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Multicellular agency: an organizational view

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Abstract We argue that the transition from unicellular to multicellular (MC) systems raises important conceptual challenges for understanding agency. We compare several MC systems (from bacterial swarms to colonies and plants, and to lower metazoans) displaying different forms of collective behavior, and we analyze whether these actions can be considered organismically integrated and attributable to the whole. We distinguish between a 'constitutive' and an 'interactive' dimension of organizational complexity, and we argue that MC agency requires a radical entanglement between the related processes which we call "the constitutive-interactive closure principle". We explain in detail that this is not possible without a regulatory center functionally integrating the two dimensions, and we also argue that, in turn, this type of regulation would not be possible without a special type of organization between the cells required for the development and maintenance of systems capable of integrated behavior.

Keywords Agency · Organization · Constitutive and interactive dimension · Multicellularity · Regulatory center · Behavior · Development · Epithelium · Closure

Introduction

Multicellularity has provided a great potential for the evolution of agents with organizations that can support various forms of complex *actions* resulting thus in the

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manifestation of versatile behaviors within their environments. But, what is the organizational basis for multicellular (MC) agency? If any MC system is endowed with the capacity to react adaptively in its environment, what is the specificity of MC agency? What is the origin of MC agency and what is its role in those evolutionary paths leading towards the increase of behavioral complexity in MC organisms?

Let us briefly advance in broad terms that by agency we mean here any type of functional modification of the environment exerted by an organism.[1] Motility-based actions are of course the most significant, but there are other forms of agency. For example, the secretion of a chemical substance by an organism in order to repel or neutralize the detected source of aggression is a form of agency regardless of whether the organism is motile. However, motility allows a much richer modulation of the adaptive interactive processes, and therefore could provide a great potentiality for plasticity and complexification of agency, as it is shown in the evolution of metazoans. Roughly speaking, motility is the capacity of a system to exert, by its own means, directional and fast movements of at least a part of its body within the environment. As Burge (2009) has remarked, tactic orientations, namely, actively taking or moving into a position in relation to the surroundings and with respect to stimulation from the environment is a characteristic instance of agency. *Motility-based interaction* (*i.e., behavior*) embeds the agent in an active sensorimotor coupling with the environment. It opens up the environment to the agent, which is now able to dynamically alter the set of environmental conditions it can detect, and accordingly, to act.[2] It is thus through motility that an agent can significantly enlarge its adaptivity.

Although a minimal form of behavioral agency can be attributed already in bacterial chemotaxis, it is in the adaptive strategies characterized (to a high degree if not entirely by motility) of animals where we find those forms of behavior that are usually considered as *full-fledged* agency (Burge 2009). Highly evolved extant animals—taken as the paradigmatic agents—demonstrate an extremely diversified set of actions such as running, swimming, flying, predating, fleeing, digging, crawling, climbing, jumping, hitting, eating, mating, navigating, nesting, parenting, protecting, communicating, constructing, building, etc. Through such activities, MC agents interact adaptively with their environments in quite plastic ways, i.e., they are able to modify in short time their movements so as to act in ways that will, above all, contribute to the maintenance of their internal organization with respect to different environmental conditions.

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[1] Accordingly, functions such as digestion, sweating, freezing in front of headlights, schreck reactions and helpless writhing, coughing or sneezing, etc., do not count as actions, since they do not provide a modification of the environment that could be functional for the system.

[2] Oriented growth and bending movements of plants and sessile animals are not considered as actively directional movements (see next section; and also Burge 2009, pp. 257–259 for a relevant discussion). A genuinely motile agent does not have to stand and passively wait to accept whatever the environment will bring at it, but on the contrary, it may move and thus take the initiative in exploiting the environmental resources.

However, practically all forms of MC systems[3] deploy a kind of collectively coordinated action in nature. Most of these MC systems comprise a number of different cell types and are characterized by specialized cell-to-cell interactions, thereby exhibiting some degree of functional integration. In many cases, this integration leads to a significantly increased capacity for displaying functional forms of collective motility and related actions (i.e., combined defense and attack strategies that enable the MC systems to escape predation, increase their efficiency for food consumption, etc. (see e.g., Shapiro 1998; Kaiser 2001; Sumpter 2010).[4] Through such interactions MC systems are able—under various environmental conditions—to maintain their collective organization (often just temporarily), to occupy new niches, and to increase the possibility of survival of the constituting units and of the associations themselves. So at first glance, all these systems seem to *act as adaptive MC agents*.

Now, it is unclear whether in all these cases the MC system constitutes a true integrated MC agent that interacts adaptively as a whole, or on the contrary, a collection of unicellular agents that are just coming together in a cohesive MC organization to improve their overall fitness and adaptation. Whereas in unicellular systems agency appears as a result ascribed to the whole organism, it is not clear whether in cases such as the swarming of a bacterial biofilm, or in the swimming of green algae, in the fast and multi-directional movements of a flock of birds or a school of fishes, in the swimming and hunting of composite MC metazoans (like the Portuguese Man-of-war), or in the rapid closing of the leaves in carnivorous plants, the actions derive from an integrated constitutive organization (Burge 2009). In other words, to what extent is the action displayed by a MC system ultimately the expression of a mere coordination of a group of unicellular agents, or is it rather something that expresses and represents the identity of the MC entity as an integrated whole? In particular, due to the fact that the parts comprising a MC system (unicellular entities) are agents themselves, the problem of *which is the subject (or the 'self') that acts* practically begins at the MC level, and consequently a central issuance attributable to the whole MC system cannot be guaranteed. To sum up, as we shall discuss and argue in detail through this paper, the transition from unicellular to MC systems raises a conceptual challenge for understanding and explaining agency, and for demarcating it from other (often morphologically coherent) patterns of activity. Our goal here is therefore to understand the organizational framework and requirements for MC agency. This research might be in turn important not only for understanding better the roots of the different degree of complexity that certain evolutionary branches have displayed, but also for understanding certain fundamental principles of cognitive processes, like the

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[3] Over the course of the history of life, cells have assembled into groups, bringing forth several types of relatively stable MC associations: biofilms, filaments, colonies, various types of aggregations, and full-fledged MC organisms.

[4] There is also a significant increase in size that these MC communities achieve, which results in the aggregative/collective effects of several unicellular actions (e.g., breaking down of large food sources by the collective excretion of enough hydrolytic enzymes, resistance to chemical substances—e.g., penicillin-resistant biofilms, etc.). We don't consider these 'passive' effects of multicellularity and their implications as pertaining to agency.

meaning of a central self or the debate about the reach of the distributed architecture for explaining the evolution of cognition.

