Brain plasticity.

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Introduction.

The main topic of my contribution is actually the question:
does or does not neurobiology justify the use of the swimming
method. I think that we may give a straight answer to it: Yes.
It might even help to develop the method a little bit more.
The basic idea I like to illustrate is that swimming reinsta-
tes an earlier phase of the ontogeny as far as it concerns
brain centres involved in the control of movement: it allows
the organism to reactivate successively higher centres in
order to learn new skills and movements.
Personally I am primarily working with animals. So I will
mainly limit myself to examples from animal kingdom. This
contribution is divided into three parts. The first part deals
with global features of the brain and its ontogeny in the
control of movement. The second part just lists particular
features of a limited number of brain structures in order to
illustrate these global features. In the final part I will try
to relate this insight of the swimming method.
As you all know, the brain is an integrated part of the body
and it allows the organism to maintain a dynamic interaction
with the environment by executing behaviour in general and
movements in particular.
Actually we know that the brain receives information from the
body - proprioceptive information - it receives information
from
the environment, and it needs this information in order to
transform it into commands to the muscles and to the glands in
order to counteract disturbances in the environment or in the
proprioceptive input. In 1934 Jakob van Uexküll has put for-
ward the concept that we are dealing with a closed loop nega-
tive feedback system (Fig. 1). Disturbances in the environment
are detected and marked by the brain, and transformed by the
brain into commands to the muscles in order to counteract the
disturbances in the environment. He called it a Subject-Umwelt
Relationship (32). Powers has added a new dimension (23-24).
What was new in Powers' concept is the recognition that the
outer shell of the organization inside the organism is the
only one that directly interacts with the physical environment
of the organism via a set of input devices such as sensory
receptors for pressure, light, vibration, chemical qualities,
etc. on the one hand, and via a set of output devices such as
muscles and glands on the other hand (Fig. 2). Systems that
are hierarchically superior yet as close as possible to these
lowest-order or first-order systems receive their input from
them. The output of these hierarchically superior, second-
order systemss can only influence the physical environment via
the first-order systems by constructing (reference) signals
for the latter systems (Fig. 3). In this way the brain is
postulated to consist of a large number of hierarchically
organized higher-order systems (Fig. 4).
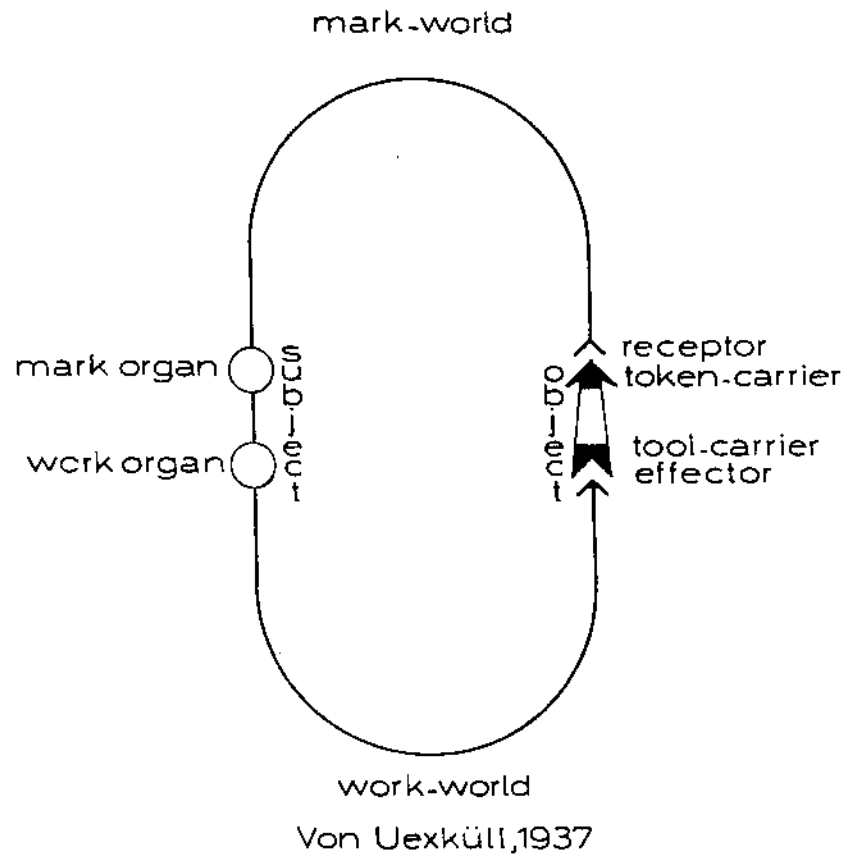
mark-world

Von Uexküll,1937

Figure 1 : The so-called Subject-Umwelt relationship:
The brain forming an integrated part of the body allows the
subject to maintain its dynamic interaction with the environ-
ment by executing behaviour that counteracts disturbances in
the environment and/or body.

To appreciate the implications of such a hierarchical organi-
zation, consider the patterning of locomotion in cats.
Although "generators" for locomotion have been localized in
the spinal cord (18), i.e. the lowest-order systems for emit-
ting signals to the trunk and limbs, experimentally induced
interventions with signals leaving higher order systems and
reaching the spinal cord also alter the patterning of locomo-
tion (19, 22, 27).
These data throw doubt upon the "localization" of locomotor
"generators" within the spinal cord. According to Powers'
concept they simply imply that supraspinal brain regions
direct the functioning of the spinal regions involved and,
thus, the resulting behaviour (11, 26). Indeed, supraspinal
structures determine the degree of freedom in the spinal cord
in programming the behaviour under discussion (10; see also
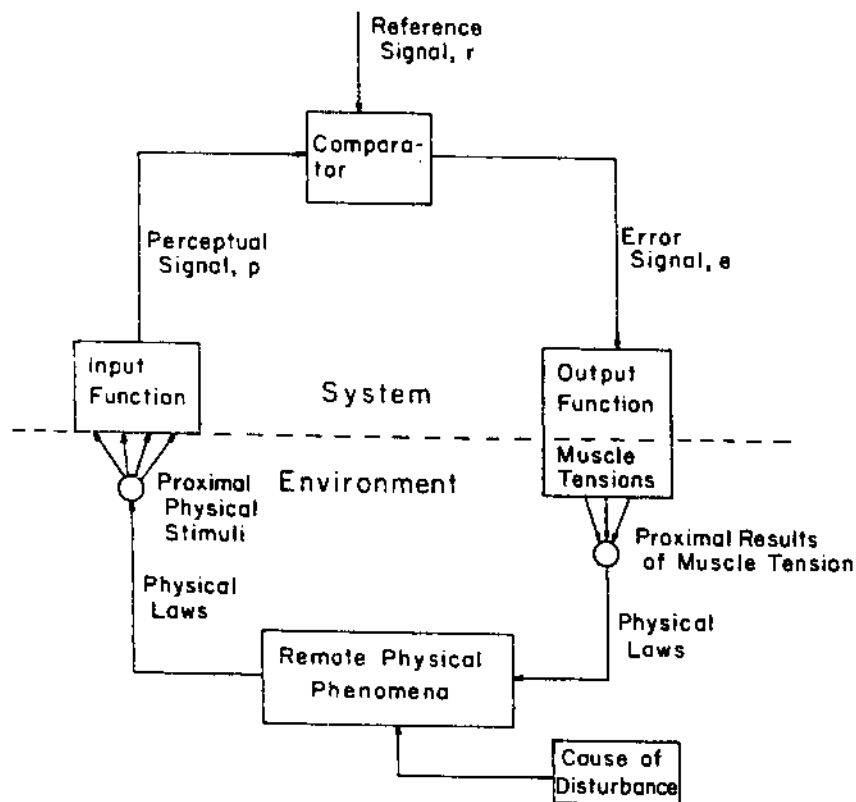below).

