CHAPTER II
THE PROBLEM OF THE INTERRELATION OF CO-ORDINATION AND LOCALIZATION

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1. THE BASIC DIFFERENTIAL EQUATION OF MOVEMENTS

The relationship between movements and the innervational impulses which evoke them is extremely complex and is, moreover, by no means univocal. I have already undertaken an analysis of this relationship in a series of previous studies (8, 9, 14, 15) and for this reason I shall present here only a short summary of such statements as may be regarded as firmly established at the present time. The main object of this summary is to serve as an introduction to a further discussion.

The degree of tension of a muscle is a function, in the first place, of its innervational (tetanic and tonic) condition $E$, and, in the second place, of its length at a given instant and of the velocity with which this length changes over time. In an intact organism the length of a muscle is in its turn a function of the angle of articulation $\alpha$; for this reason we may write that the momentum of a muscle with respect to the joint is

$$ F = F \left( E, \alpha, \frac{d\alpha}{dt} \right) . $$

(1)

On the other hand, we may assert that the angular acceleration of a limb controlled by a given muscle is directly proportional to the momentum of the muscle $F$ and inversely proportional to the moment of inertia of the limb $I$. In this way

$$ \frac{d^2\alpha}{dt^2} = \frac{F}{I} . $$

(2)

If there are other sources of force than the muscle operating on the limb, the situation is a little more complicated. Let us limit ourselves for simplicity to only one external force, namely gravity. In the simplest case which we have just described, where we are considering the movement of a single limb segment in relation to a second fixed one, the momentum due to gravity $G$ is, like the momentum of the muscle, a function of the angle of
articulation

\[ G = G(\alpha). \]  

(1a)

The angular acceleration of the limb segment under the influence of both momenta together is expressed by the equation

\[ \frac{d^2 \alpha}{dt^2} = \frac{F + G}{I} \]

If we introduce into this equation expressions (1) and (1a) for \( F \) and \( G \), we obtain a relation of the following form:

\[ I \frac{d^2 \alpha}{dt^2} = F \left( E, \alpha, \frac{d\alpha}{dt} \right) + G(\alpha). \]  

(3)

This is the fundamental equation for the movement of a single limb in a gravitational field under the influence of a single muscle where the level of innervation is \( E \). In cases where the moving system consists not of one but of several limb segments and where we are obliged to take into consideration the activity of several muscles, eqn. (3) becomes extremely complicated, not only quantitatively but also qualitatively as considerations of the mechanical effect of one muscle upon others also enter into the problem and the moment of inertia of the system becomes a variable term. However, in spite of the fact that the complications which arise in this case are so great that equations of type (3) cannot always be written even in the most general form, the physiological aspects of the problem differ only slightly, and the complications essentially involve only the mathematical and mechanical aspects of movement. For this reason in the present context we may limit ourselves only to the consideration of the most simple equation (3).

The basic equation is a differential equation of the second order which may be integrated if the functions \( F \) and \( G \) are known. Solutions of an equation of this type, that is to say, the determination of the movement which will take place in each given case, will be different depending on the so-called initial conditions of integration: that is, the initial position of the limb segment determined by the angle \( \alpha_0 \) and on its initial angular velocity \( d\alpha_0/dt \). By altering these initial conditions in various ways we may obtain very different effects of movement from one and the same governing law (3), i.e. for the same functions \( F \) and \( G \).

It must first of all be noted that eqn. (3) directly bears on the cyclical character of the relation between the momentum of the muscle \( F \) and the position of the limb \( \alpha \). The limb segment changes its position as a result
of the operation upon it of the momentum of effort $F$ and this momentum in
its turn changes because of the changes in the angle $\alpha$. A cyclical chain of
cause and effect operates in this way.

This chain would be ideally cyclical if the momentum (eqn. (1))
depended solely on $\alpha$ and $\alpha/dt$, that is, if the movement were completely
passive (for example, the falling of the arm). But, as in eqns. (1) and (3)
given in this report, the value of $F$ also depends on the degree of excitation
of the muscle $E$, which appears most clearly from the areas lying outside
the circle which we have just described. It is apparent that there are two
possibilities here; either the degree of excitation $E$ depends wholly or
partly on the values of $\alpha$ and of $\alpha/dt$, or it is quite independent of them
and is solely a function of time $t$.

The choice between the two possibilities indicated here is clearly of
great physiological significance as may be revealed with sufficient clarity
only by further discussion in this chapter. At the moment I shall only
indicate some of the consequences of each of the hypotheses we have raised.

If the degree of excitation $E$ is simply a function of position and
velocity and not a function of time, then eqn. (3) will take the form of a
classic differential equation,

$$ I \frac{d^2\alpha}{dt^2} = F \left[ E \left( \alpha, \frac{d\alpha}{dt} \right), \alpha, \frac{d\alpha}{dt} \right] + G(\alpha), \quad (3a) $$

the partial integrals of which depend only on the initial conditions. In
this case, consequently, a movement must occur if the required initial
conditions are fulfilled (from without), and once having begun it must
proceed with the same uninterruptable regularity with which a string will
oscillate if displaced to a precisely determined initial position and then
released. It is clear that this hypothesis does not correspond to
physiological reality and in effect completely ignores the role of the
central nervous system.

On the other hand, it may be supposed that the degree of excitation $E$
is a value which changes with time and depends entirely on a predetermined
sequence of impulses from the central nervous system without any relation
to the local conditions operating in the system of the moving limb being
studied. If, as in the hypotheses formulated above for the elastic
oscillation of a string, the muscle can be compared to some sort of
independent spring or rubber band, then in the second hypothesis it may be
represented as a sort of solenoid which attracts its core solely in relation
to the potential of the current which is supplied to the coil from an external source. The law of the variation in this current must be represented in the system of eqn. (3) as a function of time; in fact, whatever may be the real causes of these changes, the changes themselves are presented to system (3) in a completely finished and independent form as quite unalterable data. Equation (3) in this case takes on the form

\[ I \frac{d^2 \alpha}{dt^2} = F \left( E(t), \alpha, \frac{d\alpha}{dt} \right) + G(\alpha), \]  

(3b)

which does not permit of any concrete solution.

It is important here to draw attention to the following. In spite of the fact that the degree of excitation \( E \), as has been hypothesized, is independent of \( \alpha \) and of \( da/dt \), the momentum of the muscle \( F \) is dependent on them as before. Meanwhile, as we have shown above, the operation of this momentum, that is, the entire picture of the course of a movement, will vary with the initial conditions which in no way enter into the expression for the degree of excitation \( E \) and consequently do not in any way affect the course of its changes in time. It follows from this that the general results of interactions from eqn. (3b) cannot be foreseen or regulated in advance because the changes in excitation will be involved in the interplay of forces and dependencies which can in no way alter the further course of these changes following a fully independent law. Movements which are regulated according to the law (3b) will necessarily be ataxic.

And so we are left with the hypothesis that the excitation of a muscle \( E \) must be both a function of time and a function of position and velocity, and must be described in eqn. (3) in the form

\[ I \frac{d^2 \alpha}{dt^2} = F \left( E(t, \alpha, \frac{d\alpha}{dt}), \alpha, \frac{d\alpha}{dt} \right) + G(\alpha). \]  

(3c)

This purely analytical deduction of the functional structure of muscle excitation permits of exceptionally simple translation into physiological terms. The dependence of the variable \( E \) on time, proceeding from the absurdity of the opposite hypothesis (3a), underlies the necessity for the changes in excitation which are directly effected by the activity of the motor areas of the central nervous system. The dependence of the excitation on the position of the limb \( \alpha \) and its angular velocity \( da/dt \) is the proprioceptive reflex so well known in physiology. It necessarily follows from the preceding analysis that both position and velocity directly and independently influence the changes in the degree of excitation of the
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... muscles, and in reality both these effects have been subjected to precise physiological investigation.

Turning to clinical evidence we may say that (3a) is the equation of movement for an extremity in a case of central paralysis and that (3b) represents the equation of movement in a case of proprioceptive ataxia.

In this way we have stated in the basic equations of movement a superposition of two cyclical connections of different orders and related to different topics. The first cyclical connection is the mutual interaction of the position $a$ and the momentum $F$, and exists purely mechanically as has been pointed out above. The second connection constructed on the first one, is a similar interaction between the position $a$ (and also of the velocity) and the degree of excitation $E$; this connection is effected by means of systems of reflexes and is related to the activity of the central nervous system.

The principal significance of the general conclusions examined above may easily be deduced. The customary older representation implicitly accepted and, until the present, retained by many physiologists and clinicians, describes the skeletal link as being completely passive under the control of the central impulses and as being unequivocally subservient to these impulses. In this scheme the central impulse $a$ always produces movement $A$, and impulse $b$ always produces movement $B$, from which it is easy to proceed to a representation of the motor area of the cortex as a distribution panel with push-buttons. However, eqn. (3b) indicates that one and the same impulse $E(t)$ (ignoring the periphery) may produce completely different effects because of the interplay of external forces and because of variations in the initial conditions. Equation (3c) shows, on the other hand, that a determinate effect is possible for a movement only in a case where the central impulse $E$ is very different under different conditions, being a function of the positions and the velocities of the limbs and operating very differently in the differential equation with various initial conditions. Parodying the well known tag on nature we may say that *motus parendo vincitur* (movement is conquered by obedience).

