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Biological organisation as closure of constraints

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HIGHLIGHTS

- Biological systems realize both organisational closure and thermodynamic openness.
- Organisational closure is a closure of constraints.
- Constraints exhibit conservation (symmetry) at the relevant time scales.
- Closure draws the boundaries between interacting biological systems.
- Closure is a principle of biological stabilisation.

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ABSTRACT

We propose a conceptual and formal characterisation of biological organisation as a closure of constraints. We first establish a distinction between two causal regimes at work in biological systems: processes, which refer to the whole set of changes occurring in non-equilibrium open thermodynamic conditions; and constraints, those entities which, while acting upon the processes, exhibit some form of conservation (symmetry) at the relevant time scales. We then argue that, in biological systems, constraints realise closure, i.e. mutual dependence such that they both depend on and contribute to maintaining each other. With this characterisation in hand, we discuss how organisational closure can provide an operational tool for marking the boundaries between interacting biological systems. We conclude by focusing on the original conception of the relationship between stability and variation which emerges from this framework.

1. Introduction

In theoretical biology, an enduring tradition has placed heavy emphasis on the idea that biological systems realise what could be referred to as “self-determination”. That is, in very general terms, the capacity of a system's constitutive organisation to contribute to the determination and maintenance of its own conditions of existence through the effects of its activity (see also Mossio and Bich, 2014, for more details). Usually (Weber and Varela, 2002), the origin of this tradition is traced back to the characterisation of biological systems as “self-organising”, as Kant proposed in his *Critique of Judgement* (Kant, 1790). Over the last two centuries a number of authors, more or less explicitly inspired by Kant, have been proposing conceptual and theoretical accounts aimed at understanding the principles underlying biological self-determination.

Following Claude Bernard's seminal work (Bernard, 1865, 1878), during the first half of the 20th century self-determination was initially investigated as *homeostasis* (Cannon, 1929) and mathematically expressed in terms of feedback loops by first-order Cybernetics (Wiener, 1948; Ashby et al., 1956). Homeostasis, however, is a general systemic capacity, exhibited by both biological organisms and some artefacts (as the classical example of the thermostat shows). Accordingly, recent contributions have aimed at going beyond the limitations of the notion of homeostasis in order to better capture the *specificities* of biological self-determination. In this respect, relevant contributions were made during the 1960s by embryology (Weiss, 1968). Waddington, in particular, suggested that in the biological domain homeostasis should be interpreted as *homeorhesis* (stability of dynamics rather than stability of states), insofar as in biological systems what “is being held constant is not a single parameter but is a time-extended course of change, that is to say, a trajectory” (Waddington, 1968, p. 12).

A crucial step in the theoretical elaboration of biological self-determination is the account put forward by Piaget (1967), whose

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core idea is to integrate in a single coherent picture two inherent dimensions of biological systems: thermodynamic openness and organisational closure. On one hand, biological systems are, as von Bertalanffy (1949) had already emphasised, thermodynamically open (dissipative) systems, traversed by a continuous flow of matter and energy; yet on the other hand, they realise *closure*, which refers to mutual dependence between a set of constituents which could not exist in isolation, and which maintain each other through their interactions. In Piaget's view, biological self-determination is specifically related to closure which, through the association between division of labour and mutual dependence that it implies, captures a fundamental aspect of the idea of "organisation" as such. In a word, biological systems self-determine because they are organised, and they are organised because they realise closure.

The centrality of organisational closure and its connection to organisation, as well as its distinction from (and complementarity to) thermodynamic openness, have become givens in most subsequent accounts of biological self-determination (Letelier et al., 2011). One of the best-known formulations is the one centred on the concept of *autopoiesis* (Varela et al., 1974; Varela, 1979) which, among other aspects, places heavy emphasis on the generative dimension of closure: biological systems self-determine in the specific sense that they "make themselves" (auto-poiein). Precisely because of their dissipative nature, the components of biological systems are maintained only insofar as they maintain and stabilise not just some internal states or trajectories, but the *autopoietic system itself*, as an organised unity.[3]

In spite of its qualities, however, the concept of autopoiesis (and related computational models, see McMullin, 2004) suffers in our view from a central weakness, insofar as it does not provide a sufficiently explicit characterisation of closure. Biological systems are at the same time both thermodynamically open and organisationally closed, but no details are given regarding how the two dimensions are interrelated, how closure is actually realised, what constituents are involved, and at what level of description. In the absence of such specifications, as already highlighted by previous critical interpretations of the autopoietic theory (see in particular Fleischaker, 1988; Ruiz-Mirazo and Moreno, 2004), it remains unclear in what precise sense closure would constitute a causal regime which distinctively characterises biological organisation and its capacity for self-determination. In particular, closure might be generically understood as a causal regime involving some sort of circularity, fundamentally no different from the numerous examples of circular chains of transformations, that frequently occur in the natural (although not necessarily biological) world. Is there some *principled* difference between biological closure and all other kinds of causal cycles?