Figure 2 : An oversimplified diagram of the outer shell of the organization inside the brain: it is the only feedback system that directly interacts with the physical environment of the organism via a set of input devices such as sensory receptors of pressure, light, vibration, chemical qualities, etc. on the one hand, and via a set of output devices such as muscles and glands on the other hand.

Thus, Powers created a conceptual model for nervous system operation by conceiving the brain as an integrated whole of hierarchically ordered feedback systems controlling the input signals of the organism (23; cf. 31). In principle the cerebral organization of behaviour shares all properties inherent to any hierarchical system model. Thus, correct functioning of higher order levels and wrong functioning of lower-order levels or vice versa can occur simultaneously. Furthermore, both activation of systems at successively lower-order levels and activation of systems at successively higher-order levels are available to counteract disturbances at one or another level in the hierarchy.
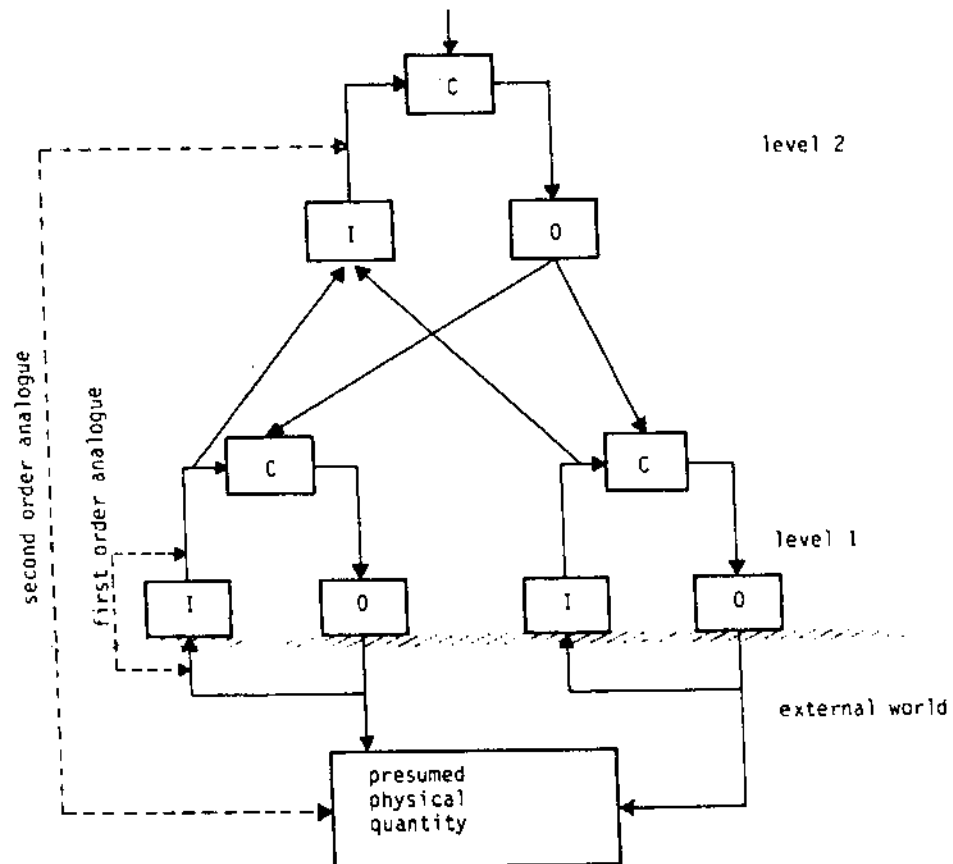
Figure 3 : Hierarchy of two first-order control systems and
one second-order system. I, input function, receiving input
signals derived from exteroceptive, proprioceptive, and inte-
roceptive stimulu; the input signals at level 2, i.e. second-
order system, are analogues of the input signals of the lowest
order, i.e. first-order, system. C, comparator function,
comparing input signals and reference signals, i.e. output
signals of higher order systems, and producing error signals.
O, output function, transforming error signals into output
signals. Output signals sent to lower order systems are beha-
vioural program signals, whereas output signals sent to output
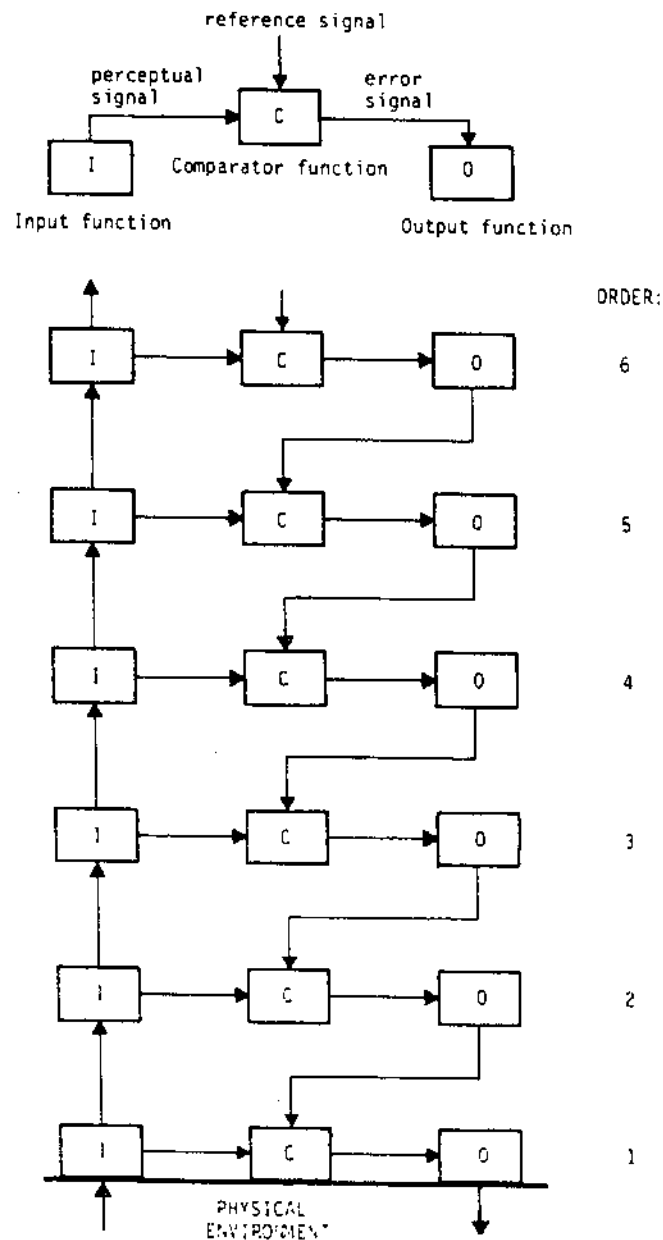devices (glands and muscles) are behavioural commands.

reference signal

perceptual
signal   C   error
signal

I   Comparator function   0

Input function   Output function

ORDER:

I   C   0   6

I   C   0   5

I   C   0   4

I   C   0   3

I   C   0   2

I   C   0   1

PHYSICAL
ENVIRONMENT

Figure 4 : Behavioural control system hierarchy; a simplified
          model.

