[41] Tashiro A, Makino H, Gage FH. Experience-specific functional modification of the dentate gyrus through adult neurogenesis: a critical period during an immature stage. J Neurosci 2007;27:3252–9.
[42] Van Harreveld A, Fifkova E. Swelling of dendritic spines in the fascia dentate after stimulation of the perforant fibers as a mechanism of post-tetanic potentiation. Exp Neurol 1975;49:736–49.
[43] Walter WG. A machine that learns. Sci Am 1951;185:60–3.
[44] Weiss P. Self-differentiation of the basic patterns of coordination. Comp Psychol Monogr 1941;17(4):1–9.
[45] Whitlock JR, Heynen AJ, Shuler MG, Bear MF. Learning induces long-term potentiation in the hippocampus. Science 2006;313(5790):1093–7.
[46] Will B, Galani R, Kelche C, Rosenzweig MR. Recovery from brain injury in animals: relative efficacy of environmental enrichment, physical exercise or formal training (1990–2002). Prog Neurobiol 2004;72(3):167–82.
[47] Yuste R, Bonhoeffer T. Morphological changes in dentritic spines associated with long-term synaptic plasticity. Annu Rev Neurosci 2001;24:1071–89.

doi:10.1016/j.bbr.2007.11.030

Research report

Reflections on the use of the concept of plasticity in neurobiology Translation and adaptation by Bruno Will, John Dalrymple-Alford, Mathieu Wolff and Jean-Christophe Cassel from J. Paillard, J Psychol 1976;1:33–47

Bruno Will[a,*], John Dalrymple-Alford[b], Mathieu Wolff[b], Jean-Christophe Cassel[a]

[a] LINC UMR 7191, Université Louis Pasteur-CNRS, IFR de Neurosciences 037, GDR CNRS 2905, 12 rue Goethe, F-67000 Strasbourg, France
[b] Van der Veer Institute for Parkinson's and Brain Research, and Department of Psychology, University of Canterbury,
Private Bag 4800, Christchurch 8140, New Zealand

Received 21 October 2007; accepted 6 November 2007
Available online 5 December 2007

Abstract

After having underlined the ambiguities of the concept of plasticity and the dangers of its purely metaphoric use in neurobiology, it is suggested that we return to a more precise definition of the structure, the operating principles and the function of the "systemic" unit or "integron" relevant to the particular level of analysis in question. Any change can then be described as a modification of function, a change in the operation principles, or an alteration of the material structure of the system.

It is suggested that the term plastic should be restricted to describing, among the possible variations in the operating principles or the function of a given system, any lasting alteration of the connectivity network of the system under the influence of an external force or environmental constraint. Therefore, systematic or random variations of performance, functional flexibility or the vicarious[1] processes or strategies that can be found in a rigidly wired system are not justified examples of plasticity.

Keywords: Plasticity; Neurobiology; Linguistic

Progress in neurobiology requires an interdisciplinary dialogue. Both the importance and abundance of various facts collected at a variety of levels of analysis of nervous system function suggest that a vertical approach to some questions in neurobiology is now possible. Molecular phenomena at the cellular level can be directly linked to processes that give rise to both basic function and behavioural phenomena that express the products of such integrated function at the level of the whole organism. It is well-known that interplay across different fields of knowledge is often restricted by different semantic limitations. From this perspective, one may question whether the concept of plasticity has been useful. The term is in fashion. A variety of expressions are used such as phenotypic plasticity, synaptic plasticity, morphological plasticity, functional plasticity, plasticity of sensory-motor coordination, behavioural plasticity, etc. Is such a generalisation of the concept justified? Are these different types of plasticity sufficiently precise to be of heuristic value in generating novel hypotheses and experiments so that the concept is useful in neurobiology? This issue merits attention because it immedi-

---

[*] Corresponding author.

[1] Vicarious process: "taking over the functions" of damaged tissue (note added by the translators).

ately poses several problems, which I would like to clarify below.

1. The trap of semantics

Every linguistic term can be used with a specific meaning or in a metaphoric sense and people naturally use a given word for a given context. The interpretative connotations linked to the concept plasticity and of the qualifier plastic lead to ambiguities. It is necessary to start by pointing out these ambiguities.