It must be pointed out, finally, that the external force field does not consist of the force of gravity $G(a)$ alone and it may even occur that this latter expression does not enter at all into the basic equation in such a simple form. Because it necessarily affects the position and the velocity of a system, and because in the norm these latter affect the changes in $E$, we may say that the *parendo* of the central impulses must sometimes go to...
Fig. 14. A semi-schematic representation of the course of a single central impulse during a rhythmic movement. \( A \), the non-rhythmic curve of changes in external forces; \( B \), the summed rhythmic result; \( C \) (hatched area), an impulse bridging the gap between the curve \( A \) and the result \( B \).

great lengths. It is obliged to adapt to all internal and external forces operating in the system while forces which do not directly depend on the operation of the impulse \( E \) may frequently play a decisive part in the general balance of forces affecting movement. In such cases (Fig. 14), if for a given movement the required changes of forces at the joint are represented by the curve \( B \) and the resultant forces in the external field are represented by the curve \( A \), then the central nervous system will be obliged to provide only the additional fraction \( C \) so that the sequence of impulses cannot maintain even a remote correspondence to the contours of curve \( B \) and frequently even less correspondence with this curve than to the changes in the external field \( A \). These supplementary compensatory impulses sometimes appear in an indirect way from cyclogrametric observation.

And so, not to enter into details discussed in the studies mentioned above, it may be said that:

(a) a unequivocal relationship between impulses and movements does not and cannot exist;

(b) the relation between impulses and movement is the further removed from unequivocality the more complex is the kinematic chain operating in the movement under consideration;

(c) movements are possible only under conditions of the most accurate and uninterrupted agreement - unforeseen in advance - between the central impulses and the events occurring at the periphery, and are frequently
quantitatively less dependent on these central impulses than on the external force field.

2. THE INTEGRITY AND STRUCTURAL COMPLEXITY OF LIVE MOVEMENTS

In the treasury of experimental physiology there are vast collections of experimental observations and facts characterizing the course of single impulses or of the more simple patterns of impulses. There are most detailed studies of all aspects of excitation, inhibition, parabiosis, chronaxie, and so on, for a single nerve pathway. However, we have up to the present only two major advances along the lines of investigation of the total or systemic operation of impulses: Sherrington's principle of reciprocity and A. Ukhomskii's principle of dominance. But even these groups of data are very far removed from the areas we touch upon - the problems of the study of structures of movements as integral formations.

It is, however, precisely this integration of movements that is the most important feature implied by 'motor co-ordination'. The fact of this integration may be investigated in many experimental situations and significant connections and correlations are observed in all these cases between the various components of the integrated processes. The simplest and most easily observed phenomenon in this category is the appearance of gradual and smooth redistribution of tensions in muscular masses, which is particularly clearly expressed in cases of phylogenetically ancient or highly automatized movements. A muscle never enters into a complete movement as an isolated element. Neither the active raising of tension nor the concomitant (reciprocal) inhibition in antagonistic subgroups is, in the norm, concentrated in a single anatomical muscular entity; rather, there is a gradual and even flow from one system to others. I shall suggest a short experiment; stretch the arm out anterolaterally and describe a great circle with the hand as shown in Fig. 15, and then find out by means of anatomical analysis how the change in muscular innervation and the process of inhibition of the antagonists are accomplished during this movement. Exactly the same process of gradual

* The concept of antagonism may be applied unconditionally only to cases of muscles operating on joints with a single axis and, further, to those which cross only this one joint. The number of muscles of this type is extremely small; in the skeletal extremities we find as examples of this type only m. brachii and internus, m. pronator quadratus, the short position of m. triceps brachii and m. vastus femoris. All other muscles may be only functionally antagonistic in a single situation and in quite different relationships in other situations.
Fig. 15. Circular movements made with the arm extended in various positions are accomplished by completely different innervational schemes for trajectories of the same type. Transfer of innervation may be clearly observed in any plastic movements; with more accurate means of registration this may be observed as a general phenomenon.

The integration discussed above is even more clearly demonstrated in the analysis of automatic rhythmical movements by the appearance of extremely marked reciprocities in the interrelationships of the components. I have described examples of such reciprocity in other studies (9, 19); I shall here merely refer to the fact that in rhythmical work with a hammer the direction of the trajectory of the elbow (forwards or to the side) gives a close correlation with such phenomena apparently far removed from the elbow as the relationship of the maximal velocities of the head of the hammer in the movements of raising and striking, the angle of inclination of the hammer to the horizontal in raising, the relationship between the length of the trajectories of the hammer and of the wrist, and so on. It seems to me that the effects of changes in tempo and the whole construction of a movement are relevant here, as I have discussed in other studies (14, 19) on striking piano keys and on locomotion. A movement never responds to detailed changes by a change in its detail; it responds as a whole to changes in each small part, such changes being particularly prominent in phases and details sometimes considerably distant both spatially and temporally from those initially encountered.
Finally, it is necessary to comment on a fact to which I have drawn attention in a number of places (14, 15, 19, 21); that the course of rhythmical live movements may be presented in the form of rapidly converging trigonometric series. I have been able to demonstrate that a diversity of rhythmical human movements (walking, striking with a hammer, filing, piano-playing, etc.) may be interpreted to an accuracy of within a few millimetres in the form of a sum of three or four harmonic oscillations, the so-called Fourier trigonometrical sums:

\[ r = A_0 + A_1 \sin \frac{2\pi}{T} (t + \theta_1) + A_2 \sin \frac{4\pi}{T} (t + \theta_2) + A_3 \sin \frac{6\pi}{T} (t + \theta_3) + \ldots \]  

(4)

The rapidity of convergence of these sums may be seen from the numerical examples of Table 7.

<table>
<thead>
<tr>
<th>Walking</th>
<th>Absolute amplitudes</th>
<th>Relative amplitudes (A_1 = 100%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A_1 cm</td>
<td>A_2 cm</td>
</tr>
<tr>
<td>Longitudinal displacement of the point of the foot</td>
<td>38.50</td>
<td>9.09</td>
</tr>
<tr>
<td>Longitudinal displacement of the centre of gravity of the whole arm</td>
<td>7.60</td>
<td>0.81</td>
</tr>
<tr>
<td>Longitudinal displacement of the center of gravity of the whole leg</td>
<td>14.47</td>
<td>1.22</td>
</tr>
</tbody>
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The fact that such an interpretation is possible is of great importance to the question under discussion. If one complete cycle of a movement lasts for 1 sec, and in this case may be represented with an accuracy of within 1-3 mm as the sum of three sinusoids, this means that all the details of this movement must have been organized with the required degree of accuracy a full second beforehand. Further, its period being known, the sinusoid is determined by two parameters, that is, it can be determined from two points.
The sum of four sinusoids may thus be theoretically determined from eight points; in other words, it is possible to reconstruct from a small section of a movement of the type which we have represented, to within a fraction of one per cent in the form of the sum of four sinusoids, the entire movement as a whole with the same order of accuracy. This experimental fact is evidence in its most cogent form of the organizational interaction and mutual reciprocity of rhythmical movements in time while the mutual interdependence between the elements of the movement which I studied (of striking with a hammer) suggests a similar interaction in terms of spatial components.

If the external expression of co-ordinational activity provides a picture of such a high degree of reciprocity and interrelatedness, then, on the other hand, its anatomical structure in terms of our present knowledge also displays a picture of no less highly organized complexity. The extreme variety of clinical studies of damage to the motor area suggests that a large number of different subordinate and variously interacting systems co-operate in order to make possible a movement in its entirety. The spinal system alone contains up to five independent centrifugal pathways (pyramidal, rubrospinal, vestibulospinal and two tectospinal pathways). In the cortical region we have a very large number of centres which in one way or another appear (most often from pathological evidence) to be necessary components in a complete movement. All attempts to describe their activity in the norm are necessarily limited at the present time to very general statements and hypothetical descriptions, but there is no doubt whatever of their synthetic activity. For example, the attempts of Bianchi, Brown, Dupré, Foerster (44), Goldstein, Gurevitch, Homberger, Jacob, Lashley, Lewy (52), Magnus (55), v. Monakow (59), and many other investigators to describe in one way or another the functional interactions of various parts of the cortex must be mentioned here with recognition of the great service these authors have rendered to the physiology of movement. A brief summary of what these authors have uncovered in areas directly bearing on the objectives of this report would be approximately as follows. An impulse reaching the terminal plates in a muscle

from the centrifugal fibre of the last neuron is the resultant of a whole series of separate central impulses which reach the synapses of the anterior horn by different pathways. Among these latter we must recognize the significant innervational independence of pyramidal impulses (the corticospinal tract) and the combined impulses from the striopallidal groups of nuclei (e.g. striatum-gl. pallidus-nucleus ruber-tr. rubro spinalis) which are found in close co-operation with centres whose functional relationships are less apparent (substantia nigra, Dark-schewitz's nucleus, corpus Luysii, and so on). Centripetal proprioceptive impulses give rise to answering effector impulses from the cerebellum and from other many stations related to the spinal cord through the quadrigeminal system. Finally, the decisive role in the production of a movement must be referred not to a centrifugal but to a central-informational system (an older physiology would have termed this 'commissural-associative') interplaying along the lines of the frontal pontocerebellar pathways. It would be possible to list the general characteristics of the functional peculiarities of each of these anatomical stations (often the details given by different authors are contradictory), but this is not my aim at present. It is important here to point out a single peculiarity which is common to all these characteristics and which has been stated as an undisputed fact for the last 20 years.

All the clinical observations noted above, as well as those of many other authors, agree on the position (quite foreign to the ideas of physiologists of the last century) that these central nervous subsystems have one and the same object of excitation at the periphery - the same muscles and most probably the same peripheral conducting pathways. The idiosyncracies and differences in the operations of the pyramidal, striopallidal, cerebellar and other systems lie not in differences and peculiarities in the peripheral objectives on which they operate but solely in differences in the forms of influence exercised on these objectives. The pallidum is concerned with the same musculature as is the brain cortex; it is not the objective but the manner of excitation which is specific. None of the data from contemporary physiological investigations contradicts the reliability of the fact that, for example, both flexion and extension in any single-axis joint can be achieved through both pyramidal and the striopallidal systems; both these systems may and do give the effect of reciprocity. In 'gross pathology' this is carried out separately and in the healthy norm both systems in some way co-operate in a rhythmical process. As accounts of the way in which this co-operation may be effected we have
in the literature many observations, impressions, and deliberations which are often quite persuasive and in many cases not contradictory. What is common to all these descriptions is not in general important; what is important, with the object of a formal examination of material, is the general tendency found in all of them – the recognition of the common presence in all cases of the qualitatively peculiar operation of central subsystems on one and the same peripheral objects.