This paper is structured as follows. In "The challenge of multicellular agency" we address the concept of biological agency, we introduce the 'constitutive-interactive closure principle', and we present the conceptual challenges for understanding MC agency. In "Analysis of the organizational support for the motility of four MC systems" section we compare the type and degree of coordination of the collective action between different MC systems, and we discuss the implications for the nature of their motility, while in "MC (behavioral) agency requires a metabolically decoupled regulatory subsystem" section we assess the operational characteristics of the sub-system necessary for functionally coherent motility-based interactions integrated at the global level of an MC system. In "The 'constitutive-interactive closure principle' explains integrated MC agency" section we further elaborate and argue with respect to the intertwining of this sub-system—operating as a center—with both the constitutive organization of the MC system and with the behavioral processes it regulates. We conclude in "Concluding remarks" section by discussing the implications of MC agency with respect to organismality.

The challenge of multicellular agency

In recent years an increasing number of researchers are focusing on the concept of agency within the biological domain, outside the realm of high-level human cognitive phenomena. The common ground is that the notion of agency should be significantly simplified. In this respect, these authors have tried to understand and explain the nature of agency in biology by adopting a minimalist perspective, through which they attempt to analyze which features would permit to infer that a biological system should be considered an agent (see e.g., Frankfurt 1978; Dretske 1988; Varela et al. 1991; Millikan 1993; Juarrero 1999; Emmeche 2000; Kauffman 2000; Christensen and Hooker 2002; Bickhard 2004; Di Paolo 2005; Moreno and Etxeberria 2005; Burge 2009; Barandiaran and Moreno 2008a; Barandiaran et al. 2009; Skewes and Hooker 2009; Arnellos et al. 2010; Shani 2012).

Despite some differences, in all the aforementioned works there is a fundamental agreement on two points: (1) a system is an agent only if it can induce functional changes in its environment (namely, changes produced in relation to the environment, and which will give a return on the agent's 'investment' by contributing to its self-maintenance)[5]; and that this requires (2) an organization able to support the continuous performance of *functional* interactions *at the level of the whole organism* with the environment, on the basis of which (interactions) the agential organization is recursively maintained. Hence, in order to tell that a system is an agent, this system should be "capable of engaging in some *modulations* of the coupling" with its environment (Barandiaran et al. 2009, p. 4), or to "*actively*

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[5] This requirement casts aside cases such as digestion, blood circulation, heart beating, tanning, sweating, etc., which are the result of endogenously driven processes that are functional for the system but they don't result in the functional changing of the environment.

regulate its own processes (Skewes and Hooker 2009, p. 286), or to be able to exert actions that are a "*whole-organismic affair*"; i.e., actions that are "imputable to the whole organism" and not "merely to subsystems" (Burge 2009, p. 262). And, it is in this context that one could argue, as Frankfurt (1978) also did, that the interaction must be "guided" if it is to be considered an action.

From this perspective, we begin by suggesting that agency implies a fundamental distinction between two concepts that we use in this paper: constitutive processes (CP) and interactive processes (IP). By the former we mean the set of processes by which a system gets constituted (development) and maintained (metabolism), while the latter refers to specific actions triggered by the system in the environment according to detected environmental conditions so as to modify these conditions for the system's benefit (Moreno et al. 2008). Besides, the functionality of interactive processes relies on the specific viability of a detection-action loop (for example, in motility the viability of the sensorimotor loops is strongly affected by size-time constraints that are significantly independent of the metabolic-constitutive dynamics (Barandiaran and Moreno 2008a).[6] And yet, in the concept of agency we find a *functional* and *reciprocal* relationship between these two dimensions: the '*constitutive dimension'* (CD), which pertains to both the construction and maintenance of the agent, is ultimately dependent on the '*interactive dimension'* (ID) i.e., the interactions that the agent deploys in the environment (see also Ruiz-Mirazo and Moreno (2011), and, Arnellos and Moreno (2015) for a discussion on the conceptual distinction between the two dimensions of a biological organization). And in turn, the latter is governed/coordinated by the former. We call this reciprocal causal relation the *constitutive-interactive closure principle.*[7]

To clarify the importance of this relation between constitutive and interactive processes for understanding the concept of agency, let us briefly reflect on how plants and animals adapt to their environment. Plants adapt to heterogeneous environments by modifying shoot and root architecture to allow optimal nutrient, water and light capture, and they continuously rebalance the allocation of resources between roots and shoots in order to favor the growth of their parts placed in the resource-rich positions (Hutchings and de Kroon 1994). Considering the sectorial nature of plants and their plasticity, plants adapt to unpredictable environments by changing their functional units through vascular re-orientation during growth and development. And they do so on the basis of the competition between shoots for changing vascular contacts with the roots (Sachs et al. 1993; but see also Oborny 2003, and Leyser 2011). As argued and explained in detail by Sachs et al. (1993), the control of vascular differentiation is sectorial; the development of a given shoot enhances the formation of only those vascular tissues that connect it with the roots. Contacts in the immediate neighborhood, ones that have other orientations and

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[6] Even in very primitive forms of sensorimotor coordination, such as in *E.coli* (and many other bacterial) chemotaxis, the Two Components Signal Transduction system, which acts as a memory and inner connection between sensors and effectors, operates in a different timescale than core metabolic processes, to the point that such kind of taxes are considered second-order processes with respect to metabolism (van Duijn et al. 2006).

[7] See Moreno and Mossio (2015) for an extended discussion on the idea of closure in biology.

connect with other shoots, are not enhanced.[8] In this respect, the growth of individual shoot branches is not only and directly determined by their local light conditions or photosynthetic production, but it is also determined by their relative competitive ability for water and nutrient transport from the root system. Hence, plants, which are intuitively not considered as full-fledged agents—though there are exceptions (e.g., Trewavas 2005; Garzón and Keijzer 2011), do not show a clear distinction between constitutive and interactive processes: in plants it is the very development and growth—viz., the constitutive processes—that adapt to environmental changes. In contrast, animals have a specific capacity for triggering fast external actions in order to adapt to environmental changes. These actions are much more rapid than growth and development, and their operation is decoupled from essential constitutive processes. This is why we shall focus our analysis of MC agency in those forms of environmental interaction based on motility.