Brain and Motor Behaviour: hierarchy of feedback systems.

By definition, the organization inside the organism (brain) is
an integration of feedback systems allowing us to operate
according to principles and definitions of servomechanism
theory. Thus the organism receives information on its current
state , i.e. "input signals", representing the difference
between current and desired states; and as a result processes
"output signals" directing motor behaviour. In principle, each
level in the hierarchy deals with input, reference, error and
output signals (for details: 4, 7, 23).
The basic aspects can be illustrated with the help of the most

simple form of (molecular) behaviour: muscle contraction. Let us start with the final common pathway through which most of the behavioural patterns are initiated: the motoneuron. It is known that the basic spinal motor reflex, the tendon reflex loop, is in fact a feedback control system (Fig. 5).
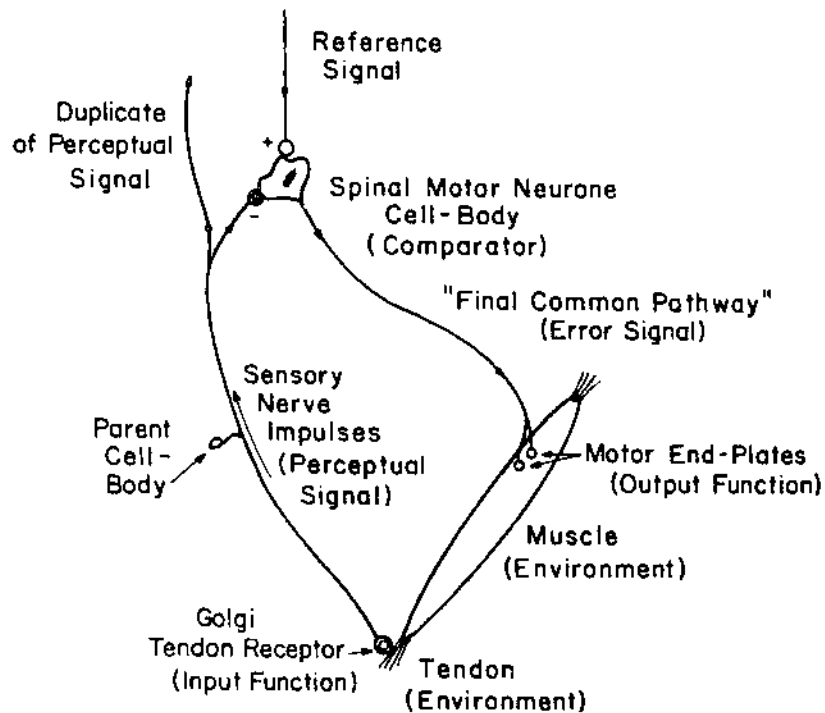

Figure 5 : An oversimplified diagram of the tendon reflex.

Action potentials generated by the Golgi tendon receptor are the input signals for the spinal motoneuron. The latter also receives neural signals from higher order centres, the so-called reference signals. The signals coming to the spinal motoneuron from the tendon receptor represent information on the current state of contraction of the muscle; the other input to the neuron contains information on the desired state, i.e. the reference signal. The neuron compares both signals and, as a result, emits neural activity representing the difference between current and desired state. This so-called error signal reaches the motor endplates of the muscle and is, by some output function, transformed into muscle contraction in order to counteract the difference between actual and desired state. The resulting output is not simply an effect, but a process by which this feedback system controls its input. The function of the motoneuron is to compare input signals and reference signals and to reduce any noted difference. In the full understanding that the given description is highly oversimplified, the properties mentioned are characteristic for all feedback control systems in the brain.

By definition, only inputs of the lowest-order systems within the hierarchy are signals emanating from the physical environment (exteroceptive stimuli), interior of the body (interoceptive stimuli), and muscles, tendon organs and joints (proprioceptive stimuli). In contrast, all input signals of higher-order systems are analogues of quantities derived from input signals of lower-order systems. Accordingly, the degree of abstraction from the observable physical effects increases at each higher-order level in the hierarchy. This lays the foundation for getting from "distal" to "proximal" stimuli. Since input signals reaching the lowest-order systems are also transformed into input signals of higher-order systems, the organism has ultimately at its disposal the weighted sum of all input signals, i.e. signals received by the highest-order systems. As the latter signals are derived from "distal" stimuli, the resulting "proximal" stimuli are still analogues of the organism's "world" and, accordingly, represent the integrated whole of all aspects of this world at the highest-order level. Since such signals are abstract, invariant functions constructed by the lower-order systems themselves, they are difficult to deduce from the physical features of the incoming stimuli. Still, it is not impossible as we will see below.

By definition, the reference signals in a feedback system are the controlled quantities of the system. When conceiving of behaviour as a process by which an integrated whole of hierarchically ordered feedback systems (brain) controls its input (Fig. 4), it follows that the reference signals for the lowest-order systems are determined by the output signals of higher-order systems. By the same token it follows that output signals of hierarchically higher-order systems are reference signals for hierarchically lower-order systems. Only the lowest-order output signals are, by some output function, directly transformed into motor behaviour. In this way one gets from "programs" to motor behaviour, with the restriction that "program" is defined as a nested set of rules reducing the degree of freedom in programming motor behaviour. As only the lowest-order output signals direct motor behaviour, in consequence of a particular interaction between input signals and internal organization of the organism, it is proposed to label these signals "motor commands", in contrast to output signals of higher-order systems reaching the lowest-order systems, which we propose to label "motor programming signals".

When one is dealing with a hierarchy of feedback control systems it is clear that information available for directing motor commands is minimal at the highest-order level, which simply contains reference signals for lower-order systems. In such a hierarchy it is evident that the information going downstream carries more and more details about the motor behaviour to be executed. In other words, the information available for directing motor commands increases at each lower level in the hierarchy, and reaches its maximum value at the lowest-order level in the hierarchy.

The reverse holds true for the degree of freedom in programming motor behaviour. This degree of freedom is maximal at the

level of the highest-order systems, reduces at each lower-order level, and ultimately becomes zero at the lowest-order level. This has great impact for the programming of ongoing motor behaviour: information going downstream can be continuously updated according to changes occurring in the input signals of levels that have not yet been set by their incoming reference signals (4, 7).