Closely related to these considerations is the currently established picture of the multiplicity of projections of peripheral organs in the central nervous system. Along the lines of the exceptionally detailed knowledge of cortical projection of the motor periphery, which was already under investigation in the 19th century, and which has been worked out in very great detail in our time (Fig. 16), we are now obliged to hypothesize localized projections of the same periphery both on the globus pallidus and on the cerebelli vermis. It is immaterial to our purpose in what way this multiplicity has occurred as a result of phylogenetic stratification and superimposition. In the human being, it is presented to us as given data, a given problem, and our task lies in the search for non-contradictory explanations of the mechanisms of a multistaged functioning of this sort.

If we attempt an examination from the point of view of such multiplicity of the equations for elementary movements (3c) which we have deduced above, we necessarily arrive at the following. A nerve impulse \( E \), which, as appears on close examination of peripheral processes, is not related in a univocal way to its consequence – a movement – and is therefore restricted to the most precise concordance between its evolution and the proprioceptive input for \( a \) and \( \Delta a/\Delta t \), is at the same time the sum of (or is in some other form of linked equivalence to) a series of impulses which have very different points of origin in the brain. Each of these impulses arises in a separate area in the brain that is distinct from other centres. Each of these centres has its particular interrelationships with other centres in the brain, its own conducting pathways, a particular degree of relationship with and form of connections to the receptors, and, finally, as clinical practice in nervous disorders shows, its own mode of operation in time and its own particular means of interaction. The difficulty of co-ordinating all these facts is very great indeed as I shall attempt to demonstrate. If the impulse \( E \) were to follow the pattern in eqn. (3b), that is to say if it had the form \( E(t) \), it would not in principle be difficult to represent a series of independent sources (a very high degree of agreement between them being
Fig. 16. Summary of data given by O. Foerster on results of stimulation of various points of the human cortical hemisphere (1926).

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implied) which would ultimately unite in a single common path of a motor
nerve and transmit the result of their common action E(t) through it to the
end plate. In exactly the same way it would not be difficult to conceive of
the possibility of multiple action of impulses in a case where the actual
form was (3c), that is, E(t, α, da/dt), if each of the separate impulses
had its own particular object of excitation at the periphery (in the form,
for example, of a particular muscle which was controlled by it alone). If
we suppose, for example, that control of a flexor group at a joint is
concentrated in the centre A and control of the extensor group of the same
joint in centre B while the proprioceptive connections secure the possibility
of either centre being able to react to α and to da/dt, then the mechanism
in this case would be merely quantitatively and not qualitatively difficult
to comprehend. The actual situation - that is, a system of impulses without
unequivocal correspondence to the movement, and controlled by proprioception,
being sent to the object from a number of sources - is one which does not
permit us any simple escape from the question. The sole (apparent) possibility
of explanation for a structure of this type lies in referring the proprioceptive
"perception" to only one of the effector centres of the brain, for example, to the cerebellum, and supposing that the other effectors function purely according to type $E(t)$. The mathematical expression of such a structure might be regarded in the following way: the summed impulse $E$ is made up of a series of central impulses $E_1, E_2, E_3, \ldots$

$$E(t, \alpha, \frac{da}{dt}) = E_1(t) + E_2(t) + \ldots + E_n(\alpha, \frac{da}{dt}).$$

(5)

However, this combination appears to be unacceptable for a number of reasons. In the first place, we have no guarantee whatever that $E$ is the sum of $E_1, E_2, \ldots, E_n,$ and not some other function of them such as would considerably alter the case and complicate for the co-ordination centre $E_n$ the possibility of suppressing the "blind" impulses $E_1, E_2$ with precisely proportional additions. In the second place, the centrifugal impulses are directed in the spinal cord not through one channel, but through a large number of channels, and reach by direct pathways at least two central nuclei, cerebellar and thalamic, attaining a further series of areas by indirect pathways; but the problem lies precisely in the interpretation of the possibility of proprioceptive multiplicity. To visualize this is about as difficult as to imagine the movement of a two-seater bicycle each seat of which is equipped with its own separate set of handle-bars. It is clear that the presence of two effector centres responding to proprioceptive input requires the closest possible co-ordination between them. I would deny neither the possibility that such connections may exist nor that they exist in fact. My aim in the first two sections of this chapter is merely to indicate the great difficulties which confront functional explanations of the co-ordination of movements. It is already apparent that eqn. (3c) is quite different from our usual, qualitatively simple models of the interaction between the centre and the periphery; when, however, we are obliged to confront their complex interaction as a result of the mutual activity of entire systems of organs which, anatomically and clinically, display varying degrees of independence, then the resulting great structural complexity becomes more obvious still. Yet this is fruitful, since a failure to realize the difficulty of a problem frequently defers the moment of its solution.

3. THE INTERRELATIONSHIP BETWEEN CO-ORDINATION AND LOCALIZATION

The discussion in the preceding sections has already largely revealed the close connection between problems of co-ordination and localization. It
is clear from all that has been said above that no nuance of a single impulse $[E(t)]$ can serve as an explanation of even the simplest case of repeated accomplishment of automatizing movements, and still less as an explanation of the involved complexity of natural movements carried out by many muscles, each of which involves control from many centres. To digress: at the beginning from the indubitable presence of functional "inter-departmental" connections between brain centres which organize these latter into hierarchical order (Über- und Unterordnung), the following innervation scheme for effector impulses will be obtained (Fig. 17). It is clear that co-ordination is determined not so much by differences in the effect of each of the impulses $Aa, Ab, \ldots, Ba, Bb$... taken separately, but also by the systematic modes of their common operation and joint effect. The term co-

![Diagram](image)

**Fig. 17.** The multiplicity of efferent pathways for the control of six muscles $a, b, c, d, e, f$, by five effector centres $A, B, C, D, E$, gives, even in this intentionally simplified case, a complex structural scheme of innervation.

ordination hints at the common actions of separate elements. The solution to the problem of co-ordination lies not in analysis of the tonal and expressive resources of a single instrument in an orchestra but in the technical construction of the score and in the mastery of the conductor.

The basic guiding thesis for investigations of co-ordination must for this reason be formulated in the following way. Co-ordination is an activity which guarantees that a movement shall have the homogeneity, integration and structural unity which has been described above. This activity is principally based not on particular processes in individual neurons, but on the determinate organization of their common activity. This organization must necessarily be reflected in the anatomical plan in the form of
localization.

This seems to me to be an extremely expedient way of formulating the question. On the one hand, organization and the forms in which it exists must inevitably be represented in the structural forms of localization. In the same way as we may derive from an examination of a diagram of an electrical circuit some idea as to the nature of its function, so data of the localization-anatomical type may serve at least as circumstantial evidence in the consideration of the new experimental problems I have put forward - the structural physiology of movement. On the other hand, such a structural analysis of movements should aid considerably in critical, evaluation of existing and future conceptualizations of the type and structure of cerebral localization. It is impossible to visualize a situation in which localizational structure would be found to contradict structural organization.

A pertinent point must be made here. One must not in any way confuse localization with topography. Topography is the geography of the brain, the study of the spatial distribution of its functionally existing points. Localization is the structural plan of anatomical interrelationships between these functional points. If we shuffle in Fig. 17 the positions of the centres A, B, C, D and E, this will change the entire topographical picture, but will not alter their localizational structure. The distribution (topography) of the elements in a diagram of a receiving set are completely different in the diagram from the topography of these elements in an actual apparatus constructed from this diagram. On the other hand, for one and the same topography completely different schemes are possible.

Figure 18 makes the latter clear in regard to circuit-diagrams which are extremely convenient for illustrating our problems; diagrams (a) and (b) in this figure have exactly the same structure for different topographies, schemes (b) and (c) have the same topography but different structures. The problem which obsessed our physiological forefathers, that of the inversion of the retinal image, and in particular whether this inversion is transmitted in exactly the same way to the cortex, and if so, how it is compensated, appears to us now to be childishly simple-minded. We still remember how some of their contemporaries hypothesized, to explain the matter, that the soul was located in the brain with its feet uppermost, without however determining more precisely whether souls have feet. Nowadays we hypothesize with great facility much more complex transpositions of elements in the representation of the retina on the cortex without experiencing structural difficulties from
this fact; indeed, in a central telephone station, for example, we do not have to worry whether the commutator links for subscribers from the northern and southern parts of a town are located respectively at the northern and southern ends of the switchboard. However, this old question permits of new

Fig. 18. Three diagrams for two-tube audio-frequency amplifiers. Diagrams (a) and (b) (a single-cascade push-pull block) are identical in all details; that of (c) (a double-cascade amplifier with transformers) is very different in principle from the other systems.

and less childish formulations; are there, nevertheless, limits to this type of transposition? And if such limits exist, what are the borders which separate transpositions that do not change structure from transpositions which inevitably destroy structure? An analysis of the problem when framed in this way shows us first of all that different structural schemes may show different degrees of tolerance to transpositions, but this aspect of the problem will be developed a little later.

Thus, in the problem of localization what is important for our purpose is not precisely where in the cortex one or another peripheral object or function is reflected, but what is represented, and how; and what are the distinguishing characteristics of those objects represented in the cortical hemispheres and in subcortical centres. Topographical problems are for the
most part clearly unrelated to the analysis of the co-ordinational structure of movements, while the problems of localization are of paramount and principal significance.