As we mentioned, motile agency is strongly affected by size-time constraints. Hence, the main problem MC systems had to solve is that as their body size increased, it also became increasingly difficult for the basic metabolic organization to efficiently support the kind of the fast and versatile sensorimotor coordination needed for motility-based adaptivity (Moreno and Lasa 2003). Biological systems demonstrate different solutions to this problem. In all cases actions exhibit certain types of functional coherence, i.e., various degrees and types of collective coordination, all of which nevertheless functionally contribute to the maintenance of the MC system. Of course, the degrees and types of the underlying functional differentiation and integration in different MC systems and the types and forms of their motility-based interactions vary significantly. On the one hand, there are diverse strategies through which the actions of various MC systems are supported by biochemically-based mechanisms that essentially operate coupled to the intercellular metabolism. Most of these cases are various forms of prokaryotic and eukaryotic aggregations that are usually constituted by a low number of cell types. They are characterized by a limited degree of functional differentiation that results mostly in relatively slow actions (with some exceptions, e.g., carnivorous plants), and generally, in a poor interactive capacity (viz., a reduced set of functional interactions achieved by the MC system), such that the MC system does not show any new movements compared to their unicellular members.

On the other hand, metazoans are constituted by many different cell types supporting a very different form of organization (and of the respective body plans), which shows the capacity for versatile and complex motility. Specifically, animals show the capacity for functional interaction with the environment based on a kind of motility, which is decoupled from morphological growth. This allows a (reversible) gain of velocity by the body (or part of it) expressed in various combinations and with a high degree of plasticity (in a time span relevant for the maintenance of the body but without fatally disrupting the underlying intercellular metabolism). As a result, all animal species (with the exception of placozoa and porifera) can interact with their environments through a wide range of combinations of different motility.

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[8] For instance, the influence of developing leaves extends to great distances along the axis of the plant, while it is severely restricted in other orientations.

This apparent *richness* (in terms of plasticity and velocity) of MC movements, which are usually understood as *behaviors*, is characterized by the high degree of functional complexity exhibited by the CD and of the relevant diversification expressed at the ID.[9]

Given all these different forms of MC motility, it is hard to find a common or unique conceptual ground to explain their agential phenomenology. As we pointed out before, above all relevant difficulties, the main challenge comes from the problematic nature of the concept of MC agency due to the fact that the parts comprising a MC system (unicellular entities) are agents themselves; hence, it is not easy to clearly identify, demarcate, and define which is the *source of MC agency capable of integrated actions.*[10]

So, considering that MC systems exhibit various degrees and types of functional differentiation and integration, our goal is *to clearly identify the type of functional integration between the various differentiated sub-systems and parts that will render the MC organization capable of deploying complex and integrated actions.* And considering also that in MC organizations several different types of cells are integrated in body plans of various types and sizes, and given the fact that a bigger and more functionally differentiated body plan is not necessarily indicative of richer interactions, then we will also analyze which type of development is capable of producing the constitutive organization necessary for complex and integrated actions in MC systems.

This analysis will help us to identify the conditions under which there is a functional and reciprocal relation between the complex integrated actions and the constitutive organization that supports them, and to suggest the organizational requirements, characteristics, and properties of MC agency accordingly.

Analysis of the organizational support for the motility of four MC systems

We begin our investigation by analyzing four different MC systems—the MC prokaryotic *Myxococus xanthus,* the eukaryotic MC green algae *Volvox carteri, the Dionaea* plant*, and the* metazoan *jellyfish,* all of them demonstrating different types of motility. In each of these cases, we will explain the MC organization supporting the related behavior, and whether (and if yes, how) it is capable of producing complex and integrated actions. We will do this by studying the way these MC systems ensure and coordinate the collective participation of their constitutive sub-systems and parts in their actions, as well as by examining the operational (i.e.,

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[9] An interactive process can be more or less complex according to the number of functional constraints required for the guidance of a given action. For example, a (successful) execution and guidance of a fast escaping swimming behavior of a fish in an irregular tridimensional marine environment (e.g., in a submarine cave) requires a much greater number of functional constraints compared to what is needed for the rigid movement of closing its leaves by a Dionaea plant in order to trap an insect.

[10] We will consider an action as *integrated* if its issuance is attributable to the whole MC system (instead of only to a part of it) and if its effects contribute to the production and maintenance of the whole MC constitutive organization (instead of only to one aspect of it). This definition will be explained and developed throughout this article, especially in "The 'constitutive-interactive closure principle' explains integrated MC agency" section.

energetic and metabolic) relation between these actions and the underlying constitutive organizations.

The organization of motility in communities of *Myxococcus xanthus*

Myxococcus xanthus is a Gram-negative common soil bacterium with a facultative multicellular phase that comprises around 100.000 cells.[11] Intercellular coordination results in a collective form of motility, which provides the MC system with the ability to engage in ‘wolf-pack’-like hunting and feeding (Berleman and Kirby 2009).

When cells aggregate into a biofilm they are aligned together through the adherence of type IV pilus-mediated social motility system (the S-engine) to fibrils (extracellular matrix polysaccharide) on nearby cells (Mauriello and Zusman 2007). The S-engine uses the pili located at the leading pole to pull the myxobacterium along, while the A-engine (used for independent sliding along a surface by pulling and pushing) pushes it by secreting slime ribbons at the tail. The MC system moves forward for almost eight minutes before it starts gliding to the opposite direction. A variation of chemotaxis based on chemosensory systems is the most probable way used by myxobacteria in order to aggregate towards a prey colony. As more myxobacteria will tend to aggregate, the swarms will often set up rhythmic waves (rippling), which pulse through the entire MC system. Rippling occurs for several days during predation, and it is confined only within the area originally covered by the prey MC system (Berleman et al. 2006). During rippling, lysis takes place and *M. xanthus* cells collectively degrade other microbial cells in order to feed.

These coordinated movements allow the cells to hunt more efficiently, hence to grow better and uniformly under nutrient-rich conditions, and to maximize their survival under starvation. In this way, cells in the MC system adapt to their environment in a better way than they can do in unicellular conditions.

The organization of motility in *Volvox carteri*

Volvox carteri is a MC alga that lives in a variety of freshwater habitats, forming spheres of up to 50,000 eukaryotic cells. In its mature state it normally consists of almost 2000 biflagellate somatic cells engaging in phototaxis, and in the biosynthesis of an extracellular matrix (ECM) and 16 germ cells, which are non-motile but can grow through photosynthesis and reproduce[12] (Kirk 2005).

Phototactic swimming of the MC system requires coordinated beating of the flagella between cells and a proper orientation of cells with respect to each other (Ueki et al. 2010). Three main structural and organizational aspects differentiate *V.*

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[11] *M. xanthus* cells form structured biofilms with motility-mediated expansion (formation of tentacle-like packs cell groups and synchronized rippling waves of oscillating cells) when other microbial nutrients are available in the environment, and massive spore-filled aggregates that rise upwards from the substratum to form fruiting bodies, mainly when exposed to low or no nutrients.