The current *Littré* (a French reference)[2] early restricts the proper meaning of the term *plasticity* to the "capacity of distortable bodies to change their shape under the action of an external force and to maintain the change after this force has ceased to act". The plasticity of clay as well as the modern term *plastic* refer precisely to this property. The notion can thus be clearly distinguished from that of *elasticity*, which designates "the property of distortable bodies to restore their original shape and volume when the force that was exerted on them has ceased". One finds the figurative meaning (of plasticity)[2] being used for adaptive flexibility in behaviour and reactions to environmental stimuli.

With respect to the qualifier *plastic*, one ambiguity comes to light from the earlier *Littré*. Etymologically, the term refers to "the ability to form, to give a shape". One finds it repeated today in the expression "plastic arts" which follows this meaning, being the "art of building new forms". Relevant here is the first use of the word "plastic" in biology in which the fundamental function of living organisms was considered to build and maintain their shape. Physiology in the early (20th)[2] century talked of "plastic nutriments" and "plastic functions" to designate that which, through nutritional functions, contributes to morphogenesis and to the maintenance of organic structure. The *Littré* dictionary illustrates this definition with a quote from Hartsoeker: "He imagined that there was a plastic and formative soul in crayfishes which provided the property of growing new legs . . .".

Biology was confronted with an ambivalence introduced by a term which referred to both the property of living entities to be "organized" organizations, that is structures that can be moulded and be malleable under the action of external environmental constraints, and "organizing" organizations, that is structures that generate order, first at the level of a genetically planned morphogenesis, then in structuring their own sensory and motor properties, and finally in transforming the physical order that characterizes their environment. Clearly, it is fundamental to appreciate both sides of this dialectic, which links the organism with its ecosystem. It appears again in modern conceptions of genesis and selective epigenesis. The "genetic" function, as revealed by the terms ontogenesis, organogenesis, embryogenesis, morphogenesis, etc., refers to the existence of structuring, organizational forces, that create and generate order, and are thus *plastic* in the etymological sense of the term. By contrast, malleability via the adaptation to environmental constraints shown by living organisms refers to the irreversible changes that outlive the initial causes, a notion contained in the modern sense of the term *plasticity*.

Today, biology has abandoned the use of the term *plastic* to characterize the self-organizing and order-generating capacity (i.e., genetic functions)[2] of living organisms (without substituting an alternative concept, which itself might be useful), but the restriction of its meaning to the ability to change shape and adapt to external constraints then also brings new ambiguities, in two respects at least.

1. In the relationship between the concepts of plasticity and elasticity, it is clear that the degree of the permanency of any modification and of its survival beyond any inductive cause is not easy to define, as one has to distinguish instances of irreversible biological phenomena and others that are more or less rapidly reversible. What time scale should one adopt to distinguish plasticity from elasticity?
2. A second difficulty arises when using the term plasticity in either its literal or figurative sense. In biology, established semantics encourage the limitation of the term to the capacity of living "structures" to change their shape in a lasting manner. However, this restriction immediately confronts us with the metaphorical use of the term structure. It is not necessary to review in any detail the numerous epistemological discussions generated by this extension of the concept of structure: material structures which characterize energy-matter conversions in a physical three-dimensional space, temporal structures which characterize the organization of phenomena in time, functional structures, conceptual abstract structures, logical structures, mathematics or other structures . . ..

By way of exploration, let us restrict the definition of the term structure to the *material substratum* of the systems of interest. Immediately, another, indeed considerable, difficulty appears: the difficulty of defining the levels of organization and the relationships between structure and function at each level under consideration.

2. The trap of levels of organization

Obviously, living organizations are composed of a series of hierarchically interlocked substructures, organized in "systemic units" [1]. Each systemic unit (the "org" of Gerard [2], also called "integron" by Jacob [3]) can be defined by its *interface structure* with the higher level system, of which it is an element, and by its *relation structure* (*or connectivity network*) which generates cohesion among the interdependent elements or "sub-systems" of which it is made. Inputs and outputs of the systemic unit can be defined at the level of the interface structure, but the specific way in which it operates (its "operating principles") are defined by its internal connectivity network. The cell, the organ, the apparatus (such as digestive systems), the organism, groups of organisms, and societies form one or more of the structural levels, or "systemic units" or "integrons", that have hierarchically embedded relationships [4]. Each level is generally approached horizon-

---

[2] Note added by the translators.