This significance may be very well explained from the example of the old conception of localization which has already been mentioned in Section 1. This conception would answer perfectly to reality if every central impulse unconditionally governed a single determinate movement, that is, if there existed a one-to-one correspondence between impulses and movements. In this case the effector impulses would be able to operate purely as a function of time \( E(t) \), giving always one and the same effect independently of what occurred at the periphery; the push-button control-board model of the cortex, similar in plan to an organ keyboard, would be suggested in the types of explanation we employed. But, on the contrary, this type of one-to-one correspondence does not exist and the cerebral motor area organizes responses by deftly adjusting and balancing between resultant external forces and the manifestations of inertia, constantly reacting to proprioceptive signals and simultaneously integrating impulses from separate central subsystems, so that ten successive repetitions of the same movement demand ten successive impulses all different from each other; and the presence in the cortex of localization of the Hitzig or Foerster type begins to seem a very dubious interpretation. I would like to recall here the failure in 1923 of the invention of "a symphony of whistles". An attempt to convert steam whistles into a musical instrument with an organ keyboard failed because any given whistle could not be relied upon to sound the same on every occasion, and its pitch would vary with the pressure of steam, with the number of whistles sounded simultaneously, with the degree to which the steam-channel was clear, and so on, so that it was impossible to obtain a one-to-one correspondence between the keyboard, on one hand, and the frequencies of the tones obtained, on the other.

It is understood that a statement of complexity, of "impracticability" from our point of view, is not in any sense a decisive argument for the acceptance or rejection of any physiological hypothesis. There is no reason to suppose that physiological structure should be maximally rotational from our technico-social anthropomorphic point of view. The localization structure of the cortex according to Foerster's scheme (Fig. 16) does not directly contradict eqn. (3c) with its proprioceptive cycle and lack of simple one-to-one relationships; it only makes the problem of functioning of its cell centres extremely difficult. The decisive argument against the theory
of direct representation of muscular systems on the cortex comes from quite another, perhaps unexpected, direction. I present this argument in its most general formulation below; here I shall employ only one of its partial modifications as applied to a particular case.

Let us suppose that the cells of the gyrus centralis are in reality the effector centre for the muscles. Let us further suppose that the activity of these cells must be (as is inevitable in the given hypothesis) sharply different from instant to instant on the multiple repetition of a given movement, in relation to changes in the external force field and proprioceptive signals. If we suppose for clarity that we may represent each excited effector cell in the cortex as lighting up like an electric bulb at the moment when its impulse is transmitted to the periphery, then under such an arrangement the effecting of every movement will be visible to us on the surface of the cortex as a zig-zag discharge. The absence of one-to-one correspondence and all the considerations which have been described above as consequences of eqn. (3c) will be obvious in this case because on every repetition of a given movement the zig-zag discharge will be visibly different. Now suppose that this repetitive movement is an automatized act, the realization of a habit of movement, in other words, a conditioned motor reflex. From the discussion above it follows as an inescapable deduction that the conditioned reflex of movement operates each time through a new zig-zag — through new cells; in other words, we arrive at the conclusion that the hypothesis of cellular localization of muscles necessarily leads to a denial of cellular localization of conditioned reflexes. One of the two chess pieces must here be taken, and it is here a very pertinent question which of the two the old-fashioned localizationist would rather sacrifice.

I do not for a moment imagine that I can overthrow the old localizationist concept at a single blow, but it is not possible to disguise the fact that it is already threatened in very serious ways. The experiments of Bethe (30) and of Trendelenburg on the extirpation of cortical tissue in monkeys has indicated the possibility of far reaching compensations and, moreover, the extensive investigations carried out by Lashley, experimenting on rats and observing the appearance of compensation and of the re-establishment of conditioned reflexes for the most varied and topographically different sites of extirpation, and very persuasive evidence in favour of a radical re-examination of the old conceptions. Lashley could not discover any clear relationship between the topographical loci of the areas he destroyed and
the degree to which the conditioned reflexes could be re-established; he
found, on the contrary, that there is a strong correlation between the time
required for re-establishment and the quantity of brain substance removed,
without reference to its locus. These results cause him to favour the theory
that there is no cortico-cellular individuality of operation, in which, it
seems to me, he is quite mistaken. His data are extremely dangerous for the
old localization theory, but they far from disprove the possibility of
any form of localization in general terms.

Lashley's error sets off very well the opposite error made by Gall in
his time. Nobody now believes that phrenology was doomed to failure because
the very principle of cortical localization was found to be defective.
Nobody ascribes its downfall to the fact that Gall did not localize avarice
or ambition to areas in which they were located in reality. Gall's theory
was essentially faulty not because of the topography he assigned but because
of the principles of selection underlying those categories for which he
thought that he could find discrete localizations in the cortex. The
categories suggested by Fritsch, Hitzig, Foerster, and others appeared to
be more physiological and nearer to reality than Gall's fantasies, which
were impregnated with the moral rationalism of the 18th century, and
appeared, as it were, to be the next approximations to the discovery of
reality. The evidence which has accumulated against these Foersterian
categories up to the present time must inevitably lead to their abandonment,
but this does not yet threaten the fall of the principle of localization in
general. It should be recalled that immediately after the abandonment of
phrenology the idea of localization also appeared for a long while to be
compromised until it gradually became apparent that it was possible that
the baby had been thrown out with the bath water. Now, again, after the
development and establishment of the understanding of conditioned reflexes,
to deny the structural anatomically engraved specificity of the brain would
amount to an affirmation that its nature is absolutely beyond knowledge.

Our experimental aim at present lies in the correct formulation of
categories which are really represented in the brain centres. The key to
this search for the true categories clearly must lie in structural analysis:
of the receptor moment, as it appears in experiments with conditioned
reflexes; and of the effector moment, as it appears in the co-ordination of
movements.
4. ECPHORIA OF THE ENGRAMS OF MOVEMENT

So far I have touched in this report only on those phenomena which point to the momentary, extensively structured nature of the co-ordination of movements. It appeared important to me to demonstrate that a movement could not be understood in terms of some nuance in operation of a single impulse, but that it is the result of the simultaneous co-operative operation of whole systems of impulses, while the structure of this system - its structural schema - is important for the understanding of the result. It is only a short step from this to the central argument in this report, that the innervation and localization of this structure is in reality not only not contradictory to the observable structure of the movements of the organism but is necessarily an exact representation of the latter. To proceed further it is now necessary to attend to another side of the phenomenon, that is, its duration in time. It is necessary to elucidate experimentally whether a simple parallelism exists between the duration in time of a series of system-related impulses or whether there also exists on the co-ordinalational time axis the same mutual structural interdependence as has been described above for every separate moment of force.

This formulation of the question may be clarified by the following illustration. In order to achieve a given co-ordination at a given moment, we have Schema I (for example that illustrated in Fig. 18). Is it possible to regard all co-ordinations over all possible durations of time as uninterrupted functionings of Schema I, or do they exist, and may be regarded as a sequence of changes of Schema I to some other schema, qualitatively different from it (Schema II, and then to Schema III, Schema IV, and so on), while the law of the transition between the schemas and their order of transition, in its turn, has its own determinate structural features? Our factual data on this problem are so far extremely scanty but some observations may still be made.

Firstly, we must turn to the facts described above of the homogeneity of a movement and its unity in terms of the interrelations of its parts in space and in time. Having established our model for a rhythmical movement in the form of a three-four term trigonometric series of the type of eqn. (4), it is possible to prove beyond doubt that this homogeneity also exists in time, and that this particular homogeneity is indeed not peripheral or mechanical but certainly originates in the operation of the central nervous system. This demonstrates that there exist in the central nervous system exact formulae of movement (Bewegungsformeln) or their engrams, and that these
formulae or engrams contain in some form of brain trace the whole process of the movement in its entire course in time. We may affirm that at the moment when the movement began there was already in existence in the central nervous system a whole collection of engrams which were necessary for the movement to be carried on to its conclusion. The existence of such engrams is proved, however, by the very fact of the existence of habits of movements and of automatized movements.

A problem of considerable structural significance now arises. Let us suppose that to a given co-ordinated movement there correspond, in the brain n engrams by means of which it is ensured that the movement will take place with successive ephoria in a determinate time sequence and with determinate tempo and rhythm. All these n engrams exist in the central nervous system at any given moment as the habit of movement exists, but they exist in a hidden, latent form. How are we to explain the facts that, firstly, they do not all undergo ephoria simultaneously but in sequence, secondly, they do not lose their order of ephoria, and thirdly, they observe determinate time intervals between ephoria (tempo) and quantitative relationships in their duration (rhythm)? There are here two basic possibilities, two "temporal structures"; either (a) each successive ephoria of the engram (or perhaps a proprioceptive signal of its effect at the periphery) serves as an ephorator for the next engram in order; or (b) the mechanism for ephoria, the ephorator, lies outside the engrams themselves and directs their order by a hierarchic principle of Überordnung. The first hypothesis may be called the "chain" hypothesis, the second the "comb" hypothesis (Fig. 19).

Very weighty considerations may be found to support both these hypotheses. The chain hypothesis brings to the fore proprioceptive moment, and in this connection it explains independently and satisfactorily the observation of tempo and rhythm referring them to a regular synchrony with events occurring at the periphery. Because, on this hypothesis, the stimulus for the arousal of each successive ephoria is the existence of the preceding one, it is possible to explain both the maintenance of an order of succession and the impossibility of separate links being left out of a succession of ephoria in this way. Finally, the hypothesis recommends itself by its simplicity, and by the fact that it is unnecessary to postulate any particular structure for the ephorator.

The arguments in favour of the comb hypothesis are no less cogent. The presence in the C.N.S. of "the plan of a movement", the homogeneity of its
Co-ordination and Localization Problems

![Diagram of a chain and a comb with labeled points a, b, c, d, e, and f.]

Fig. 19. Two theoretically possible schemes for successive ecphoria of motor emgrams a, b, c, d, e, and f.

