, while analyzing the purposeful structure of movements we noted the far-reaching variability and interchangeability of elements in their motor composition and in the combinational interrelationships among separate motor elements of the chain. This diversity is similar to what we encounter in stringing letters together to produce words. Extending this metaphor, we may note a high degree of variability in the letters themselves, that is, in the motor elements per se. Not only do the number and the order of stitches with a needle or movements of a scalpel by a surgeon or the turns of a drill by a mechanic vary from operation to operation, but so do the very movements involving these instruments. Movements of the hand with a needle, scalpel, scythe, or file while functionally equivalent are never completely identical. One immediately discovers that various separate motor elements (both simultaneous

and sequential) differ among themselves with respect to the degree of their intrinsic variability. In certain motor behaviors, two elements are adjacent in the sequence, one of which is as stable as facial features, and the other as variable as facial expressions. Further analysis reveals the reasons for such differing degrees of variability. The degree of variability of a given motor element depends on the background level that controls it. Automatisms controlled by the level of synergies are the least variable, while those controlled by the spatial-field level reveal, on the other hand, the maximum degree of interchangeability and plasticity which is a characteristic of that level.

In Chapter V the feature of "specific variability" which characterizes various levels of coordination has been discussed. This feature reflects predominantly qualitative but also qualitative peculiarities of observed variations. Analysis in terms of this feature can be useful not only for determining the level at which a particular movement is organized but also the structures and levels involved in the background "higher automatisms" of the level of actions.

The second characteristic of the variability of the motor composition of actions is related to the clearly pronounced difference between the right and the left hands, i.e.. to the presence of dominant and subdominant sides of the body, etc. This distinction was either completely or almost completely absent in the movements controlled by the lower levels including that of the spatial field. On the level of synergies . . . . . . *[translation not finished beyond this point]*

Footnotes:

Footnote 1. This example was told to me by Professor S. G. Gellerstein, to whom I express my thanks.

Footnote 2. Here we might also use the term ekfors," coined by Semon, which correspond; to his view of these matters.