Please cite this article in press as: Will B, et al., Reflections on the use of the concept of plasticity in neurobiology, Behav Brain Res (2008), doi:10.1016/j.bbr.2007.11.008

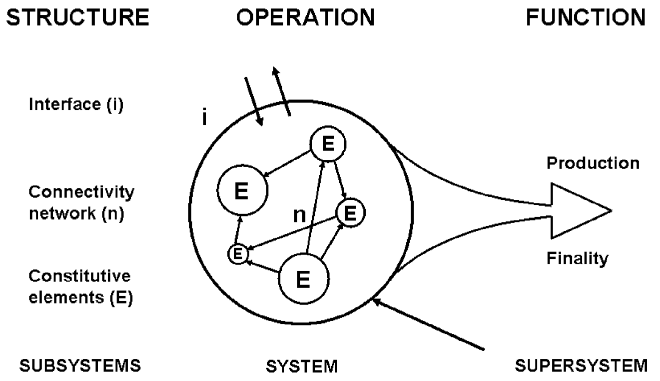

Fig. 1. Schematic drawing showing an integron considered as a systemic unit. The specification of the system by its structure requires: (1) its *interface* (i), the site of interaction between the system and its environment, (2) its elementary constituents or *subsystems* (E), and (3) the *connectivity network* (“n”) that binds these elements together. To define the system in terms of its operating principles requires knowledge of the “function” of the individual elements (sub-systems). The function of the system is the product of its operating principles and is expressed through its network of connections and functional relationships with its superordinate-system(s), of which it is an element.

tally by scientists. Each level requires technologies, questions, theories, specific concepts that constitute the main branches of physics, chemistry, biology, psychology, sociology.

Each of the integrons of living organizations must thus be considered as an open system specified by its Structure, its operating principles and its Function (an “S.o.F. system”) (Fig. 1).

The *Structure* of the system is defined by its *interface*, the place of interaction with its environment (but not necessarily, its shape) and by its *internal connectivity* which defines the interactions among its constituent elements or sub-systems.

The *operating principles* of any system reflect the modalities and the spatiotemporal layout of the sub-systems which themselves respond to the exchange dynamics occurring at the level of the system’s interface.

The *Function* is the product of these operating principles and requires some product or reaction to the environment. Any function presupposes a purpose or functional aim. The functional aim of an integron only has biological significance when the consequences of its expression can be identified at the higher level system to which it belongs. That is, the significance of a function can only be understood within the context of the operating principles of the super-ordinate system in which the integron is integrated. This approach avoids the traditional confusion between how a system works (its operating principles) and its function.

When the level of the integron (or “system”) corresponds to the whole “organism”, which is our primary concern, the behaviour of the organism can be described as a sequence of events at the interface between the organism and its environment or eco-system (i.e., the superordinate system of the organism). The behaviour of the organism is the product of the operating principles that are expressed through the actions of multiple organs and sub-systems. The functional sub-systems involved at this level (nervous, endocrine, respiratory, circulatory, assimilation, excretion functions, etc.) have significance within the integrated superordinate system (i.e., the “organism”) to ensure its integrity and structural survival. The organism is actually “behaving” when it interacts with other components of its ecosystem (sexual partners, predators, food or prey). Research on the operating principles that underlie behavioural expression raises specific problems that have not been recognised. Indeed, such research supposes that one can identify the neuronal ensembles, or subsystems, responsible for different behavioural characteristics. The connectivity of the neuronal ensembles and how they work (i.e., their operating principles) provide a new level of organization to explain a given function.