[12] Somatic cells are terminally differentiated, they have an eyespot—a primitive visual system used like radar to scan the environment for light sources—and they do not divide. Hence, contrary to germ cells, they have flagella that continuously beat and provide the MC system with a phototactic motility.

carteri from its unicellular ancestor (*Chlamydomonas reinhardtii*) so that the MC alga can coordinate the participation of the somatic cells in its phototactic swimming. First, during its development the spheroid expands its volume (at least 10000-fold) by deposition of large quantities of ECM that come to constitute more than 99 % of the volume of a mature adult spheroid. This huge ECM plays the role of a sharp and discrete boundary layer over the surface of the spheroid, which contains compartments surrounding individual cells. The second aspect concerns the formation of spheroid's polarity and of anterior-posterior asymmetry. The somatic cells are endowed with eyespots, and are located such that the largest and most light-sensitive ones occupy the anterior part of the spheroid. The third aspect is the re-orientation of the flagella in each cell. This is accomplished by a rotation of the basal bodies of the somatic cells, resulting in the parallel beating of the flagella in each cell. The resulting distinctive morphological polarity is characterized by a stronger light sensitivity for the anterior pole, a much heavier posterior, and the parallel beating of the flagella toward the posterior. This suffices for efficient phototactic coordination. Accordingly, the MC spheroid can move relatively forward up to 2-3 meters per hour (Ueki et al. 2010).

The coordination of flagella beating between the somatic cells provides *V. carteri* with the capacity for movement (swimming), and consequently, with the ability to better use and exploit the nutritious resources in euphotic conditions (Kaiser 2001).

The organization of motility in Dionaea plants[13]

Venus flytrap (also known as *Dionaea muscipula*) is a plant formed by billions of eukaryotic cells. These cells form a relatively large (at least, compared to the two other cases) MC entity through a process of development, in which they differentiate into several cell types constituting tissues and organs with specific functions. Its characteristic leaves end in two main lobes. The lobes excrete nectar, thereby attracting many insects and small animals that are then trapped within the lobes, which close in about one-tenth of a second while prey crawl over them.[14] The trap will then excrete digestive juices to dissolve and absorb the prey (Chamovitz 2012). How does this happen?

Roughly speaking, when plant cells are filled with water, they have a high turgor pressure (due to their rigid cell walls) and they push the lobes open. When they lose water and the turgor pressure decreases, the leaves close. The way this hydraulic spring is loaded and triggered is not clearly understood. According to the most likely and experimentally consistent explanation, the mechanism involves the generation of action potential (Hodick and Sievers 1988), which induces mechanical closing resulting from either acid growth response and wall loosening of the individual outer cells of the lobes (Williams and Bennet 1982), or from a loss of turgor pressure in the upper epidermis (Hill and Findlay 1981). The hydraulic spring

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[13] Besides the well-known case of the Venus flytrap there are other examples of plants capable of fast movement, such as *Mimosa pudica*, the Telegraph plant (*Codariocalyx motorius*), sundews (*Drosera*) with relatively slow movements compared to the other cases, and bladderworts (*Utricularia).*

[14] This way of getting nutrients and energy is an adaptation found in several plants living in soils poor in nutrients (Ellison 2006).

is loaded by energy produced by the electric membrane potential, which is used by the cells to accumulate mineral ions (mainly potassium), which in turn will draw water into the cells via osmosis. This will open the lobes. When one of the several large black hairs of the inside surface of the lobe is touched, an electrical membrane potential (mainly calcium ions) that radiates intercellularly across the lobes and in the midrib between them is activated. This triggers the opening of the gates from which potassium ions and then water flows out of the cells, resulting in the closing of the lobes.[15]

The organization of motility in jellyfish

Jellyfish (jellies or medusas) are free-swimming marine metazoans of the phylum Cnidaria. Despite their diversity, all jellies have the same basic body plan characterized by one body opening (a sac with a central digestive compartment, the gastrovascular cavity), the outer epidermis, and the inner gastrodermis, separated by a layer of jelly-like mesoglea. Inside the bell-like cavity there is a falling elongated body (the manubrium), and several tentacles are extending downward from the rim of the umbrella. Specialized stinging cells (cnidocytes) that contain the nematocyst (which is discharged when a prey touches the tentacles) are located primarily at the tips of the tentacles, and secondarily in gastrodermis or epidermis.

Through the coordination of the movements of these body parts, jellyfish can swim slowly to feed, and rapidly to avoid predation. They demonstrate maneuverability, and some species have the capacity for efficient orientation, compass navigation, and daily migration. All species can catch prey by means of fast and directed movements of their tentacles and the activation of nematocysts. Some bigger jellyfish (such as box jellies) are agile swimmers that can reach speeds of 1.8 m per second (thousands of times faster than *Volvox*). Let's discuss in some more detail the organization of jellyfish supporting this rich motility.

The collective participation of distant cells in the motility of jellyfish is realized through 'epithelialization' (formation of an epithelium).[16] Epithelial tissue spreads over the whole jellyfish body and can withstand and counteract a wide range of self-generated contraction forces. Thus, the body itself acts as the muscle's antagonist, extending the contracted surface again when activation ceases. Though in jellyfish there are no definitive muscles, the epithelial cells of the gastrodermis (and the epidermis of hydrozoans) have myoepithelial[17] extensions on their basal surfaces. These anatomical structures act as a uniform sheet of conductive tissues and satisfy

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[15] It has been hypothesized and experimentally supported that when a hair is touched there is a threshold of ion buildup, which is stored as an increase in ion concentration for a short time. The touch of a second hair within about twenty seconds will cumulatively trigger the passing of the threshold, thus activating the closing of the leaves (Volkov et al. 2007).

[16] An epithelium is defined as a sheet of polarized cells that are joined by belt-like junctions around their apical margins, and with an extracellular matrix (ECM) being present only apically and basally (the basal lamina). Jellyfish are almost wholly epithelial and the simplest MC animals at the tissue grade of organization (Tyler 2003).

[17] Two types of cells with contractile properties are known across MC animals: true muscle cells and epitheliomuscular cells. All muscular structures described so far in Cnidaria are epitheliomuscular (Burton 2008).

the need for synchronized coordination of distant effectors in the movement of the MC body (Mackie 1970). Epithelial cells are excited by chemical and tactile stimuli, triggering thus a change of electric potential that is propagated symmetrically—though in a spatiotemporally limited way—along the cells (Anderson 1980).