Formulas and the homogeneity of the movement itself and of its course from beginning to end does not answer to the hypothesis that a movement is fractioned in this way, or that there is no guiding principle of succession among elements of the chain type other than events at the periphery. We do not see in this case any sign of a guiding principle unifying the whole. Further, if we recall the facts discussed above which indicate that the central impulses merely adjust to, and compensate for, the external forces field so that the pattern of the impulses over time may have very little in common with the picture of the movement, the comb hypothesis finds a new and important reinforcement. At the same time, a glance at Fig. 14 shows that the central impulse C, which is represented by a hatched area (and is entirely unlike the summed rhythmical equilibrium B which is finally achieved because of the presence of external disturbing forces A), shows a succession of elements which in no case resemble each other. The possibility of obtaining the homogeneity and regularity of B on every repetition, agreeing at the periphery with the law expressed in eqn. (4), necessarily requires the existence in the C.N.S. of some type of guiding emgram which encompasses the entire law of succession of B. If a guiding emgram of this type exists (we may refer to it as the motor image of a movement) it must have a dual nature; it must contain within itself, in some way uniquely and simultaneously existing like an embryo in an egg or track on a gramophone record, the entire scheme of the movement as it is expanded in time. It must also guarantee the order and the rhythm of the realization of this scheme; that is to say the gramophone record mentioned above must have some sort of motor to turn it. To pursue this metaphor, what I have called the gramophone record is
the directing engram, and what I have compared to a gramophone motor is the ephorator.*

Both of the hypotheses which we have examined are completely bound up with the structure of the peripheral impulse which we have deduced above in terms of eqn. (3c), that is, its dependence on the form \( E(t, a, da/dt) \), but they only illuminate this dependence in different ways. On the chain hypothesis the critical agents which determine the development of the process are the dependence of \( E \) on \( a \) and \( da/dt \), that is, their proprioceptive relationships, while the temporal moment of the relationship to \( t \) is determined in this case only by the tempo and by the maintenance of each individual element of the chain \( a, b, c \) (Fig. 19). In the comb hypothesis, on the other hand, the dominant relationship is \( E(t) \), that is, the independent initiative and the regulating activity of the C.N.S., and proprioceptive effects merely play the role of correctors to the general whole.

It must not be forgotten that the hypothesis of the necessity for an effector mechanism which is distinct from the engrams themselves and is in some sense dominant over them, is not necessarily related to the comb hypothesis but is necessary in equal degree for both hypotheses. Whatever we may ascribe to the regulating engram in the comb hypothesis and to the elementary engrams \( a, b, c, ... \), in the chain hypothesis they are all alike bound to contain in latent form the impulse \( E \) in dependence not only on \( a \) and \( da/dt \) but also on \( t \). It makes no difference whether the central mechanism of tempo – this "gramophone motor" – is related in its action to the duration of the physico-chemical intercellular reactions or to some other physiological rhythms;** they must in any case exist as some functions which differ from the collection of engrams which they activate, because real time cannot be incorporated in the latter. A decision between alternatives in favour of one or other of

* It is interesting to note here that the question which I have raised of the ephoria of movements in a chain system or a comb system is a repetition in new terms in the area of the physiology of movement of the ancient psychological dispute of association (Bleuler, Adler) versus action (Berze) in the manner in which psychological processes are carried on. The chain model corresponds to the concept put forward by the associationists and the comb model is very similar to Berze's hypothesis. I am in no sense a partisan of the latter opinion in view of its deeply idealistic basis (the psychology of voluntarism), but I cannot deny that the attacks made on the opinions of pure associationists were extremely opportune.

** For example, the velocity of the dispersion of waves of excitation through the C.N.S., time phenomena related to the interference of these waves, rhythmical heart activity, etc.
motor is the only bound up chord above in da/dt), but chain hypothesis ess are the relationships, in this case ment of the hand, the active and the merely play sity for an ess and is in e comb hypothesis we may ascribe memory engrams to contain in it but also on sop - this of the physico- al rhythms; ** on the collection incorporated in or other of have raised of em is a ovement of the er) versus action carried on. The associationists, I am in no sense alistic basis e attacks made ofortune. citation through these waves, these two hypotheses, or perhaps in favour of some other more complex organizational synthesis which incorporates both of them, is a topic for further investigation. At present is is important for us to discover what, in principle, is implied in the actual manner in which the problem is framed.

What is important is that the motor image of a movement (that has been termed by neurologists "the program of a movement", Bewegungsformel, Bewegungsgestalt, and so forth) must necessarily exist in the C.N.S. in the form of an engram. This directional engram does not merely exist on the comb hypothesis; indeed, the same fact of successive "stamped-in" connections between elementary engrams a, b, c, d, e, ..., in the chain hypothesis is also the engram in the other scheme, only in this case it is represented by an arrow rather than by a circle; this is the engram that determines the law of systematic succession of ecphoria and that consequently controls it. This motor image corresponds to the real, factual form of the movement, that is, to the curve B in Fig. 14, and in no way to the curve of the impulse C; it is indeed true that its presence makes it possible to control the course of the impulse C so that, as a result, a smooth performance of the movement habit B is achieved. Therefore it is necessary that there should exist in the supreme nervous organ an exact representation of what will later occur at the periphery; meanwhile, the unfolding of the activity in the field in the intervening operational stages and the realization of the impulse C (which by the argument given above is accordingly dissimilar to the peripheral effect), must therefore also be dissimilar to the contents of the controlling engrams. We may use the following metaphor: it is as if an order sent by the higher centre is coded before its transmission to the periphery so that it is completely unrecognizable and is there again automatically deciphered. In Section 3 above I have said that the possibility of a habit of movement, of the establishment of a conditioned motor reflex, necessarily implies its unitary localization in the central areas, and that a unity of this type cannot be related to the theory of the representations of muscles in the higher centres of the cortex. The considerations which have just been raised once again confirm this theses, on this occasion from the point of view of the time structure of movements; that level of the C.N.S. in which the centrifugal impulse C is formulated and in which we might consequently expect to find a representation of the muscular system is not the supreme level of the C.N.S., but is in fact that level at which the elementary engrams a, b, c, ..., etc., of the comb hypothesis are located. Between the mechanism represented by the comb hypothesis and the mechanism
involved in the case of muscular representation we are obliged to insert
another process of the coding of the image of the movement and its
presentation in the form C. In the terms of our equation this coding
process is the transformation of the relationship \( E(t) \) in the pure form
prevalent in the higher level into a full dependence of the form \( E(t, a, a, \)
do/dt); that is, the adaptation of the impulse to proprioception.

In this way, the analysis of the course of a movement in time again
brings us to a recognition of the structural complexity of an act of movement,
and consequently also of the complexity of its representation in terms of
localization. Here, also, the recognition of the necessity for the existence
of directional engrams and mechanisms of ephoria demands that we postulate
a series of hierarchical levels, each of them, inevitably, having a degree
of qualitative independence.

5. TOPOLOGY AND METRICS OF MOVEMENTS. THE MOTOR FIELD

If we now turn from the temporal moment to the spatial it will be
necessary to touch on two considerations: the distinction between the metric
and topological properties of physiological space, and the peculiarities of
the motor field of the central nervous system. Because of their fundamental
importance these two points should really be the objects of separate reports.

* The formation and development of new habits of movement, that is, the
engraphy of conditioned reflexes of movement, also appears to be a
structurally complex process in the light of the analysis undertaken in
this report. It is in fact the case that new directional engrams with
their spatio-temporal details must be built up in the C.N.S.; however,
those auxiliary proprioceptive mechanisms which I have just described as
"coding" the impulse, and which provide the higher engram with the
possibility of an actual detailed existence, must also be built up. The
fact that the habit of movement is not engraphed in those centres in
which the muscles are localizationally represented is at once demonstrated
by the fact that an acquired habit may exist while incorporating very
different muscles in various combinations. When a child learns to write
he can only form large letters, but a literate adult can form either large
or small letters with equal facility and write either straight ahead or
sideways, etc. Apparently the motor directional engrams are developed,
generally speaking, later than the auxiliary coding mechanisms and
correspond to a higher degree of mastery in the acquisition of a habit.

** The term "topology" as used here does not coincide exactly with the strict
mathematical definition. For lack of a more adequate expression I have
adopted this term for the whole of the qualitative characteristics of
space configurations and of the form of movements in contrast to the
quantitative, metric ones. The more detailed definition of what is meant
here under the term topology will be understood from the text.
I will for this reason discuss them only as much as is necessary to develop my basic thesis.

In any geometrical representation we may make a distinction between topology and metrics. By the topology of a geometrical object I mean the totality of its qualitative peculiarities without reference to its magnitude, form, any distortion in its reproduction, etc. As topological properties of a linear figure, for example, we may discuss whether it is open or closed, whether the lines composing it intersect with each other as in a figure eight or whether they do not intersect as in the case of a circle and so on. Besides these properties, in the determination of which quantitative considerations are irrelevant, we may also consider such topological properties as incorporate the concept of number, not, however, including the concept of measure. Among these properties we may refer, for example, to that of quadrangularity, membership in the group of five-pointed stars, and so on. I shall arbitrarily describe this group of properties as topological properties of the first order while the former may be considered zero order properties. All figures in the upper row in Fig. 20 belong to one and the same topological class of figures of the first order (being, however, completely dissimilar in metric relations); they are indeed identical in respect to the numbers which characterize them. All of them have five angles or points, all of them display five intersections of the lines composing them, and so on. No. 6 in this illustration belongs to another class of the

\[ \begin{align*}
1 & \quad 2 & \quad 3 & \quad 4 & \quad 5 \\
6 & \quad 7 & \quad 8 & \quad 9 & \quad 10 & \quad 11 & \quad 12 & \quad 13 & \quad 14
\end{align*} \]

Fig. 20. 1-5, topological class of five-pointed stars; 6, topological class of figure-eights with four angles; 7-14, topological class of letters A.
same order containing four angles and one intersection, but it is located, as are the first five figures, in the class of zero order, being as they are a closed figure with intersecting lines. In order to illustrate characteristic properties of the first order with an example with which we are all familiar I shall point out that every printed letter is a separate topological class of the first order, while to the single class of letter A there belong letter A's of all dimensions, scripts, outlines, embellishments, etc. (see 7-14 in Fig. 20), though we ignore certain additional details of purely calligraphic significance. The chalk figures for the game of "hopscotch", which appear in great numbers on our pavements every spring, are also all representatives of one and the same topological class of the first order for each equivalent representation of the game, and in this respect the scale of the figure or the age and skill of the draughtsman do not matter. The habitual scheme on which a given child draws a house or a face is also usually a determinate topological class and nothing more.

