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How prokaryotes 'encode' their environment: Systemic tools for organizing the information flow

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ABSTRACT

An important issue related to code biology concerns the cell's informational relationships with the environment. As an open self-producing system, a great variety of inputs and outputs are necessary for the living cell, not only consisting of matter and energy but also involving information flows. The analysis here of the simplest cells will involve two basic aspects. On the one side, the molecular apparatuses of the prokaryotic signaling system, with all its variety of environmental signals and component pathways (which have been called 1–2-3 Component Systems), including the role of a few second messengers which have been pointed out in bacteria too. And in the other side, the gene transcription system as depending not only on signaling inputs but also on a diversity of factors. Amidst the continuum of energy, matter, and information flows, there seems to be evidence for signaling codes, mostly established around the arrangement of life-cycle stages, in large metabolic changes, or in the relationships with conspecifics (quorum sensing) and within microbial ecosystems. Additionally, and considering the complexity growth of signaling systems from prokaryotes to eukaryotes, four avenues or "roots" for the advancement of such complexity would come out. A comparative will be established in between the signaling strategies and organization of both kinds of cellular systems. Finally, a new characterization of "informational architectures" will be proposed in order to explain the coding spectrum of both prokaryotic and eukaryotic signaling systems. Among other evolutionary aspects, cellular strategies for the construction of novel functional codes via the intermixing of informational architectures could be related to the persistence of retro-elements with obvious viral ancestry.

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1. Introduction: stating the "signaling code" problem

The essential aim of the present work is to re-examine critically and constructively the new panorama on cellular communication –actually, a smallish part of it, as our essential focus will be on characterizing the prokaryotic solutions. We will look for an informationally rich interpretation addressed from a code biology perspective, including the exploration of some new computational and evolutionary aspects.

Does the prokaryote organize signaling codes? Of what kind? Even the simplest cells are open systems regarding both energy flows and information flows; but it is not clear that thermodynamics adequately distinguishes between them. Although the way *metabolic inputs* are processed differs radically from the way *signaling inputs* are processed, that difference rarely appears in the literature. The former are slowly depleted of their *enthalpy* or internal energy in a long series of metabolic reactions, step by step within a vastly interconnected metabolic network, while the latter are rapidly analyzed once they have transiently landed upon some receptor and their respective *information* is subsequently propagated throughout a lean signaling system, with very little energy changes involved.

This singular difference about the hands-off processing that signaling pathways perform with respect to metabolic pathways was elegantly commented by Gerhart (1999, p. 228):

> *"As information transfer pathways, these signaling pathways are basically different from metabolic pathways, even though both are called 'pathways'. In a biosynthetic metabolic pathway, a carbon compound passes through a series of enzymatic steps, with appropriate energy inputs, undergoing modifications until it emerges as an end product ready for incorporation into a macromolecule or complex lipid. But in a signal transduction pathway, carbon atoms and energy are not passed along. Only an impulse is relayed by way of successive reversible changes of state of switch-like intermedi-*

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ates. At the end of the pathway, the transduced signal activates or inhibits some target protein [. . .] the most frequent target of signaling is transcription, and some pathways affect only transcription."

Both the energy flow and the information flow are densely intertwined in the regular functioning of the cellular system. They have been schematically represented in Fig. 1. The energy flow, pioneeringly described by Morowitz (1968), actually comprises interrelated ingoing and outgoing flows of matter, energy, and entropy–generically represented by the two blue arrows in the right part of Fig. 1. Apart from compounds containing the basic elements of life (C, H, N, O, S, and P), many other metallic bioelements (such as Fe, Ni, Mo, Mn, Zn, Cu, Co, etc.), and quite many potential nutrients and metabolic waste products are actually involved in this general "energy flow". As we will see, all of them have to be previously sensed before being internalized–so to speak, the information flow precedes, anticipates, and makes possible the handling of the energy flow. Complementarily to charting these material flows, the energy/entropy balances may be used to ascertain the local/global biophysical backgrounds and the organizational constrains of the cell in its environment (Haynie, 2001).