Myoepithelial conduction lacks directional and selectively targeted propagation of impulses—epithelial conduction cannot circumvent an intermediate tissue without activating it, nor can it modulate or regenerate a signal (Keijzer et al. 2013). But this limitation is overcome by a neural network (NN) that coordinates and synchronizes the self-organized contractile activity of the muscle tissues. In general, jellyfish have a rudimentary nervous system (NS), which is composed of distributed nerve nets associated with simple sensory receptors that are distributed radially around the body of the animal (Mackie 1990, 2004; Satterlie 2002).[18]

The effect of this arrangement of the nerve nets permits the generation of action potentials by the rapid communication of a stimulus (through the release of neurotransmitters) from any part of the animal to all parts, over relatively long distances and with a significant degree of modulation, which is not possible in 'simpler' MC systems lacking neurons. By integrating a large set of signals coming from the external and the internal environment the NN achieves fast and plastic actions. In this way, the rudimentary NN of jellyfish permits rapid and plastic communication over longer distances of conducting cells within or connected to the myoepithelium. This allows for both quick responses and enhanced myoepithelial patterning capabilities, whose combination has resulted in functional diversification (swimming, hunting, stinging, eating, etc.).

Comparison of the four cases of MC motility

In each one of these four cases, we see the formation of a cohesive MC organization that displays functional actions at the global level. In all cases, the motility of the MC systems is the result of the collective participation of their cells (and their respective sub-systems), and of the specialized coordination between them, and in turn, it contributes to the maintenance of the whole system. However, as we have seen, the type and degree of coordination of the collective action vary significantly between these MC systems, an aspect with significant implications for the nature of their motility. Indeed, as we shall discuss next, the way jellyfish have organized their actions is characteristically and qualitatively different from the other three cases.

During the swarming phase of myxobacteria, there is no cellular differentiation. Therefore, there can be no specialized sensory and motor functions. All cells have their own, selfsame sensorimotor capacities. Each individual cell exerts motor

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[18] Despite the underlying distributed nature of these nervous systems, some jellyfish present a nerve cell density that is at least six times higher in the head region than in the body column. In certain medusas, the RFamide sensory neurons are more abundant in the manubrium along the bell margin, in the tentacle bulbs, and along the tentacles. For example, *Aglantha digitale*, in addition to their diffuse nerve net, possess an elaborate nerve ring around their central opening (manubrium) and around the oral opening. These characteristics are considered to reflect a considerable degree of centralization (Galliot et al. 2009; Satterlie 2011).

actions on the basis of its own detection of the local chemical environment, which is influenced only by cells to which it is adhered, since each cell can detect the signals produced only by neighbor cells (Kaiser and Warrick 2014). Coordinated swarming movement, then, is the net effect of the self-organization of individual chemotactic movements; the resulting collective coordination is the emergent outcome of many local interactions.

Moreover, the swarming MC bodies cannot manage their own energetic needs and the construction and maintenance of their fruiting bodies at the same time. The constitutive cells depend highly on the environment. When nutrients are exhausted or waste accumulates, these cells will stop moving in a swarm. They continue to be organized collectively, but in a different, almost completely static way, by forming a transient MC structure that supports the spore head (the cells positioned inside the spherical mounds differentiating into spores that wait to be carried to a nutrient-rich environment). In other words, myxobacteria cannot be at the same time motile and participate in the MC structure of the fruiting body. During this process the cells at the top of the stalk tube form a more rigid structure with rings of cells that can form an impermeable barrier, and with the secreted proteins used as food or intercellular signals (Cereijido et al. 2004). However, such an intercellular milieu would gradually degrade. All these aspects result in the inability of the MC system to express a plastically coordinated movement in a time relevant to the biochemical and energetic requirements of its body.

The way motility is organized in *V. carteri* has some characteristic differences from that of myxobacteria, both in the type and degree of coordination of the action. In *Volvox* there is a specialization of sensorial function–stronger light sensitivity for the greater somatic cells, as well as effector function.[19] However, there is no direct transmission of sensed signals of any kind between distant cells and even between those positioned in the immediately adjacent spot in the spheroid, since there is no known direct communication among cells (Ueki et al. 2010). Each individual somatic cell exerts motor actions (i.e., flagellar activity) on the basis of its own detection of the local environment. The sensorimotor coordination in *V. carteri* is structurally supported by the morphological and anatomical constraints introduced during development (the spheroid's polarity and asymmetry combined with the re-orientation of the flagella beating in each cell towards the always heavier posterior). It cannot be changed during the lifetime of the adult spheroid. Thus, the phototactic swimming of *Volvox* (as in *M. xanthus*) is the net effect of the individually organized phototactic swimming of each one of the somatic cells, though in this case the net effect is much more explicit due to their rigid placement in the maternal spheroid. Specifically, in *Volvox*, the absence of local interactions coordinating the somatic cells has been structurally compensated by their constrained placement in the ECM, which enhances their spatio-temporal coordination, thus making phototactic swimming a more immediate and precise action than swarming of *M.*

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[19] The complete germ-soma differentiation in *V. carteri* concerns the separation of somatic and reproductive characteristics that used to be integrated in the unicellular ancestor, and not the development of new structures related to the production and execution of new actions.

xanthus. This coordination of swimming based on structural components spanning the whole MC system provides a globally coordinated but rigid action.

In such conditions, the movement is merely a direct function of the beat frequency of the flagella of individual cells. Unlike groups of myxobacteria, *V. carteri* can move continuously, without interruption for reproduction and development. But it uses the same mechanism to coordinate the exchange of nutrients and metabolites between cells and of waste between cells and environment as for swimming. Due to its spherical body plan and the numerous somatic cells, it achieves molecular transport of nutrients and waste due to the self-generated flows created by collective flagella beating (Solari et al. 2006). The result is a strong dependence between motility and metabolism in the sense that a great part of the latter is dedicated to the former. Consequently, the way *Volvox* is constituted precludes further diversification of the repertoire of movements. As a matter of fact, *V. carteri* can only swim slowly following a phototactically-driven direction, just like Chlamydomonas do.