A “modular” view of the structure and operating principles of the nervous system has become popular [5]. For example, the search for interdependent, wired modules as constituents of motor programmes constitutes an important trend in neurophysiology (see [6]). This modular perspective can lead to useful clarifications. However, would the concept of plasticity also then be clarified? Will we be able to justify its use to describe some specific malleability of function, some variability of the operating principles, some alteration of the material structure of the system? At minimum, can we hope to be able to establish causal relationships between structure, operating principles and function and the general utility of the concept in neurobiology?

But there would then still be a third problem: that which arises from the stability of a given system.

3. The trap of stability

Speaking about the “plasticity” of a system implies that there exists the possibility of identifying a change in its state, that is, its shape or properties. This state modification itself can only be defined by reference to a given invariant stability. The “plastic” change of a given structure expresses the transition from one state of stability to a final state of stability that can be distinguished from the initial state.

With respect to living systems, and even ignoring temporal and spatial factors, the concept of stability concerns several issues:

- *non-changeable* (*rigid*) *stability* (skeleton; the neural system blueprint);
- *changeable stability* that is irreversible (long term memory);
- *changeable but reversible stability* that returns to the initial state as soon as the constraint disappears (flaccid structures of the organism; short-term memory?);
- *equilibrium stability* which results from the implementation of antagonistic forces (a nearly universal model nervous system organization);
- *steady-state* which is a specific characteristic of living organizations both from a structural and functional point of view.

The morphological invariance of the system is maintained only at the expense of a vast number of micro-reorganizations of the basal structure. Stability of function is itself underpinned by a multitude of random micro-events at the various levels of the systemic organization.

The invariance of the system is dependent on phenomena at lower levels of analysis. That is, the homeostasis of the organism

Please cite this article in press as: Will B, et al., Reflections on the use of the concept of plasticity in neurobiology, Behav Brain Res (2008), doi:10.1016/j.bbr.2007.11.008

is maintained only at the expense of a continual modification of its internal operations. These functional variations generally do not necessitate any structural modification of the connectivity network. Conversely, a change of the inner structure (following a lesion for instance) may have no effect at the functional level because a vicarious process contributes to maintain functional invariance.

From a theoretical point of view, Ashby [7] specified several possible forms of stability in systems that show properties of homeostasis, habituation or adaptation,

(a) *Stability* of a state of thermodynamic equilibrium that characterizes systems that react to any unbalancing disturbances (within a given margin) by a compensatory reaction that aims to restore the initial state.
(b) *Ultra-stability* of unbalanced but stationary states as defined in the thermodynamics of irreversible phenomena which corresponds to the ability of the system to have several possible states and to react to unbalancing actions by modifications of its connectivity structures until it reaches a new stable state.
(c) *Multi-stability* in which a system is able to modify the pattern of activity of its sub-systems in response to a "disruptive" stimulus without becoming unstable.

An additional important characteristic of multi-stable systems is that they cannot exist without a given amount of background noise, as shown by some random quality of their connections, and are characterised by heterogeneity of their components.

Atlan [8] has made the interesting comment that the reliability and adaptive flexibility of a system increases as the heterogeneity of its components increases, to decrease the redundancy of the system when faced with random environmental stimuli.

Thus, one has instability as a condition of stability, random disorder as generating organization, diversity as being at the source of unity: all these seemingly contradictory notions are compatible with what one may call the "logic of life".

Is there hope that the concept of *plasticity* will be fully justified in describing a general notion of function, operating principles and the material structure of the systemic units that can be identified at various levels of neurobiological organization? In its present form, is the term one of those generalizations condemned by Bachelard?[3]

4. Arguments for restricting the concept of plasticity

The increasing trend of using the term plasticity in its general metaphoric sense generates the fear that it will rapidly become a source of interdisciplinary confusion. Such a metaphoric use will not easily prevent the interpretative connotations that are attached to this term. Will this connotation lead us to ascribe a change in function because of a change in the structure of the system that results either from the action of an external force or environmental constraints?