After this general introduction we may turn from geometry to psychophysiology. If we draw the attention of a psychologist or a teacher to our collection of letter A's in Fig. 20, he will immediately remark that the whole set displays a common characteristic in terms of its essential sign, that is to say without circumlocution, that the topological characteristics of a figure are of paramount psychologico-pedagogical importance in comparison with properties of a metrical sort. Our psychologist or teacher will be quite right, because the recognition of the letter A does not require the presence of any metrical properties and is, on the contrary, entirely dependent on the presence of determinate topological cues. This great affinity between the process of recognition and topology, which has also been noted and studied for some considerable time by adherents of Gestalt psychology, is certainly a psychophysiological phenomenon and may even be of general biological significance, but in any case it cannot be deduced from purely geometrical considerations. The biological characteristic of the predominance of topological categories over metric ones may be pursued in a multiplicity of examples. A maple leaf differs from a birch leaf in respect to topological properties of the first order, while at the same time all maple leaves belong to one and the same topological class in spite of all the thoroughly investigated biometric variation between separate specimens. The structure of the brain and the disposition of the main convolutions of the cortex again provide an example of an object having the same topology for all possible metrical variations. It is possible to say with certainty that in the area of
is located, as they are characteristic of purely one psotschotch", etc. (see also all scept the not matter. face is also to psychoachter to our k that the ential sign, characteristic ce in comparison or will be quite he presence dependent on ity between the i and studied , is certainly logical y geometrical ance of ultiplicity of o topological le leaves the thoroughly The structure the cortex ry for all possible at in the area of biological morphology those cases in which metrics is of importance together with topology (for example, the lens of the eye) are rare exceptions*. This overwhelming importance of topology in the case of living objects should be attentively compared, for example, with the morphology of crystals where the essential relationships are all metric ones.

A whole series of biologically important morphological signs must unquestionably be referred to topology, although they cannot be numbered either in the zero or in the first order. Every child will naturally distinguish between a cat and a dog; the distinction is certainly not made on the basis of anatomical considerations such as the comparative structure of the claws and the teeth, on which topic he may be fully ignorant, but on the general appearance - on a certain je ne sais quoi - that indubitably appears to be a topological category. However, the difference between the appearance of a cat and a dog cannot be related to topological signs of the first order. It is likely that some higher orders which await future analysis are operating here.

Insufficient attention has so far been given to the fact that the movements of live organisms, to no less a degree than their perceptions, are determined by topological categories. This is illustrated with great clarity by the example of drawing, perhaps because this type of movement leaves a record which may be conveniently studied. It is easy for everyone to draw a five-pointed star, but we can say with certainty that this picture is made by using only topological and not metric relationships. As proof on this I suggest the experiment of drawing ten such stars in succession and comparing the pictures. I doubt if it is at all possible to make a metrically perfect copy of a similar object without the help of a compass and a ruler, that is, the human motor system cannot attain any high degree of metric proficiency, but it can be said that our motor system is very sensitive to topological distinctions of higher orders than one and zero. It is sufficient, for example, to draw attention to handwriting. I pointed out above that the letter A belongs to a single topological class of the first order no matter how or by whom it is written. Besides this, all letter A's written in my hand are similar to each other and are simultaneously different from letter A's written by second and third persons. The similarity between my A's is far from metrical, but is topological; the differences between my A's and those written by other hands must in the same way be related to topological

*It may never cross the mind of an anatomist or a topographical anatomist that all his life he considers only various topological categories - a new variation of Molière's M. Jourdain!
differences involving higher orders than the first. The topological
propensities in our perception seize upon what may be regarded as common
features within the limits of a given handwriting - once again in a form
which it is not easy to subject to analysis in terms of impressions - a je
ne sais quoi, the analysis of which is not yet practicable for us because
of our lack of acquaintance at present with whatever may constitute higher
topological orders and what properties we must ascribe to them.

Such of our movements as do not leave a trace upon paper have drawn
less attention to themselves in the manner indicated. Parallel with the
knowledge on handwriting there exist structurally similar bodies of knowledge
on gait, touch in music and accent of voice, although the analysis of these
phenomena has not been carried very far. One thing may, however, be already
affirmed with certainty; all attempts to draw distinctions of this type in
terms of quantitative metrical signs (as can be done, for example, with
pitch) are doomed to failure in advance. It is here necessary to make new
discoveries in qualitative geometry, but consideration of the perspectives
which are now unfolding in this direction would be for us at present too
far from our main goal.

A circumstance of great and immediate interest in the structural
analysis of movements is the fact that topological peculiarities in visual
perception display marked similarities to some signs of idiosyncrasies in
the topology of motor organization. So, for example, the category of
dimension is equally indifferent to visual perception and to movement. I
find it equally easy to recognize a triangle, a star or a letter whether it
is presented to me in a large or in a small form. The same indifference to
the absolute dimensions of a geometrical object was demonstrated in dogs by
Pavlov and in rats by Lashley. In precisely the same way I find it equally
easy to draw a star or write a word large or small, and to do this on a
piece of paper or on a classroom blackboard. It would be interesting to
make a study of the quantitative relationship between the variation in these
drawings and their size; but we may say in any case that, whatever the size,
they retain their topological properties not only of the first but also of
higher orders; so, for example, all the characteristics of handwriting which
are peculiar to a given person when writing on paper are also apparent in
writing on a blackboard, although, in a word, the entire muscular structure
of the movement is absolutely different in the two cases.

Visual perception, however, shows great sensitivity to such concomitantly
metric cues as symmetry, a category that is at the same time completely
ical as common in a form ions - a je us because tute higher have drawn with the is of knowledge sis of these ; be already this type in ple, with to make new perspectives resent too uctural es in visual norasies in ory of movement. I or whether it difference to red in dogs by id it equally this on a test or intation in these sever the size, t but also of xdwriting which apparent in ular structure uch concomitantly completely ignored by the motor system. On the other hand, the metrical category of extensity is, without doubt, of greater importance to the motor than to the visual receptors because the estimation of dimension in perception (for example, visually) is always ultimately based on deep-seated kinaesthetic associations related to the field of sensitivity of the receptor. The perceptual and motor systems are to all appearances equally indifferent to the category of position in space (right, left, above, below), which is of exceptional interest for the structural analysis of localization. In fact a figure which may be placed in the most diverse portions of the visual field is recognized with equal facility as being the same; in the same way the process of carrying out an habitual action, for example, writing a word or playing over a passage which one has learnt by heart on the piano, is carried out with approximately the same facility and with the same degree of accuracy independently of the position of the hand or of the register on the piano. It is interesting that the purely metrical abilities of the kinaesthetic apparatus (for example the estimation of length or of distance) are characterized by gross differences in various zones of the spatial field.

Both perceptual recognition and motor reproduction are extremely sensitive to the orientation of a figure in space. The identification of a triangle after it has been rotated 180° is incomparably more difficult than the identification of triangles of different size with the same orientation. In just the same way it is extremely difficult to draw figures upside down with a pencil.

* I consider this fact to be an extremely clear illustration of the structural complexity of every conditioned reflex, even what is apparently the most simple one. In presenting a conditioning stimulus visually to a dog neither the head, and still less the eyeballs, are in any way immobilized and for this reason the visual stimulus may fall on the most various points of the retina, and consequently on different points of the first visual centre. If the visual stimulus is, for example, a triangle, on each presentation of this stimulus to the animal's retina a whole series of sensory elements are excited, and here, every time the animal turns its head and eyes this series is either wholly or partially different. The appearance of a single reaction in all these cases proves, it would seem, that the engram for a given conditioned reflex is not located at those points (the primary visual centre) on which the separate lines and points are represented but at some structurally higher centre, the connection of which to the former is very similar to that which has earlier been described in the case of the successive levels of the centres of movement. Here we find an example of the same fact which was employed above (section 3, p. 29) as proof of the impossibility of localization of the muscles and of conditioned reflexes in one and the same centre.
It is an important fact that in a very large percentage of cases children draw the mirror images of letters, that is to say they change about the right and left sides although they never turn the letter upside down. Another fact is also interesting (being indicative of some sort of structural hierarchy); children never either read or write an entire word from right to left, they only do this separately and successively for individual letters of the world. It is clear that in both these cases there must exist different mechanisms which cannot be compared to each other.

These analogies and differences may be pursued to great lengths: a study of these and others promises to be extremely fruitful. At present, however, it is necessary only to summarize all that has been said above about the topological properties of perception and movements.

First of all, it may be stated that the totality of the topological and metrical characteristics of the relations between movements and external space can be generalized under the term motor field, analogous with the concept of the visual field recognized by psychologists. An immediate task of physiology is to analyse the properties of this motor field. The preceding statements permit us to assert that the physiological motor field is as widely different from objective external space as is the visual field. Its typical differences from theoretical Euclidian space consist, first of all, in an obvious preference of the motor field for topological categories as compared with metric ones, in the presence of some evident tropisms, or tendencies toward certain directions, in the absence of bilateral symmetry (which is peculiar to the visual field), and so on. The predominance of topology is revealed also in the fact that straight lines and their distinction from curved ones are not proper to the motor field (in this it differs from the visual), nor are stable, identical lines. In biomechanics this is manifested in that successive

Fig. 21. Cyclogram of a series of successive poorly automatized movements taken on the same plate.
movements of cyclical nature never exactly repeat themselves (Fig. 21). The co-ordinational net of the motor field must be regarded, in distinction to a net in Euclidian geometry, firstly as non-rectilinear, and secondly as oscillating like a cobweb in the wind. Its "oscillation" does not, however, in every case proceed so far as to destroy topological relationships either of zero order (for example the category "between") or of the first and perhaps of even higher orders.