In Dionaea (as also in all carnivorous or touch-sensitive plants–e.g., *Mimosa pudica*) the movement is limited to a part of the body. Only the leaves are sensitive and motile. Plants exhibit a much higher cellular differentiation than algae and bacterial aggregations (see Bell and Mooers 1997 for a comparison of numerous different species). However, they have no way to produce signals that can act on different levels as integrators of signals produced locally and which are limited to specialized cites (Leyser 2011). This is obvious also in Dionaea, where the traps operate independently of each other, since the triggering and closing mechanism operates independently for each pair of leaves. As discussed, the driving force of the closure is the result of the difference between turgor pressures. Specifically, it is due to the hydrostatic pressure differences between the lower and upper layers of the leaves when the water run from the upper to the lower level during the closing of the trap. To sum up, each trap has what is needed in order to operate. It does so independently of other traps, which could in the meantime be eating, digesting, or remain open.

But the key to understand the limitations of the motility of Dionaea lies in the specificity of the organization of its constitutive processes. Being a MC system with differentiated cell types, tissues, and organs, Dionaea is the result of a complex development process. But as in all other plants, this development is organized so as to intimately and continuously connect the tissue establishment and organ formation to environmental adaptation through the regulation of post-embryonic growth and the relevant developmental events. In other words, the whole MC system of Dionaea is organized so as to relate adaptive interactions to the time scale of developmental processes. This is the reason why Dionaea's fast sensorimotor-like interactions show a radical incoherency between the developmental structure—evolutionary selected long ago to respond to environmental changes through internal constitutive adaptation—and the subsystem supporting its motility, which has been evolutionarily selected within this developmental structure. This is the fundamental reason why Dionaea (like any other plant) cannot display complex actions.

In jellyfish, things are substantially different. Jellyfish exhibit an epithelial organization that allows distant cells to stay together by forming various sustainable effector structures (the bell, the tentacles, the manubrium, etc.) that can execute locally coordinated contractions. Moreover, their neuromuscular structure is integrated in a specific body plan with a set of primitive and differentiated organs that provides the whole MC system with the metabolic and biomechanical requirements for its complex behavior.

The body plan of jellyfish is organized in a specific way. It includes a kind of skeleton, a digestion system, a circulation system, etc., all of which are functionally adapted to constitute a highly plastic and fully integrated MC motile entity. Even though jellyfish do not possess distinct organs (they have no head and no central NS, and they don't have any *discrete* gas exchange, secretory or circulatory systems), there is sufficient complexity in the body plan to support functionally rich motility. In particular, the jellyfish body plan is characterized by a very low (but necessary) degree of functional internalization.[20] The nerve cells are internalized as baso- and sub-epithelial cells between the two epithelial layers. They are thus lying in an internal milieu, due to the belt-like apical junctions that secludes them from the environment (Koizumi 2002). The same happens with the muscle cells, which are the most primitive in eumetazoa,[21] and which also lie under the epithelial cells, thus being in an internal environment gradually secluded from external physicochemical disturbances. Additionally, the partial internalization of the epithelial digestive cavity from the external environment gives jellyfish the advantage in feeding on larger prey, as they can release and concentrate enzymes within a partially enclosed space. It is through this epithelial gastrovascular cavity lining the gut that jellyfish partially carry digested food through their body. This central cavity could also be considered as a simple internal organ for digestion and partial transport of materials. Last but not least, the mesoglea provides support in motility by playing the role of a primitive hydro-gelatinous skeleton supporting unified body displacements. The mesoglea is also an oxygen storage, and germ cells storage for some species.

In a complete contrast to the other three cases, jellyfish can deploy a functionally diverse and complex interactive behavior because of their epithelial structure, and because of the existence of a specialized subsystem—the NS—*able to exert a fine-tuned control of the structures responsible for the execution of the necessary sensorimotor interactions with the environment*. But these complementary subsystems are functional only in the context of a very specific body plan that is adapted to plastic motility. We will explain in the next two sections how these conditions are related, and why they are jointly necessary for full-fledged MC agency.

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[20] The wide repertoire of neural-based movements demonstrated by the eumetazoa was physiologically and metabolically possible only through the formation of body cavities, and as such, through the creation of extra internal space for the development of organs. The internalization of physiological functions is a common characteristic of the evolutionary developments that accompanied the explosion of behaviors in MC animals (Rosslenbroich 2009).

[21] Eumetazoa is the clade comprising all animal groups except the Porifera (sponges) and Placozoa.

MC (behavioral) agency requires a metabolically decoupled regulatory subsystem

We have shown how complex action in jellyfish is linked with a subsystem–the NS–operating as organizer and coordinator of the contractile epitheliomuscular tissues, which enabled the development of diverse and versatile behavior. As explained in Prescott (2007), the NS supports multiple distinctive behaviors generated by different patterns of neural activity. Behaviors such as swimming, fast escaping, eating, attacking, and their combinations, are complex forms of sensorimotor coordination issued from the combination of signals operating both locally and globally, thereby modulating the coordination of whole-body movements (Anderson et al. 2004; Mackie 2004; Satterlie 2008). This coordination is possible due to the existence of *the NS operating as a regulatory sub-system* that spatiotemporally coordinates the combinatorial execution of local contractions of distant bundles of epitheliomuscular cells throughout the whole MC system, thereby *controlling sensorimotor loops*.

The emergence of such a subsystem exerting a regulatory control of the epitheliomuscular structure of the body is not a purely contingent event.[22] The appearance of early animals endowed with contractile tissues permitted potentially complex movements. As Keijzer et al. (2013; Keijzer 2015) have argued, it is likely that before the appearance of NS, animals endowed with epithelial tissues were able to deploy self-organized patterns of body movements.[23] In these conditions, a fundamental step to functionally organize this potentially rich motility was the creation of a subsystem able to exert a (meta)functional regulatory control on the contractile tissues.

As Christensen (2007) has argued, a regulatory subsystem is required when a system has to deal with an increasing number of functional possibilities and needs to achieve a globally functional integration. Of course, functional coherence can be achieved through self-organization, i.e., through parallel local interactions that generate ‘emergent’ outcomes (outcomes are not directly regulated or controlled), as the ones we have seen in MC ‘agents’ like *M. Xanthus* swarms. However, this solution only works when the number of different functions to be coordinated is not high. Christensen argues that self-organization has significant limitations for achieving functional coordination. In the absence of regulation, the achievement of a global state depends only on the reliable propagation of state changes through local interactions, which also adds a delay as the size of the system increases. Then, for global coherence to be reliable, self-organization must be robust against

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[22] Due to lack of space, the deep relationship between epithelial-based development and the building a body organization that permits a complex form of motility will not be discussed in this paper. For a detailed treatment see Arnellos and Moreno (2015).