Brain and Motor Behaviour: ontogeny of the hierarchy.

The first stage in ontogeny is characterized by the sole presence of the outer shell: the comparator does not yet receive information from supraspinal levels. In other words, the reference value is zero: the muscles only contract when the α-motoneurons receive information from the muscles. Thus, changes in the environment actually dictate the response: there is no individual-specific variance at all. At this stage in the ontogeny we are a pure automaton or reflex-machine. But as soon as the second-order feedback system maturates, this system starts to produce an output which actually becomes the reference value of the first-order feedback system: the variability of the lowest-order system increases, and the reflex is now replaced by a reaction as McMillan calls it. The form of the movement is the same, but the degree of freedom to direct the reflex is different: the reflex is not anymore invariant. During maturation of the organism the degree of freedom in moving increases because of two reasons.
First, the number of superimposed feedback systems increases, enhancing thereby the variability of the lower-order systems (Fig. 4): the ontogeny is characterized by a strict order, in which the higher-order levels become successively involved. Second, once the linear hierarchy is fully maturated, the higher-order feedback systems become part of a so-called non-linear hierarchy, implying that the output of a particular level in the brain is sent not only to the next inferior level in the organization of the brain, but also to lower levels bypassing thereby intercalated levels; the same holds true for the input (Fig. 6). Since both the input and the output of each level has anyhow to be transmitted via the lowest-order level, which ultimately produces the commands for the muscles, it is evident that an adult organism can use different supraspinal pathways - implying different strategies - to perform exactly the same movement with the same form, and with the same changes in the E.M.G.: only the strategies, the schemata or the programmes used are different (7, 21). Normally, it is the requirement of the task - including the context in which the task has to be executed - that determines which strategy will be used.
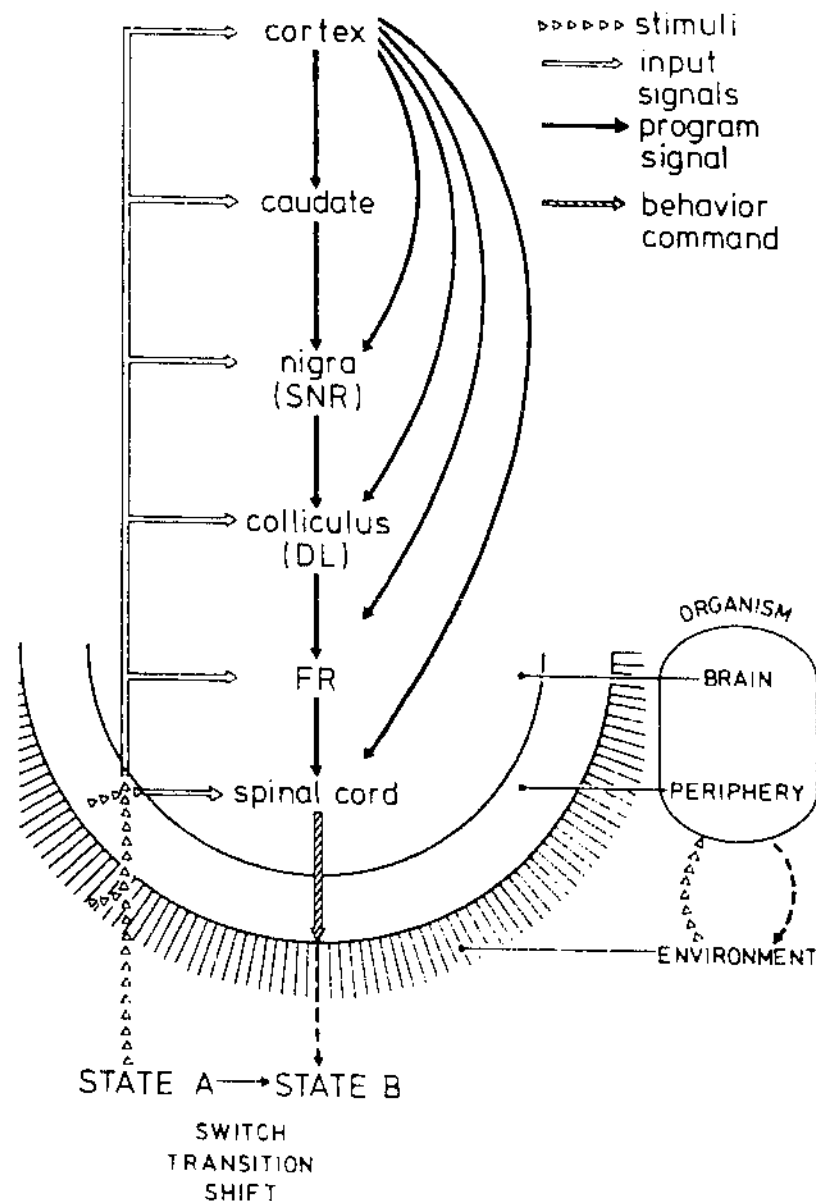
STATE A ⟶ STATE B

SWITCH
TRANSITION
SHIFT

Figure 6 : Oversimplified diagram of the flow of information going downstream in the hierarchy from the cortex. Signals leaving the caudate nucleus (caudate), substantia nigra, pars reticulata (nigra, SNR), deeper layers of the colliculus superior (colliculus, DL), and reticular formation (FR) and bypassing structures inferior to them are ommitted. The information carried by the output signals toward successively lower order levels is transformed as follows: Cortex: code for arbitrarily programming behavioural states. Caudate: code for arbitrarily programming the ordering and sequencing of behavioural states. Nigra: code for arbitrarily programming the ordering and sequencing of behavioural states with the help of propriotopic codes. Colliculus: code for arbitrarily programming the ordering and sequencing of behavioural states with the help of propriotopic and exteroceptive codes. FR: not yet specified. Spinal cord: detailed code for programming the behavioural state to be executed. (Note: This diagram deals

with the flow of a particular cortical code that goes downstream in the hierarchy. It will be evident that other codes follow different pathways).

At the moment we assume that expecially the complexity of the incoming stimuli, viz. essential features of the context in which the task has to be executed, determine which input level in the hierarchy is activated. On the other hand we assume that the requirements of the task determine which pathway downstream in the hierarchy is selected for the programming of the task, viz. providing the details of the movement to be executed. In other words, a healthy organism has not only the ability to use its incoming stimuli in order to activate a particular higher-order level- bypassing thereby lower-order levels -, but also the ability to send the output of the activated feedback system to hierarchically lower-order feedback systems - bypassing thereby one or more intercalated feedback systems. Thus, a healthy organism can just plug into the sequence of the different levels of the non-linear hierarchy.

Due to a disease as occurring in disabled organisms with brain disorders, it is not anymore possible to plug into the sequence. To relearn them certain skills is to bring them back to the lowest-order level in the hierarchy, and then to learn them to activate the higher-order levels according to the principles used in the ontogeny to build up to the non-linear hierarchy of superimposed feedback systems.