Some of the properties of the motor field which we have now disentangled are of great interest for the theory of localization. Firstly, there is the deeply seated inherent indifference of the motor control centre to the scale and position of the movement effected, as we have discussed above. It is clear that each of the variations of a movement (for example, drawing a circle large or small, directly in front of oneself or to one side, on a horizontal piece of paper or on a vertical blackboard, etc.) demands a quite different muscular formula; and even more than this, involves a completely different set of muscles in the action. The almost equal facility and accuracy with which all these variations can be performed is evidence for the fact that they are ultimately determined by one and the same higher directional engram in relation to which dimensions and position play a secondary role. These engrams, which determine the muscle structure of each of the concrete variations, clearly lie still lower than those described in section 4 and in particular in the area C of Fig. 14, whereas the engrams of dimension and spatial position may already be referred to area B. We must conclude from this that the higher engram, which may be called the engram of a given topological class, is already structurally extremely far removed (and because of this also probably localizationally very distant) from any resemblance whatever to the joint-muscle schemata; it is extremely geometrical, representing a very abstract motor image of space. This makes us suppose - for the time being merely as an hypothesis though it forces itself upon us very strongly - that the localization areas of these higher-order motor engrams have also the same topological regulation as is found in external space or in the motor field (and that in any case the pattern is by no means that which maintains in the joint-muscle apparatus). In other words there is considerable reason to suppose that in the higher motor centres of the brain (it is very probable that these are in the cortical hemispheres) the localizational pattern is none other than some form of projection of external space in the form present for the subject in the motor field. This projection, from all that has been said above, must be congruent with external space, but
only topologically and in no sense metrically. All danger of considering the possibility of compensation for the inversion of projection at the retina (section 3) and many other possibilities of the same sort are completely avoided by these considerations. It seems to me that although it is not now possible to specify the ways in which such a topological representation of space in the central nervous system may be achieved, this is only a question of time for physiology. It is only necessary to reiterate that the topological properties of the projection of space in the C.N.S. may prove to be very strange and unexpected; we must not expect to find in the cortex some sort of photograph of space, even an extremely deformed one. Still, the hypothesis that there exist in the higher levels of the C.N.S. projections of space, and not projections of joints and muscles, seems to me to be at present more probable than any other.

6. THE PRINCIPLE OF "EQUAL SIMPLICITY"

It is now time to give a general formulation of an heuristic principle which I have already presented in a partial modification in section 3 above, and to examine its application in terms of a few examples. I shall call it the principle of equal simplicity.

I begin with non-physiological examples. I have three devices with which it is possible to draw a circle; a circular template, a compass and an ellipsograph. A circle of the same radius as the template may be drawn as easily with the template as with the compass; a circle may also be drawn with the ellipsograph, as it is a particular case of an ellipse, but it will be a little more complicated to do this than with either the template or the compass. If we have a circle of some other radius the template immediately becomes useless. The compass draws circles of all radii with equal facility. A given actual ellipsograph may only describe a circle of a single determinate radius, and for this reason it is eliminated together with the template. If we wish to draw an ellipse we may do this using the ellipsograph with exactly the same difficulty, no more or less than we had in drawing the circle, but both the compass and the template are useless.

In this example we are considering a set of curves of the second order which differ (a) in radius and (b) in eccentricity. One of our instruments, the template, gives us with great simplicity one curve and no others. The second instrument gives us equally easily all variations in radius, but only a single eccentricity, zero, peculiar to a circle. The third instrument gives us with equal ease - although in absolute terms the process is slightly
more complicated than in the case of the compass — all eccentricities, but only one radius. A circle of the same radius as the template may be drawn by means of all three instruments but the functional relationship between their simplicity and the possible variations in all three cases are quite different. The type of this functional relationship is determined with great accuracy by the scheme of construction of the instrument.

In mathematical language the preceding example may be presented in the following way. We designate the degree of simplicity (for example the speed with which the task can be completed, or unity divided by the time of completion, etc.) by \( S \), the radius of the circle by \( r \) and the eccentricity by \( e \). Then, for all our devices,

\[
S = f(r, e).
\]

For the template of radius \( r \) we have:

\[
f(r, 0) = 0; \quad f(R, 0) \neq 0. \tag{6a}
\]

For the compass:

\[
f(r, e)_{e \neq 0} = 0; \quad f(r, 0) = \text{const} \neq 0. \tag{6b}
\]

For the ellipsograph:

\[
f(r, e)_{e \neq 0} = f(R, e) = \text{const} \neq 0. \tag{6c}
\]

Equations (6b) and (6c) may be represented by a line; eqn. (6a) is the point of intersection of the lines (6b) and (6c).

Examples are possible in which the degree of simplicity does not change abruptly from zero to some final value as in the preceding case, but changes from one value to another with a certain regular continuity. So, for example, in multiplying numbers with Odner’s calculating machine the degree of simplicity (or the speed of the work) decreases in parallel with an increase in the number of multiplication signs and with the number of units involved with each of these signs. At the same time the degree of simplicity is invariable with respect to the number of digits multiplied. In the Millioner calculating machine the degree of simplicity is invariable in respect to the number of digits in the multipliers and depends only on the number of multiplication signs. Finally, on a slide rule the degree of simplicity is almost invariable with respect to both components involved.

In all these cases we encounter the same fact, that different structural schemes may carry out the same set of operations but the differences in their structures are always accompanied by differences in the form of the function
S. We may say with certainty that the more marked are the changes in $S$ in
the transition from one element of the set to another adjacent to it, the
smaller is the degree of the adaptation to this transition possible with the
structural peculiarities of the system in question. On the other hand, for
any given system there are "lines of equal simplicity", that is, those
transitions from one element of the set of possible tasks to another which
do not result in any change in the simplicity of manipulation, corresponding
to transitions which are most closely related to the structural scheme of
the device.

We arrive from this case to the following formulation of the principle
of equal simplicity: for every system which is capable of undertaking a set
of different elementary processes of a given range, the lines of equal
simplicity correspond to those directions in this range along which movement
does not involve any change either in the structural principles or in the
principles of operation of the system. Instead of the expression "simplicity"
which does not have any concrete association we may insert a whole series of
parallel expressions in relation to the case under investigation: the
expressions of speed of completion, degree of accuracy, degree of variance
and so on. For a general formulation I have selected the term simplicity as
being the most general in spite of its lack of concrete associations.

We may extract an heuristically valuable principle from the discussion
above. If we are concerned with any given system, the structure of which is
unknown to us but whose operation we may observe under a variety of conditions,
then by a comparison of the changes in the variable $S$ (speed, accuracy,
variation, etc.) encountered as a function of each of the variables in the
conditions, we may come to determinate conclusions as to the structure of
the system which are unattainable by direct means.

Let us imagine, for example, that we are invited to see a film without
having any idea of how cinematography works. We may suppose that we are
attending it in a puppet theatre (as our grandfathers might have). We are
astonished by the wealth and variety of the material we are shown, exceeding
by far all that could be met with in these days, but we still have an
indisputable right to consider that we are watching only marionettes which
have been greatly improved in principle. It is true that in a puppet theatre
we never, for example, saw the sea; but then (says grandfather) it is obvious
that here they have only an extremely cunning mechanical imitation of the sea.
In the old puppet theatre figures could not be made to diminish as they grew
more distant, as this occurs in the cinema, but once again it is possible to
consider this as a new achievement of the technology of the marionette theatre. All this, although extremely difficult, is possible. It is, however, very easy to show that we are not in a puppet theatre and to do this precisely with the help of the principle of equal simplicity. It is sufficient, for this purpose, to select two objects which are sharply different in their difficulty of representation in the puppet theatre, for example, a rotating wheel and a stormy sea, and without reference to cinematic technique (let us suppose that its technical structure is inaccessible to us) to turn to the studio's accountant and ask how much it would cost to obtain representations of both these objects on the screen for one minute. As soon as we discover that a strip of 20 m of film costs about the same for either object (or, to put it more accurately, that the cost of the film is related to some other arbitrary factors and in no way to the mechanical properties of the objects on the screen), the hypothesis of a puppet theatre collapses. In general, a skilful interview with an accountant may give many positive technical details - we may recall that it was just this way that Mendeleev discovered the secret of an important French explosive.

For the puppet theatre all is possible (at least potentially) that is possible to the cinema. But the "all" is, in principle, unattainable with the same degree of simplicity as operates in the cinema. We encounter the same interrelationships between the gramophone and such talking machines as were experimented with a hundred years ago by von Kempelin, for example. The whole structural nature of the gramophone lies in the fact that the sounds to be reproduced make no difference to it, whereas von Kempelin would have been obliged to construct a new mechanical gullet for each new pitch. A rural deacon in L. Andreev's story was brought into an extremely amusing collision with the principle of equal simplicity as applied to the gramophone when he could not conceive how the gramophone could reproduce with equal ease both a music-hall song and the voice of the Son of Man. The principle described proves to be extremely fruitful in its application to the structural analysis of the function of the central nervous system, both in its receptor and in its effector aspects. In section 2 I used a circular movement of the extended arm of the type shown in Fig. 15 as an example of the smooth redistribution of muscle pull. We may return to consideration of the same movement from a new point of view. If a circle is described with the arm directly to the front, then directly out to one side and then about some intermediate axis, both the muscle and the innervational schemes of the three movements will be sharply different. However, all three movements are
subjectively very much alike in terms of difficulty and objectively they
display approximately the same amount of accuracy and of variation. This
allows us to conclude with a high degree of probability that the structure
of the central complex which governs the production of a given series of
movements is much more closely related to spatial form than to muscle scheme,
because all three variations of the circular movement which we have attempted
lie on lines of equal simplicity in regard to the properties of the movement
and the properties of their forms, but not the properties of the muscular
schemes. This conclusion may be made more clear from the following example,
which I have thoroughly analysed in another study (23). In order to carry
out with precision any given automatized movement, for example, cursive
writing, the positions and the means of fixation in the intermediate links
of the arm are almost completely indifferent. I write with the same
handwriting and with almost equal ease when I rest my forearm on a table-top
and when my arm supports its own weight, as well as in a variety of
positions. All these variants are sharply different from the point of view
of muscle structure and if it were assumed that the object of the working
out of a habit of movement were one of these structures we would be obliged
to suppose that the others would lie completely outside the range of this
habit, that is to say, on a quite different level of simplicity. The fact of
identical simplicity and the retention of the characteristics of the habit
is immediate evidence that the habit of writing is not a habit of the muscle
scheme and consequently that the traces in the C.N.S. which govern these
habits are closely related to the topology of handwriting and considerably
removed from joints and muscles. All these, and many similar examples, must
be experimentally analysed both qualitatively and quantitatively and each
such analysis allows us to arrive at new basic conclusions as to the structure
of the activity of the motor centres of the C.N.S.