[23] Porifera and Placazoa—the only metazoans lacking NS—are essentially sessile. Only some marine and freshwater species of sponges can move (very slowly) across the seabed through the cumulative amoeboid or crawling locomotion of the individual cells that compose their lower surfaces (Bond and Harris 1988). Some tufted larvae (mainly in their parenchymella stage) similarly show phototactic responses that are the result of independent responses (either photonegative or photopositive) of individual cells (operating both as sensors and effectors) in the ciliated posterior tuft of the larva (Maldonado et al. 2003).

variations in specific conditions. However, the capacity of the system to generate multiple finely differentiated global states will be limited. Alternatively, the system will have to sacrifice the reliability of attaining a specific state for the generation of multiple states. In general, "slow action and poor targeting capacity severely limit the capacity of self-organization to achieve the kind of coherence that functional complexity requires (…) Consequently, the most effective means for achieving the type of global coherence required for functional complexity is through regulation, including feedback mechanisms and instructive signals operating at both local and larger scales. The key feature that distinguishes regulation from self-organization is the presence of a functionally specialized system that differentially specifies one or a restricted set of states from the range of possible states the regulated system might take, based on the sensing of system conditions and the production of control signals that induce changes in functional state" (Christensen 2007, pp. 265–266). Thus, what is required for achieving effective control when functional diversity increases (i.e., the potential diversity of sensorimotor loops) is a subsystem that is sufficiently independent of the dynamics of the controlled processes, so that it can be varied without disrupting these processes, but it is still linked to parts of the controlled system so as to be able to modulate its operations (Bechtel 2007; Bich et al. submitted).

This is precisely the fundamental organizational task fulfilled by the NS: it produces patterns of signals that ensure viable sensorimotor loops while being decoupled from metabolic dynamics. Only neural signals can do this work in a MC body. In contrast, chemical signals interact directly with metabolic processes. Even when they are of a neuro-epithelio-secretory nature (e.g., hormones) and they can travel a distance in the body, they will however be received from all compatible cells (i.e., they do not have the same specificity as electrical signals). Unlike chemical signals circulating within the body, electrical interchanges among neurons provide the possibility for recurrent interactions within the dynamic domain of the NS. More specifically, the NS constitutes a cellular infrastructure that converts metabolic energy into modifiable and recurrent electrodynamic processes, thus creating a new dynamic level of highly plastic sensorimotor patterns, which are almost free from the thermodynamic constraints of the biochemical level of intercellular metabolism. Therefore, the NS operates in a dynamically decoupled way from the metabolic processes (Moreno and Lasa 2003; Moreno and Etxeberria 2005; Barandiaran and Moreno 2008a; 2008b).

Thus, the NS of Cnidaria, though constituted as an essentially distributed network, lacking centralized/hierarchical mechanisms of control, is still able to (1) functionally modulate muscles and other organs involved in sensorimotor interactions, and (2) to operate as a controller of the intercellular metabolic processes that support biochemically body movements). This is why the NS works as a regulatory organization able to support a diverse set of complex and integrated actions.

In sum, the appearance of NS, thanks to its capacity for exerting regulatory control of contractile epiteliomuscular tissues, allows MC organisms to display complex viable sensorimotor loops. The result is a diverse forms of functionally coherent motility.

The ‘constitutive-interactive closure principle’ explains integrated MC agency

We will now explore two implications of the arguments developed so far. The first implication is that the regulatory control of the NS goes beyond the active and global coordination of motility, and affects the whole constitutive organization of the MC system. Without this global regulatory control, the MC system would not be properly developed and/or could not be maintained. The second implication is that in turn, the maintenance of the NS is itself dependent on the interactive (behavioral) processes it generates. Therefore, complex behavior is necessary for the maintenance of the regulatory subsystem (the NS) that controls the constitutive organization of the MC agent. Let us discuss these points.

First, besides its role in controlling behavior, the NS plays also a regulatory role regarding other functions of the body, and even in late developmental processes. This regulatory control is realized via the neuroendocrine system comprised of neurosecretory and other neurally controlled cells. In Cnidaria, the role of neurosecretory cells is played by both sensory cells integrated into the epidermis and by sub-epidermal ganglion cells, where endocrine cells are epidermal epithelial cells and gastrodermal neurons. Neuropeptides are abundant in Cnidaria. They play a variety of different functions, such as the enhancement of neural differentiation, the pumping activity of the body column, the tentacular movement leading to prey capture and ingestion, etc. For example, neuro- and epithelio-peptides have been shown to act like true hormones in reproduction and development (Hartenstein 2006). Additionally, Cnidaria show a high capacity for regeneration, where a small piece of the body can develop into the full organism. Neuro- and epithelio-peptides as well as epithelial cells may trigger, induce, enhance or inhibit all reproductive and growth phenomena of neuronal differentiation, neurogenesis, and oocyte maturation. They also control morphogenesis and spawning by regulating the related differentiation events (see e.g., Schaller et al. 1996; Koizumi 2002; Fujisawa 2008; Takeda et al. 2013).

Since, as we have argued, the NS does not only regulate the sensorimotor loops by generating complex behavior, but also controls intercellular metabolic processes (so as to ensure global homeostasis), development and growth, *the NS, then, operates as a unified regulatory center* that functionally integrates all dimensions of the organization of the MC agent. It achieves functional integration of a potentially variable set of complex interactive processes (sensorimotor loops). It also functionally integrates the control of these behavioral processes with the control of metabolic/constitutive ones. In other words, the NS acts as an *integration center* or ‘self’ of the multicellular agent, and *this ‘self’ is ultimately the source of the action*.

Nothing similar occurs in the other MC motile systems we have studied. For example, since any kind of coordinated activity in *M. xanthus* is based on a distributed process of self-organization, the coordination of swarming is carried out equally by each individual cell. It is in this respect that swarming cannot be considered an integrated action, since—due to the type of coordination—there is no central issuance attributable at the level of the whole MC system. In the case of *V. carteri*, functional coherence is achieved through structural constraints introduced in development. As Christensen (2007) also suggests, this strongly predetermined way to achieve globally functional coherence has the advantage of simplifying processing requirements. Indeed, this rigid coordination produces a more cohesive, specific and timely move (compared to the swarming of *M. xanthus*), and the resulting swimming appears to have been issued centrally due to the rigid structural constraints. But in fact, each somatic cell swims independently of the others, hence, this kind of phototactic swimming is not considered an integrated action. The reason is that there are as many local initiations as somatic cells capable of phototaxis. In this respect, there can be no initiation of phototactic swimming clearly attributable at the level of the whole MC alga. Even in the case of some species of sponges that contract their whole bodies, or in others that can close their oscula and ostia, the effects are mediated through local signals (mainly through paracrine and much less through electrochemical signaling) that open calcium channels and cause calcium influx producing thus cellular contraction but also the release of an extracellular signal propagating the contraction from cell to cell (Leys and Meech 2006). But due to the lack of complete epithelia (Abedin and King 2010) and of a subsystem organizing their collective contractility, these contractions are relatively very slow, and their coordination is poor and rigid (Nickel 2010). As a result, sponges display neither integrated nor plastic contractility.