Concerning the information flow, we must initially distinguish between the *inner information flow* related to the self-construction process, and the *external information flow*, which is characterized by a series of ingoing and outgoing signals. The former is characterized by the now classical Central Dogma of Molecular Biology "DNA makes RNA makes proteins" (Crick, 1956). They are represented in Fig. 1. As we will discuss later, the prokaryotic signaling solutions also known generically as "component systems" are in charge of managing this external information flow (or signaling flow) which, not to forget, implies both ingoing and outgoing signals, the latter strikingly absent from the signaling literature. It is significant that understanding the signaling system of bacteria (i.e., the organization of its "information flow") has been delayed more than 30 years regarding the knowledge of its metabolism (i.e., the "energy flow"). Even more, regarding the former system, attention was only devoted to modeling the very complex, and rather exceptional, chemotactic system of motile bacteria, like *E. coli,* versus the predominant and very simple one component systems that will be described below (Koshland et al., 1982; Galperin et al., 2001; Ulrich et al., 2005; Marijuán et al., 2010).

Actually, the cellular self-construction process and the advancement of the life cycle imply the organizational congruence among all the above flows. Guiding signals from the interior and the exterior of the system are needed to adequately fine-tune protein and enzyme populations to the ongoing circumstances, so as to make possible the advancement and completion of a life cycle in a variety of environments. Arguably, the final relationship with the cycle is what provides its 'meaning' to any inner or outer signal –which is nowadays efficiently describable in molecular terms. It may be stated that the energy flow fuels the advancement of the life cycle, while the information flow orientates the life-cycle decisions.

In this paper our main question is whether the cellular management of the information flow implies the organization of signaling codes—or not. In order to respond, first we are going to examine in depth the different components involved in the prokaryotic signaling system, concretely those of *E. coli K-12*, and their respective characteristics (in Section 2). As we will see, the three main options imply very different information processing capabilities and metabolic/synthetic costs (Marijuán et al., 2010). Thereafter, in Section 3, we will consider the integrated functioning of the prokaryotic signaling system coupled with the transcriptional apparatus. Additionally, in Section 4 we will consider the complexity growth of signaling systems from prokaryotes to eukaryotes, distinguishing four avenues or "roots" for the advancement of signaling complexity—a comparative will be established between the signaling strategies of both kinds of cellular systems. It is in this juncture where we shall ponder on the plausibility of signaling codes (Section 5). We will argue that amidst the continuum of energy, matter, and information flows there seems to be evidence for different kinds of coding relationships, mostly established around the arrangement of life-cycle stages. Arguably, most of these codes cannot be considered as strict codes (according to Barbieri, 2016), rather they would form a sort of 'representational mosaic.' However, with the emergence of second messengers in bacteria, as well as with the appearance of eukaryotic signaling systems and complex cytoskeletons, a new orientation is established towards more global, quasi-formal representations of the most strategic inner/outer environmental signals (Tozzi et al., 2017).

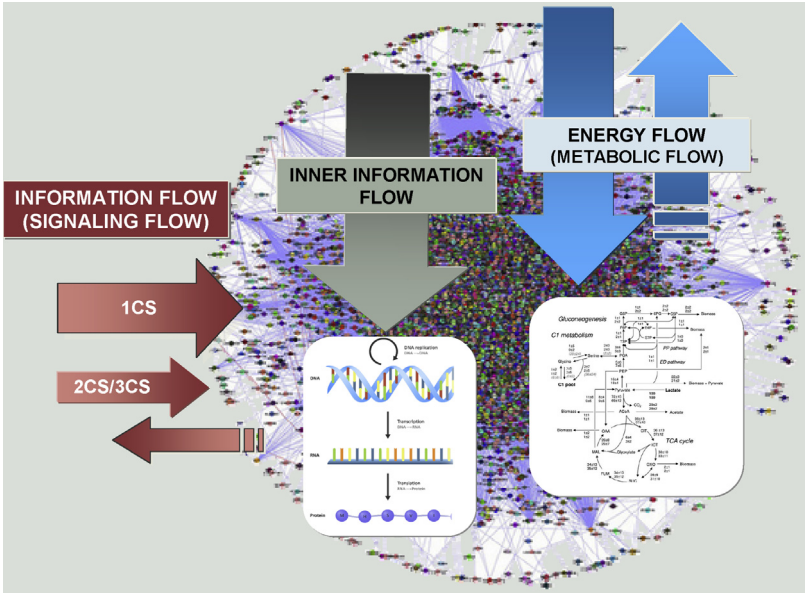

Fig. 1. Energy flows and information flows are represented as the basic exchanges of the living cell with its inner/outer environment. They are shown respectively as blue arrows in the right part (energy flow), grey ones in the center (inner information flow), and red arrows in the left part (external information flow or signaling flow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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