As mentioned above, the outer shell or lowest-order level in the hierarchy consists of the spinal motor reflex loop (Fig. 5). Stretching of the muscle produces changes in the spindle receptor. The resulting signal is sent to the αmoto-neuron. This signal (input) is compared with a signal which is sent to the spinal cord by supraspinal systems (reference signal). It is the difference (error) between both signals which determines the command (output) sent to the muscle. This is the closed loop feedback system forming the outer shell of the organism. There are famous experiments in which the supraspinal pathway is cut-off in so-called spinalized animals: such animals are paralyzed. Still, such an animal can walk and, even, gallop after being put on the running belt of a treadmill. Although several authors use this phenomenon to prove that the so-called locomotor generator, viz. the mechanism that contains the complete programme for locomotion, is localized in the spinal cord (18), this phenomenon actually illustrates that decerebration takes away the supraspinal signal and, accordingly, produces a reference value zero at the level of the spinal cord: as long as changes in the exteroceptive and/or proprioceptive input remain absent, the organism does not move and appears to be paralyzed because of the lack of any difference between the input (being zero) and the reference value (being zero): the resulting ouput remains zero (4). Once the organism is put on the running belt of a treadmill, the proprioceptive input as well as the exteroceptive input changes. It will be obvious that the difference between the changing input and the reference value being zero produces an output analogous to the input: the organism reacts as long as changes in the input are produced. In other words,

such a preparation does not show any movement without changes in the proprioceptive and/or exteroceptive input.
Let us now reconsider the knee-tendon-reflex in healthy organisms.

Under certain conditions I agree with the definition given by McMillan: a constant response being invariant. However, this holds only true for a very immature individual, in which there are no supraspinal centres maturated, viz. organisms which are unable to change the reference value of the lowest-order system. If one activates a particular part of the reticular formation in a healthy individual, the amplitude of the knee-tendon-reflex increases: in fact, one activates a second-order feedback system which directs the reference value of the lowest-order system. A similar effect can be produced by activating much higher-order feedback systems in the brain. For instance, "solving a mathematical problem" or "fixating visually an object" alters the threshold of the knee-tendon-reflex: again, these processes change the output of higher-order systems and, accordingly, the reference values of lower-order systems including that of the lowest-order system. In other words, the movement made during the knee-tendon-reflex is only a reflex in those organisms in which the supraspinal centres have lost their ability to change information to be sent to the spinal cord. In healthy organisms there are as many degrees of freedom to manipulate or to play with this reflex as there are distinct hierarchical feedback systems in the brain.
This hierarchy is far more complex than that depicted in Fig. 6.
Realizing that the organization within the brain is even more complex than the one shown in Fig. 7, it becomes evident that the brain is too complex to fully understand the available degrees of freedom in this respect. In this context it is useful to cite Watson: if the brain was so simple that we could understand it, we would be too simple to understand the brain. Anyhow, such a non-linear hierarchy of feedback systems has several advantages (4, 23).
First, there is no need to make complete schemata for particular movements, although it might do this. For, the higher-order levels can just produce reference signals for the next hierarchically lower-order level. In that case, it provides only global information as far as it concerns the execution of the movement: the required details can be filled in at any lower-order level. Only at the lowest-order level all details about the execution of the movement have to be available. The most important feature of the above-mentioned cerebral organization is the non-linear nature of the hierarchical organization.
To elaborate these features a little bit more, it might be useful to follow the neural information sent by the supplementary motor cortex (SMA) downstream in the hierarchy to the spinal cord (Fig. 6)
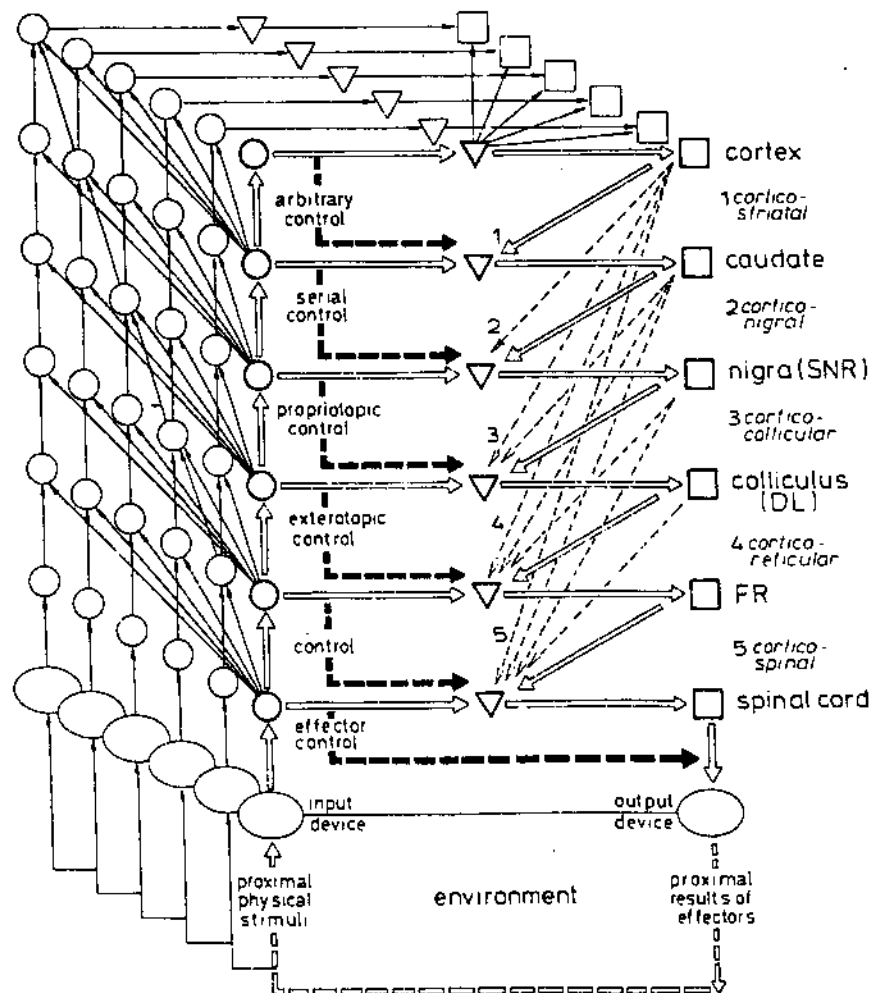
Figure 7 : Schematic diagram of the non-linear, overlapping hierarchy of negative feedback systems controlling the input signals of the organism. Stimuli delivered by 1) the ongoing behaviour itself, 2) immediate surroundings, and 3) proprioceptive and interoceptive receptors are transformed into abstract, invariant input signals whose degree of abstraction increases at each higher level within the hierarchy. The latter input signals are compared with so-called reference signals, i.e. output signals of hierarchically superior systems, resulting thereby in error signals which, in turn, are transformed into output signals. Only the output signals of the lowest-order system are transformed into behaviour. Note: for the sake of simplicity the output signals leaving the caudate nucleus, substantia nigra pars reticulata, colliculus superior (deeper layers), and reticular formation respectively, and bypassing one or more hierarchically lower-order systems, are omitted.