There are three main types of enduring structural changes in living organisms that remain:

(1) The first is the evolutionary scale of the transformation of the species in terms of its morphology and adaptive capacities. It indicates some ability for structural mutation of the genome. This can be called "*evolutionary*" *plasticity*.
(2) The second concerns individuals and epigenesis. It concerns the structural malleability of the system during its development. It also concerns the structural changes due to the influence of external forces rather than any distortion. It implies that performance is selected within the range of genetic competence. This can be called *"genetic"* *plasticity*.
(3) The third corresponds to the capacity of the fully developed system to change its own structure and to expand its behavioural repertoire. It corresponds to an *adaptive plasticity* of a system which has already completed its maturation.

From the perspective of interdisciplinary dialogue in neurobiology, between specialists from cellular to behavioural levels, it is appropriate to distinguish the observable behavioural variations that are dependent on structural changes from those that do not imply such changes. Only the earlier category, in my opinion, expresses a plasticity of the system (see Fig. 2).

Computer controlled robots display functional flexibility. This shows that a rigid network of pre-established connections can be the substrate of variable operating principles, but with fixed (invariant) functions. For instance, the performance diversity of Walter's turtle[4] not behavioural plasticity. Any modulation of the possible responses of an organism to environmental variation does not obligatorily express a property of plasticity. It may simply express the presence of a given repertoire of competences that may be solicited. The range of possible responses in a fixed situation is also not structural plasticity. It may simply reflect the current state of the organism in selecting the response programmes that are already available in its behavioural repertoire.

Any operating principle that gives rise to function can show flexibility despite any rigid wiring (its connectivity), such as tolerance towards errors, which are automatically corrected because of compensatory feedbacks. This adaptive flexibility based on the principle of self-regulation and non-stereotyped responding does not assume any structural modification of the inner connectivity networks of the system.

Today, neurophysiologists are trying to identify the wired modules underlying the executions of some rigid motor pro-

---

[3] Professor of philosophy at the universities of Dijon and Paris (Sorbonne), Bachelard got his degrees in mathematics and philosophy. He was also professor of physics and chemistry at a junior high school. He was a member of the Academy of moral and political sciences (note added by the translators).

[4] W. Grey Walter was a physiologist and electronics engineer who used his wartime exposure to radio detection and ranging (RADAR) to build a simple "brain" that endowed his "turtle", an artificial autonomous robot with complex adaptive behaviour. Grey Walter stated that such robots could be used in research to achieve a better understanding of animal behaviour (note added by the translators).

Please cite this article in press as: Will B, et al., Reflections on the use of the concept of plasticity in neurobiology, Behav Brain Res (2008), doi:10.1016/j.bbr.2007.11.008

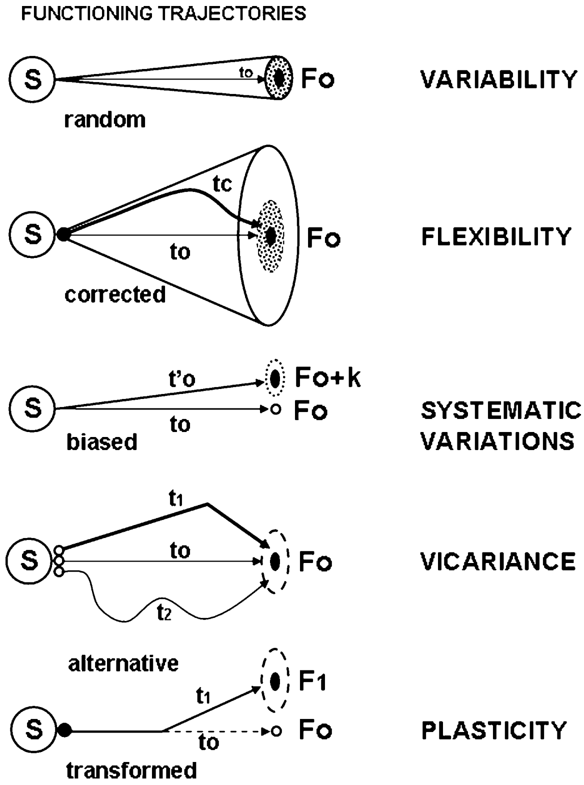

Fig. 2. Classes of observable variations, considered either at the level of the system's function (performance, aim or finality, F0) or at the level of its internal operating trajectory (t0) (see comments in the text). In principle, the first four classes of trajectory do not suppose any modification in the material structure of the system (interface, connectivity network, constitutive elements). The term plasticity is only appropriate in terms of the ability of the system to achieve novel functions (F1), either by transforming its internal connectivity network (t0, t1) or by changing the elements of which it is made.