A concerted attempt to answer this question has been made by Robert Rosen, who has explicitly claimed that a sound understanding of biological organisation should account for the distinction between closure and openness *in terms of a distinction between two causal regimes*. In Life Itself (Rosen, 1991), Rosen's account of closure is based on a reinterpretation of the Aristotelian categories of causality and, in particular, on the distinction between efficient cause and material cause. Let us consider an abstract mapping f between the sets A and B, so that $f: A \twoheadrightarrow B$. If we interpret the mapping in causal terms, and look for the causes of B, Rosen claims (and develops a detailed conceptual and formal justification, that we will not repeat here) that A is the material cause of B, while f is the efficient cause. By relying on this distinction, Rosen's central thesis is that "a material system is an organism [a living system] if, and only if, it is closed to efficient causation" (Rosen, 1991, p. 244). In turn, a natural system is closed to efficient causation if, and only if, all components having the status of efficient causes within the system are materially produced by the system itself.

An analysis of Rosen's account in all its richness would by far exceed the scope and limits of this paper. Let us just mention that, recently, several studies have made substantial contributions to reexamining, interpreting and developing Rosen's ideas (Piedrafita et al., 2010; Letelier et al., 2003, 2006; Wolkenhauer and Hofmeyr, 2007). What matters for our present purposes is that closure, and therefore self-determination, is located at the level of efficient causes: what constitutes the organisation is the set of efficient causes subject to closure, and its maintenance (and stability) is the maintenance of the closed network of efficient causes.

In this paper, we develop an account of organisational closure which is directly inspired by and, we believe, consistent with the theoretical framework established by Rosen. Nevertheless, although Rosen made clear progress in the understanding of biological organisation with respect to previous formulations, we do not believe that his characterisation of closure is fully satisfactory. The main limitation is that it remains too abstract, and therefore hardly applicable as a guiding principle for biological theorising, modelling and experimentation. Closure is defined by Rosen as involving efficient causes but, without additional specifications, it might be difficult to identify efficient causes in the system: what entities actually play the role of efficient causes in a biological system? How should the relevant level of causation at which self-determination occurs be characterised?

To deal with this issue, decisive insights have emerged from more recent literature which emphasise, in line with Piaget's initial view, the "thermodynamic grounding" of biological systems (Bickhard, 2000; Christensen and Hooker, 2000; Moreno and Ruiz-Mirazo, 1999). In particular, Kauffman (2002) suggested retrieving the classic idea of "work cycle" (in the sense of the Carnot engine), and applying it within the context of self-maintaining biochemical reactions. Based on Atkins's ideas about work, conceived as a "constrained release of energy" (Atkins, 1984), Kauffman argues that a circular relationship between work and constraints must be established in a system in order to achieve self-determination, in the form of a "work–constraint (W–C) cycle". When a (W–C) cycle is realised, constraints which apply to the system are not independently given (as in the Carnot engine) but rather are produced and maintained by the system itself. Hence, the system needs to use the work generated by the constraints in order to generate those very constraints, by establishing a mutual relationship, i.e. a cycle, between constraints and work.

In a fundamental sense, the account of closure that we provide in this paper lies at the intersection between Rosen's and Kauffman's proposals. In specific terms, our central thesis is that closure should be understood as *closure of constraints*, a regime of causation which is at the same time distinct from – and related to – the underlying causal regime of thermodynamic openness. It is important to underline that our purpose is by no means to provide a *model* of closure which would adequately capture the complexity of real biological systems. Rather, we conceive this paper as a contribution to characterise in precise terms some of the general features of closure, which might subsequently be used to develop models of biological organisation. Our aim, in other words, is to explicitly state what makes closure a distinctive causal regime, characteristically at work in biological systems.[4]

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[3] The generative nature of closure seems to adequately encompass one of the main differences between biological systems on one hand, and artefacts and other categories of natural systems on the other hand. Intuitively, it seems correct that those situations in which the existence of the parts depends on that of the whole system are indeed characteristic of biological organisms. The parts of a rock do not dissolve if the whole is broken into pieces, just as the components of a computer do not disintegrate if the whole machine is disassembled.

[4] The question of whether or not closure is a necessary and sufficient condition for characterising biological systems is not discussed here. Consequently, we do not

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