Programming Voluntary Movements: adulthood

Today, there is little doubt that the SMA contains the code for "arbitrary" or "voluntary" programming of (motor) behavi-

our (9, 25). For instance, studies on man with lesions in this
area have shown that such patients have lost precisely this
capacity. As mentioned, the output signals of the SMA are
actually the reference signals of the system hierarchically
inferior to the SMA, viz. the striatum (caudate nucleus).
The latter reference signals are compared with the input
signals of the striatum, viz. signals derived from the overall
input of lower centres in the brain, the body and the environ-
ment. The resulting output signals of the striatum allow the
organism to rearrange arbitrarily the serial ordering of non-
exteroceptively directed behaviour (1-5, 21). Increased stria-
tal activity dissociates behaviour programs, making possible a
rearrangement of the resulting elements: it improves the
organism's ability to alter non-exteroceptively directed
behaviour. Decreased striatal activity prevents such dissocia-
tion and, consequently, impedes rearrangement; still, the
organism remains able to shift proprioceptively and/or extero-
ceptively directed behaviour.
Such disturbances in programming the serial ordering of non-
exteroceptively directed behaviour have been found at the
cognitive and motor level in man, at the level of social
communication in monkeys, at the level of motor behaviour in
cats, and at the level of behaviour strategies in rats (1-5,
21).
Given the fact that the cortex contains the code for "arbitra-
ry" programming of (motor) behaviour, it is evident that the
striatum reduces the degree of freedom in programming (motor)
behaviour by adding concrete details about the serial ordering
of non-exteroceptively directed (motor) behaviour. In this way
the striatum contributes to the necessary transformation of
motor programming signals into motor commands (3, 21).
The striatal code for programming (motor) behaviour is sent to
the substantia nigra, pars reticulata (SNR; Fig. 6).
The SNR is known to reduce the remaining degree of freedom in
programming (motor) behaviour by adding details about the
serial ordering of (motor) behaviour with the help of static
or tonic proprioceptive stimuli. Thus, an organism with a
hypofunctioning SNR is unable to restore abnormal postures or
positions because of the fact that only static or tonic prop-
rioceptive stimuli are available. In this manner the SNR forms
a next step in the process of transforming motor programming
signals into motor commands (7, 14).
The nigral code, in turn, is sent among others to the deeper
layers of the superior colliculus (CS; Fig. 6). And this CS is
known to reduce the remaining degree of freedom in programming
(motor) behaviour by adding details about the serial ordering
of (motor) behaviour with the help of static or tonic extero-
ceptive stimuli. Thus, an organism with a hypofunctioning CS
is unable to use visual fixation of a static object in order
to reduce the distance between him and the object (7, 14).
Although it is not yet possible to mapp the whole process of
transformation of motor programming signals into motor com-
mands, we know that the levels hierarchically inferior to the
CS, viz. the reticular formation, reduce the degree of freedom
in programming (motor) behaviour (1) by adding details about
the serial ordering of (motor) behaviour with the help of

dynamic or phasic proprioceptive stimuli and, then, (2) by adding details about the serial ordering of (motor) behaviour with the help of dynamic or phasic exteroceptive stimuli. At the lowest levels in the hierarchy, viz. the spinal cord, the degree of freedom in programming (motor) behaviour is reduced to zero because all details about the motor behaviour itself are filled in (7).
Given this information it is relevant to make two remarks. First, the order in which the hierarchy of distinct levels of feedback systems maturates is exactly the mirror image of the order mentioned above. And, second, knowledge about the pro- gramming function of the distinct levels in the hierarchy tells us which kind of stimuli have to be chosen in order to activate the level under discussion. For instance, activation of a hypofunctioning, but not yet destroyed, SNR may be achie- ved by challenging the organism to use static or tonic propri- oceptive stimuli in order to alter its posture or position.

Until now we have just discussed the information stream going downwards in the hierarchy as if we were dealing with a linear hierarchy. However, this is not at all the case: it is the non-linear nature of the hierarchy that provides the functio- nal plasticity known to be present in healthy organisms. In fact, each healthy organism is able to use a great variety of alternative pathways to send information from the SMA towards the spinal cord in order to programm the execution of a single movement (Fig. 6). Since each pathway allows the organism to programm the motor behaviour in its own characteristic manner, the availability of alternative pathways implies that the organism can use one out of many different strategies to execute a particular movement: the form of the resulting movement may be exactly the same, but the strategy may be completely different (7, 8, 21). Below I will illustrate this feature a little bit more with the help of the following example. Once we were confrontated with a cat which turned out to be born without a striatum (Fig. 8).
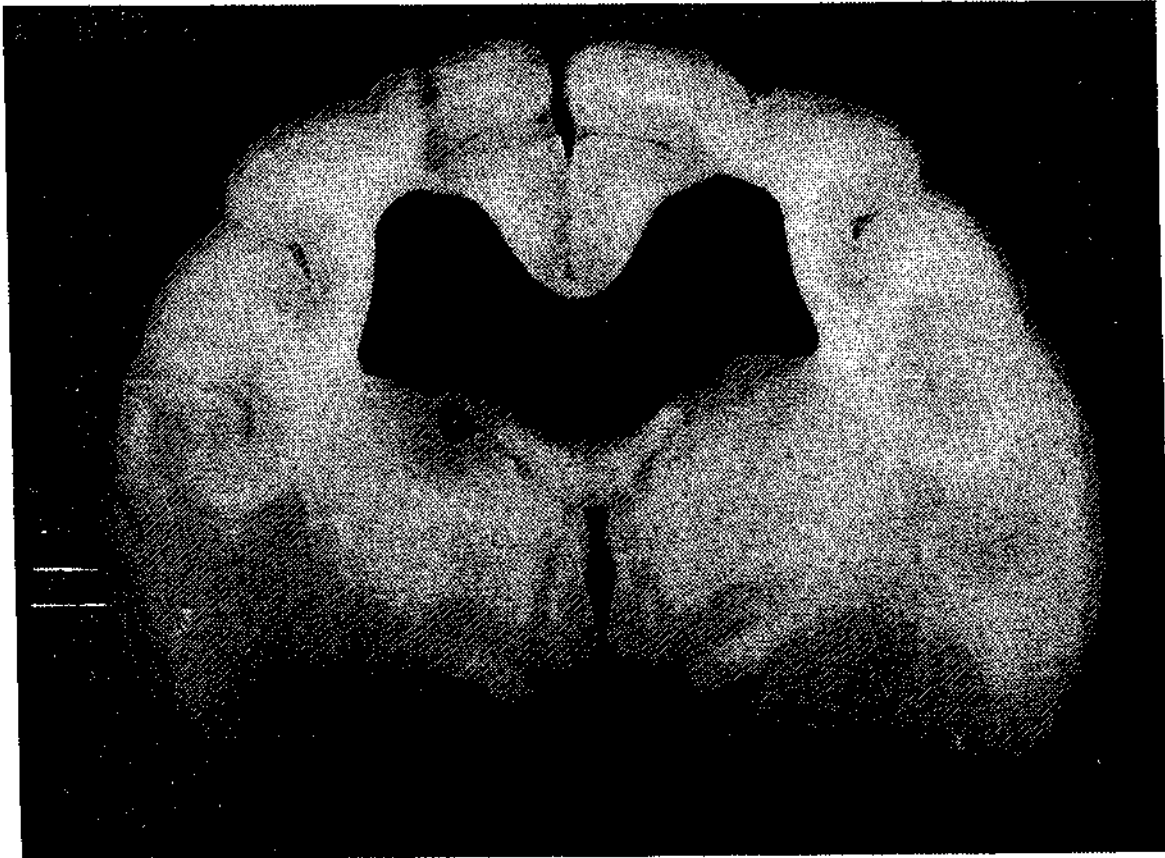
Figure 8 : Frontal section of the brain of an adult cat born
without a striatum: only a thin layer at the bottom of the
enormously enlarged lateral ventricles is left. This cat had
intact reflexes, walked, galloped, played, jumped and moved
like any other healthy cat.