An extremely interesting example of the application of the principle of
equal simplicity may be taken from the psychology of perception which is, at
the moment, far more developed than the structural physiology of movement.
This example refers to a theory of hearing. A whole series of hypotheses
have been put forward in order to explain the mechanism operating in the inner
ear and allowing us to discriminate sounds (Helmholtz, Ewald, Hering, Gray)
among which the most popular at the moment is Helmholtz's hypothesis. On
this hypothesis each of the numerous fibres of the basilar membrane is supposed
to act as elastic string tuned to a particular frequency. When this particular
frequency operates on the organ of Corti and the basilar membrane the given
fibre goes into a condition of resonant oscillation and mechanically stimulates the auditory receptors attached to it. In this way each of the sensitive endings of the acoustic nerve are stimulated only by a single sound frequency and the recognition of the frequency in the C.N.S. is achieved by the same process which effects the perception of tactile local signs (Lokalsetzen). Complex sounds or harmonics are analysed in this way which explains the recognition of pitch and the discrimination of chords.

Many serious psychological objections have been raised against this hypothesis. Additions and corrections were soon made. Helmholtz himself was not able to explain in these terms the perception of consonance and dissonance for which he was obliged to hypothesize the presence of a separate system perceiving beat (Schwabungen). There have been numerous later additions and emendations (F. Alt, A. Gray, L. Hermann Waetzmann, Budd-Feldafing, W. Köhler, G. Revesz, F. Brentano, and others), and the very fact of their necessity has cast serious doubt on Helmholtz’s hypothesis. It is very probable that should a new hypothesis appear which adequately explains all the requisite phenomena and is at the same time simpler, it would be preferred to the older hypothesis on the principle that the true explanation is the simpler one * (although there is nothing objective in this guarantee). However, no hypothesis of this type has so far appeared. Meanwhile, there are serious objections to Helmholtz’s hypothesis independent of its simplicity or complexity. It is only necessary for this purpose to show (and there are in the literature an enormous number of experimental and clinical facts pointing in this direction) that the lines of equal simplicity are distributed in an essentially different way for the function of auditory perception and for a resonant harp. So as not to encumber this report I shall limit myself to two points.

We are making a comparison between a system whose functional operation is unknown to us, the apparatus of auditory perception and a known physical model – a set of resonators which for the sake of vividness I have called a

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*This conviction may very easily be false. Contemporary physics provides various examples of this. The theories of de Broglie, Einstein, Heisenberg, Schrödinger or Dirac are far more complicated than the concepts which they have supplanted. To set up simplicity as a criterion of reliability would be to affirm in principle that the categories of logic and psychology dominate the categories of objective reality and determine them, and we have no authority for apriorities of this type.
resonant harp. For this latter structure the simplest of all operations is the determination of the absolute frequency of a tone; this follows from its very structure. The determination of the relationship between the frequencies of the components, and is for this reason more complicated. However, the statistics of musical pedagogy (J. v. Kries, O. Abraham, G. Revesz) show that the possession of absolute pitch is a very rare occurrence while a majority of people have relative pitch. In other words, for the organ of hearing relative determinations of intervals are easier than those of absolute tones.

On the other hand, a pure musical tone is simpler in its acoustic structure than the sounds of the human voice - vowels with their numerous formants, and consonants with their characteristic phonation. For a resonating harp these can be recognized in no other way than by their analysis into simple components and only after the determination of these components; consequently, on this model the discrimination of speech sounds is more complicated than the discrimination of pure tones and is based entirely on the latter process. As far as the human organ of hearing is concerned, many people have musical (relative) discrimination while all understand and perceive speech. Very striking cases of tone deafness have been described (L. Alt, W. Köhler). Köhler's patient not only did not understand what was meant by a melody, but was even unable to distinguish between a low and a high tone, while he could distinguish all shades of speech and accent very well, indeed, imitating provincial accents quite well in telling anecdotes (such persons have no physical defects of hearing). We again find an inversion of the levels of difficulty with respect to the resonator apparatus which we have hypothesized.

It is clear from both comparisons that the organ of hearing gives an essentially different gradation of simplicity than that of the hypothesized resonator mechanism - a gradation amounting in some examples to a direct transposition of the order of difficulty. It is this circumstance which is critically dangerous for Helmholtz's hypothesis, independently of its simplicity or complexity.

The discussion in section 3 of the example of the lack of correspondence between the theory of muscle localization in the cortex and the idea of the localization of conditioned reflexes is clearly a particular case of the use of the principle which has here been described in full. Further experiments and observations on changes in the accuracy of movements in their different variations and for corresponding changes in the irradiation of a habit of
movement may disclose for us a whole series of structural regularities in
the motor field, and the motor functions of the brain in their entirety —
regularities which cannot be foreseen at present. Only one thing may
already be foreseen with certainty. Every new discovery in the field of
coor-ordinational structure will at the same time be a new discovery along
the lines of localizational structure; and on that day when we understand
the one we shall be able to say that we understand the other.

Symbols Used in this Chapter

I. SPATIAL COORDINATES

x: longitudinal (sagittal) coordinate.
y: vertical coordinate.
z: transversal coordinate.

For x, positive direction is forward.
For y, positive direction is upward.
For z, positive direction is to the left.

II. SYMBOLS FOR PARTS OF THE BODY

<table>
<thead>
<tr>
<th>Initial letter</th>
<th>Latin term</th>
<th>English term</th>
<th>Centre of gravity of the limb segment</th>
<th>Proximal joint of limb segment</th>
</tr>
</thead>
<tbody>
<tr>
<td>c</td>
<td>caput</td>
<td>Head</td>
<td>gc</td>
<td></td>
</tr>
<tr>
<td>b</td>
<td>brachium</td>
<td>Upper arm</td>
<td>gb</td>
<td>b shoulder joint</td>
</tr>
<tr>
<td>a</td>
<td>antebrachium</td>
<td>Fore arm</td>
<td>ga</td>
<td>a elbow joint</td>
</tr>
<tr>
<td>m</td>
<td>manus</td>
<td>Hand</td>
<td>gm</td>
<td>m wrist joint</td>
</tr>
<tr>
<td>t</td>
<td>truncus</td>
<td>Trunk</td>
<td>gt</td>
<td></td>
</tr>
<tr>
<td>f</td>
<td>femur</td>
<td>Thigh</td>
<td>gf</td>
<td>f hip joint</td>
</tr>
<tr>
<td>s</td>
<td>sura</td>
<td>Shin</td>
<td>gs</td>
<td>s knee joint</td>
</tr>
<tr>
<td>p</td>
<td>pes</td>
<td>Foot</td>
<td>gp</td>
<td>p ankle joint</td>
</tr>
<tr>
<td>H</td>
<td>homo</td>
<td>The whole body</td>
<td>gh</td>
<td></td>
</tr>
</tbody>
</table>

III. TERMS FOR THE CENTRES OF GRAVITY OF SYSTEMS (EXAMPLES)

The centre of gravity for the system (shin + foot) \( g(sp) \).
The centre of gravity for the system (whole + leg) \( g(fsp) \), etc.
Other points along the long axes of the limbs are indicated by Greek letters corresponding to the initial letters of the Latin term for the limb. For example:

*α* a point on the longitudinal axis of the thigh (*f*).

*ω* a point at the end of the foot (*p*).

**IV. SYMBOLS FOR THE MECHANICAL FUNCTIONS OF MOVEMENT**

*S* displacement (along a line described by real coordinates).

*V* velocity.

*W* acceleration.

*F* force.

*M* moment of force.

The symbols for joints or centres of gravity of a limb segment are attached to these letters as subscripts. Symbols for coordinates are given in parentheses. For example:

\[ S_\alpha(y) \]
the vertical component of the path followed by the elbow joint.

\[ V_\alpha(z) \]
the sagittal component of the velocity of the knee joint.

\[ W_\alpha(z) \]
the transversal component of the acceleration of the end of the foot.

\[ F_{g\alpha}(y) \]
the vertical component of the force at the centre of gravity of the shin.

\[ F_{gsp}(z) \]
the longitudinal component of force at the centre of gravity of the whole leg system.

\[ M_f \]
the moment of force at the hip joint.

**ADDENDA**

1. A point on the facial plane of the head in the region of the upper edge of the aural helix is projected upon the centre of gravity of the head in profile photographs, and is provisionally termed the semi-centre of gravity on these photographs, and is designated by *gα/2*.

2. The angles mentioned in this handbook are designated as follows:

*α* the angle of the longitudinal axis of the thigh to the horizontal, directed forwards.

*β* the angle of the longitudinal axis of the shin to the horizontal, directed forwards.

*φ* the angle between the longitudinal axes of the thigh and shin.
REFERENCES