grammes that are controlled by self-regulatory circuits [6]. That is, these modules are endowed with operating flexibility and a tolerance margin of error. Numerous fundamental behavioural activities employ such rigorously wired programmes. These programmes use self-adjustment to produce adaptive flexibility and avoid stereotyped responding.

Moreover, operating errors beyond the correction capacities of the system and thus beyond its flexibility margins constitute either *systematic variations* of the system's performance (ongoing errors) or *random variations* (its variability, its background noise) (see Fig. 2).

Finally, the *variety of strategies* used to achieve the same behavioural goal does not imply that new connective structures are generated, but simply that vicarious alternative strategies pre-exists within the system and the rules by which these strategies are induced can be defined. Physiology provides many examples of parallel circuits that are able to maintain functional invariance when one or more circuits fail. This is a well-known principle used to optimise reliability in engineering. It is likely that behavioural regulation also follows this rule.

The real problem with the concept of plasticity is to highlight lasting structural reorganization and the construction of new functional modules. Actually, it is exactly the same problem as that of learning and memory.

It is therefore of interest, both for the neurophysiologist and the cellular neurobiologist, to be able to link any structural changes both to the operating principles of the structure and to behavioural (functional) variations.

A more precise taxonomy of behavioural variations that cannot be ascribed to structural changes in connectivity networks would be valuable. It might help us distinguish *flexibility*, *strategy substitution* and *systematic or random variability* (background noise) by focussing on mechanisms or functional models that explain them in the context of a rigidly wired machine. At the same time, it would help specify the *plasticity* of the system and the modifiability of its inner structures (see Fig. 2).

From an interdisciplinary perspective, such semantic clarification is useful between behaviourists, neurophysiologists and "cellular" neurobiologists. This may seem less obvious to the individual scientist, for example the behaviourist who is focussed on his/her immediate (behavioural) level of analysis.

Finally, one may wonder whether the S.o.F. (Structure-operating-Function) model of analysis can be extended to the super-ordinate system in which individual behaviour is no longer considered simply as the functional expression of the organism, but also a structural element supporting the operating principles that give rise to function at the level of the super-ordinate system. This is the case, for instance, for the inter-individual relations in a social group, where the connectivity structure characterizing this organizational level of the system finds precisely its material structural foundation in the stereotypy of movement patterns, attitudes, and other various signals that make up its behavioural products with a social aim. If the concept of plasticity is restricted to the lasting capacity of the connectivity network of the system to change its structure that links together the elements of any system, then it may have some heuristic value to advance knowledge.

References

[1] Weiss P. Self-differentiation of the basic patterns of coordination. Comp Psychol Monogr 1941;17(4):1–96.
[2] Gerard RW. Neurophysiology: an integration (molecules, neurons, behavior). In: Field J, editor. Handbook of physiology, Section 1, Neurophysiology, vol. III. Washington, DC: Am. Physiol. Soc.; 1960. p. 1919–65.
[3] Jacob F. La logique du vivant. Paris: Gallimard; 1970.
[4] Miller JC. Living sustems: basic concepts. Behav Sci 1965;10:193–411.
[5] Szentagothai J. The "module-concept" in cerebral cortex architecture. Brain Res 1975;95:475–96.
[6] Paillard J. Le codage nerveux des commandes motrices. Rev EEG Neurophysiol 1976;6(4):453–72.
[7] Ashby WR. Design for a brain. London: Champman and Hall; 1954.
[8] Atlan N. L'organisation biologique et la théorie de l'information. Paris: Hermann; 1972.

doi:10.1016/j.bbr.2007.11.031

Please cite this article in press as: Will B, et al., Reflections on the use of the concept of plasticity in neurobiology, Behav Brain Res (2008), doi:10.1016/j.bbr.2007.11.008