This animal did not show any abnormal behaviour: it had intact
reflexes; it could walk and gallop on the running belt of a
treadmill; and it played, jumped and moved like any other cat.
Given the abovementioned information, we now understand why
such an animal did not show any gross motor deficit. Instead
of using its dysfunctioning corticostriatal pathway, it simply
used cortico-nigral, cortico-collicular, cortico-reticular and
cortico-spinal pathways to execute its voluntary movements
(Fig. 6).
Thus, organisms with a hypofunctioning striatum can still use
tonic or static proprioceptive stimuli to voluntary change
their position and posture, since they are able to activate
the cortico-nigral pathway (21). They can also continue to use
tonic or static exteroceptive stimuli to voluntary approach or
grasp an object, since they are still able to activate the
cortico-collicular pathway (7). And, finally, they can still
use dynamic proprioceptive and/or exteroceptive stimuli to
voluntary move, since they are still able to activate the
cortico-reticular and cortico-spinal pathways (7). Apart from
this, such organisms are still able to learn a complete schema

including all details required for the execution of a voluntary movement. In that case, they use their cortex to fill in all required details, and send this information straight forward towards the spinal cord via the cortico-spinal pathways. When using the latter strategy, the organism gains speed at the cost of losing the ability to update the programming of the ongoing movement: for, changes in the environment cannot anymore be used to adapt the output signals of the intercalated systems.

Today, we know that a long-lasting progressive dysfunctioning of the striatum initially leads to a reduced ability to arbitrarily shift from one movement to another: the organism does not yet suffer from dysfunctioning output stations of the striatum (see above). However, when the progressive pathology within the striatum increases, the first-order output station of the striatum, viz. the SNR, starts to dysfunction as the result of the arrival of distorted reference signals sent by the striatum to the SNR (Fig. 6). When the pathology of the striatum further increases, the second-order output station of the striatum, viz. the CS (Fig. 6), starts to dysfunction as the result of the arrival of distorted reference signals sent by the SNR to the CS (7, 12-14, 20).

In practice, this successive disconnection of lower-order outputstations of the striatum occurs in patients suffering from Parkinson's Disease. In fact, the definite diagnosis can only be made at the moment that motor disorders inherent in a dysfunctioning CS or, even, reticular formation become evident.

In this context it is of utmost importance to realise that these patients have still morphologically and neurochemically intact output stations of the striatum: they show only these deficits because the latter stations dysfunction as the consequence of a long-lasting morphological and neurochemical deficit within the striatum. This implies that the above-mentioned output stations of the stratium can still correctly function when correct signals are offered.

In practice, we have been able to show that adequate input signals can indeed re-activate such malfunctioning output stations of the striatum in parkinson patients (6). In fact, we have tested a small number of patients (n=5) who had reached the stage of various degrees of akinesia: two of them had to be supported by nurses in order to stand. Their motor behaviour was analyzed when they were put on the belt of a treadmill of which the speed was slowly increased from zero on. The basic idea was that the running belt produces both changes in the exteroceptive input (tactile, visual and related stimuli) and changes in the proprioceptive input as consequences of the passive movements of their body and limbs. These experiments showed that even fully akinetic parkinson patients could walk in a perfect manner, when the belt was running. They were even able to run when the belt of the treadmill had a speed of 5 km./hour. They moved not only legs in a correct manner, but also their hanging arms, viz. a typical fealture of such patients. Apart from these phenomena, two patients started to laugh, while their typical parkinsonian mask face disappeared. In addition, these two patients

started to sing, viz. a capacity which is gone in patients marked by a progressive stage of this disease. Given the fact that these patients were unable to see their own movements, we wondered whether they were aware of the experimentally induced improvement of their motor behaviour. Analysis of their answers following the question "how did you move on the treadmill" revealed that they were fully unaware of the artificially induced improvement. These data led us to the conclusion that the treadmill produced changes in stimuli which were sufficient to reactivate the lower-order output stations of the striatum, but not yet sufficient to re-activate the cortex (see: Fig. 6).

In other words, the complexity of the stimuli created by the running belt was too small in order to activate the cortex. It is our firm belief that additional research will reveal what kind of stimuli are required to re-activate the cortex. For, practice has already provided anecdotical examples showing that parkinson patients can create imaginary stimuli to execute voluntary movements, viz. a typical cortical phenomenon (28).

It is up to physiotherapists, neurobiologists, neurologists and psychologists to deduce from practice, animal studies and clinical observations which kind of stimuli have to be selected in order to reactivate those brain structures in the non-linear hierarchy of feedback systems which per se are not morphologically and/or neurochemically affected by the disease, but are just dysfunctioning because of the arrival of distorted information sent by morphologically and/or neurochemically affected brain stuctures.

Programming Voluntary Movements: ontogeny

Like puppies in animal kingdom, human babies have just a maturated outer shell at birth. At that time there are no maturated supraspinal centres which produce variance in the reference signals sent to the spinal cord. We are more or less stimulus-bound organisms at that stage of the ontogeny. For instance, a baby can only drink when it passively touches the nipple: it needs a _dynamic change in this exteroceptive stimulus_ in order to drink. At that time the baby can flex its arm only when the latter is passively extended: again, it needs _dynamic changes in proprioceptive stimuli_ to move. About 10 months later it becomes able to crawl on all fours to grasp a resting object. Only at that stage of the ontogeny it is able to activate the higher-order system that uses _static or tonic exteroceptive stimuli_ as input. Still, later on, the baby becomes able to stand alone. The system necessary for using _static or tonic proprioceptive stimuli_ apparently maturates only at that stage of the ontogeny. Again months later, the child starts to arbitrarily shift motor behaviour, indicating the maturation of the striatum.

Programming Voluntary Movements: moving on land and moving in water

Let us now return to the swimming method used to mobilize

disabled patients. As described by McMillan, there are signi-
ficant differences between moving on land and moving in water.
Below I will elaborate three of these differences.

A. Standing on land implies maintenance of balance around the
vertical axis of the body, whereas floating in water implies
maintenance of balance around the lateral axis of the body.
Today, it is known that the ability to rotate around the
lateral axis preceeds the ontogenetic stage during which the
organism can rotate around its vertical axis. We even know
which brain structures are involved as far as it concerns the
control and development of these movements in rats. Young rats
start to move around their lateral axis: they pivot. Once
these movements are developed, the rats develop the ability to
move along their longitudinal axis: they move forwards. Once
the latter movements are developed, the rats develop the
ability to rotate around the vertical axis: they rear. This is
a general principle in animal kingdom (17). Today, we know
that rotations around the lateral axis are mediated via dopa-
minergic, nigrostriatal neurons which terminate in the dorsal
striatum, viz. fibres of which the number is decreased in
Parkinson's Disease. Rotations around the longitudinal axis
require intact dopaminergic, tegmento-mesolimbic neurons which
terminate in the ventral striatum. And, finally, rotations
around the ventral axis require intact dopaminergic neurons
which terminate in the olfactory tubercle (6).
When adult rats are placed into an unfamiliar environment they
display the whole sequence of different movements within a
split second. In other words, the order in which adult ratss
successively acativate the distinct systems, of the hierarchy,
is identical to the order typical for the ontogeny. In additi-
on, however, adult rats are also able to plug in this sequence
(16, 17). It is not necessary to initially perform a lateral
movement and, then, a longitudinal movement in order to make a
vertical movement. We, like other primates and rodents, can
just start to make a vertical movement. That is the degree of
freedom we have reached after the integrated network within
the brain is fully developed. The ability of adult organisms
to successively activate hierarchically superior systems
according to principles inherent in the ontogeny is also clear
when one considers the process of recovery from brain damage
(15, 29-31). For instance, rats with hypothalamic lesions are
completely akinetic in the beginning, but slowly recover.
First, they become able to rotate around the lateral axis:
they behave like puppies. Then, they become able to rotate
around the longitudinal axis and, finally, they become able to
rotate around the vertical axis. The whole recovery process
takes several weeks to months.
Once we are acquainted with these properties, it becomes
possible to understand the value of mobilizing disabled pa-
tients in water. First, the water forces the patient to return
to the lowest-order levels in the hierarchy. Subsequently, we
have, created a condition during which we can offer exterocep-
tive and/or proprioceptive stimuli allowing the patient to
successively re-activate higher-order systems according to
principles inherent in the ontogeny.

So: water forces the patient to return from the higher-order
system that allows him to balance around the vertical axis
to the lower-order system that allows him to balance around
the lateral axis. In this manner, swimming or floating
reinstates an earlier phase of the ontogeny. This reinstate-
ment, in turn, allows the patient to successively activate
higher centres in the brain in order to learn new skills and
movements.

I will be evident that this holds only true for those disor-
ders of movements which are due to brain structures which
dysfunction as the consequence of distorted information recei-
ved from morphological and/or neurochemically deficient brain
structures, but not true for disorders of movement which are
due to morphologically and/or neurochemically deficient brain
structures.

B. When standing on land and being asked to rotate the head 10
degrees to the left with closed eyes, a healthy subject will
have no problem with this task: he uses static or tonic prop-
rioceptive input to activate its SNR (Fig. 6) with the result
that the latter brain structure produces correct reference
signals for the lower-order systems of the SNR. When floating
in water, a healthy subject cannot use this system. Instead,
he uses dynamic or phasic changes in the proprioceptive input
to produce a so-called contra-rotation of the head.
As mentioned above, the system that allows the subject to use
dynamic or phasic proprioceptive input is maturated before the
system that allows the subject to use static of tonic proprio-
ceptive input. In other words this example again underlines
the notion that water forces the patient to reinstate an
earlier phase of the ontogeny, allowing thereby the patient to
successively activate higher brain centres in order to learn
new skills and movements.

C. When standing on land, a healthy subject is balancing on
his feet. In water, however, he is balancing his head, shoul-
ders and, sometimes, trunk and pelvis. Again, these differen-
ces between balancing on land and balancing in water reflect
differences in the order in which the involved capacities
develop in ontogeny. In fact, any movement develops along the
so-called rostro-caudal or head-feet axis: first, the head is
involved; then, the neck, shoulders and arms; and, finally,
the trunk, pelvis and legs become involved (17).
In other words, this example too shows that water forces the
patient to reinstate an earlier phase of the ontogeny, allo-
wing thereby the patient to successively activate higher brain
centres in order to learn new skills and movement.

Epilogue.

Knowledge of the non-linear hierarchy of feedback systems
controlling motor behaviour lays the foundation for a number
of approaches which may help us to improve the available
methods to rehabilitate patients suffering from disorders of
movement inherent in brain damage.

1. <u>Swimming in general and the Halliwick method in particular</u>. It reinstates one of the earliest stages of the ontogeny as far as its concerns brain centres involved in the programming of movement. This reinstatement makes it possible to assess principles inherent in the ontogeny in order to successively activate higher brain centres which are not yet morphologically and/or neurochemically deficient, but are producing disorders of movement because of the fact that they just receive distorted signals sent by higher-order systems in the brain.

2. <u>Selecting and offering adequate exteroceptive and proprioceptive stimuli to activate a paricular dysfunctioning level in the hierarchy.</u> Although we already know that the degree of complexity of the incoming stimuli, viz. essential features of the context in which the movement has to be executed, determines which input level in the hierarchy will be activated, our knowledge is far from complete in this respect. Still, there is little doubt that distinct levels in the hierarchy are differentially controlled by dynamic resp. static exteroceptive stimuli, by dynamic resp. static proprioceptive stimuli, and by imaginary stimuli. It is of utmost importance to get more insight into the nature of stimuli which are needed to (re)activate particular levels in the hierarchy. Anyhow, this approach is complementary to the above-mentioned swimming method.

3. <u>Designing motor tasks requiring the use of particular strategies to programm circumscribed movements</u>. It is this approach that allows a patient with a particular morphologically and/or neurochemically deficient brain structure to activate pathways downstream in the hierarchy which bypass the affected brain structure. In order to develop such tasks, it is important to have knowledge about the programming features of the distinct parallel pathways in the brain. Until today, our knowledge is limited to the different pathways leaving the supplementary motor area of the cortex.

The above-mentioned approaches have one common feature: they are intended to reactivate intact parts of the brain rather than to change affected parts of the brain. It is my firm belief that the plasticity of the brain forming part of a non-linear hierarchy of feedback systems, in which both the body and the environment are incorporated, is much greater than one usually accepts. It is this feature of the brain that should challenge physiotherapists, neurobiologists, neurologists, and psychologists to open perspectives for actual progress in the field of rehabilitation of patients suffering from disorders of movement. Anyhow, intense cooperation and willingness to integrate theoretical and practical knowledge are essential prerequisites for a blooming future in this respect.

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