A regulatory center appears only in eumetazoa. Since eumetazoa are complex MC systems where many (spatially and/or temporally) local regulatory subsystems operate—each of these subsystems operating according to its local norms—and functional behavior requires unified body movement (and this in turn requires functional coordination with metabolic and even developmental processes), a higher-order *integration* is required. Accordingly, control of eumetazoan behavior cannot be achieved without functional coordination of all its different local regulatory subsystems. When a global regulatory subsystem functionally integrates all these norms according to a higher-level normativity, the latter practically operates as a *regulatory center*. A regulatory center implies therefore a system with many local regulatory subsystems, which are regulated in turn according to a global (meta)norm that underlies global integration.

Second, since the NS's ongoing operations are based on sensorimotor loops, interactive processes play a crucial role in the maintenance of NS. Hence, the expression of the constitutive-interactive closure principle that we formulated in "The challenge of multicellular agency" is realized in MC systems as follows: *the regulatory action of the NS, maintains, through the behavioral interactions, its own activity, and derivatively governs functionally the integrated MC organism*. It is not only the fact that the ongoing activity of the NS is maintained through the patterns of activity that the animal exerts in its environment—which continuously feed the sensorimotor loops. The closure between the CD and the ID happens even before the adult stage of Cnidaria. The development of neurons expressing neuropeptides appears at the larval stage. Examples of their diverse function include: the role they play as inducers of the planula larva's migration by swimming toward light, as transcription factors triggering several cascades of internal signaling, which regulates cell cycle activity, cell differentiation and death, and morphogenesis, and as inhibitors and enhancers of neurogenesis (Kass-Simon and Pierobon 2007;

Galliot et al. 2009). In the metamorphosis of the planula larva to the adult stage of the polyp, a concentration of nerve cells in the aboral part seems to be typical (Nakanishi et al. 2008). External chemical stimuli trigger a signaling cascade, which leads to the release of LWamide neuropeptides by the apical tuft and eventually to the triggering of metamorphosis (Plickert et al. 2003). Metamorphosis also involves patterns of planula migration. Planula larvae migrate over the substratum scanning the environment for places suitable for settlement. Their migration is also partly regulated by neuropeptides (LWamide and RFamide peptides), which are secreted by the apical tuft[24] in response to environmental cues, and which regulate the phototactic interactions of the planula by increasing motility and stimulating free swimming migration, when the conditions of the environment are unfavorable (see e.g., Katsukura et al. 2004; Piraino et al. 2011).

But the closure principle that we are explaining here implies in turn, that the agency deployed by the MC system should be functionally complex. Otherwise, it could not support the operations of an equally complex regulatory center like the NS. This complexity is of course correlative: the more complex the NS, the more complex the type of agency necessary for its ongoing maintenance, and vice versa. In contrast to plants that can create food almost everywhere through photosynthesis powered by solar energy, animals have to actively search for concentrated sources of energy in order to nourish themselves. They thus have to often change their environments and to confront the related environmental adversity and precariousness through reversible changes in their behavior and/or physiology. Therefore, in jellyfish as in any other animal, viable agency primarily requires fast and plastic connection between sensors and effectors for adaptive motility. The achievement of successful coordination of movements with the environment requires in turn both plastic MC motility and an increasingly diverse and complex sensing capacity. Many of the free-living Cnidaria (mostly at their medusa stages) have ‘sense organs’ in the form of eyes and statocysts (Jacobs et al. 2007), which allow them to engage in targeted, precise behaviors. The appearance and development of all these increasingly complex detectors of environmental conditions goes hand in hand with the increase in complexity of the behaviors, but also with the development and internalization of organs for the metabolic and biomechanical requirements for such complex behavior. Fine tuned sensing occurs because complex behavior requires it. As it has been argued by O’Reagan and Noë (2001) the agent’s movement cause changes in sensors, which in turn influence motor actions, and so on, as to achieve viable sensorimotor loops. Accordingly, deploying complex interactions is both a consequence and a condition of the development and maintenance of increasingly complex sensors and organs, and neural nets.

To sum up, the existence of a global regulatory center is not only the cause of a complex and integrated form of agency; in turn, this form of agency is also fundamental for the maintenance of the former. And moreover, the *Constitutive–Interactive Closure Principle* is at work, since the NS, by its very appearance, acts

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[24] The apical sensory organ seems to play the role of chemo- and mechano-sensory structure with neuroendocrine functions involved in larvae migration and metamorphosis also in free swimming invertebrate as well as in bilaterian larvae such as gastropods, nematodes, etc. (Voronezhskaya and Khabarova 2003; Marlow et al. 2014).

as a regulatory subsystem of interaction that actively affects not only the maintenance of the MC system but also its development.

Concluding remarks

Living systems have an organization that (re)produces itself and that actively intervenes in its environment so as to be maintained. In this sense, all biological systems are agents. The basic self-re-producing organization of living beings is the cell. But many living systems are MC organizations, which means that they are constituted by parts–cells–that are ultimately agents that can themselves coordinate their interactions. These parts, on the other hand, should in some way satisfy the conditions of the realization of the MC system as a whole. In turn, and with respect to the constitutive dimension of such systems, this implies that the cells should modulate their MC organization so as to satisfy the requirements for global MC (re)production. Accordingly, the implication with respect to the interactive dimension, is that, at least in a minimal sense, many cells should interact together so as to satisfy the global adaptive needs of the MC system. In other words, the parts of a MC system should be organized so as to ensure that the system interacts with its environment functionally (i.e., in a way that contributes to its own maintenance), and they should do this without interfering with its developmental logic.

Whereas in a unicellular system there is necessarily a complementary, symmetric relation between its constitutive processes (its metabolic organization) and its interactive processes (the functional actions that the organism triggers in the environment), in a MC system this relation can take very different forms. As we have seen, for example, prokaryotic MC systems such as groups of *M. xanthus* exhibit poor constitutive and interactive complexity. Eukaryotic systems such as *V. carteri* exhibit a slightly higher constitutive than interactive complexity (always compared to their unicellular antecedents, the *chlamydomonas*), and Dionaea plants, instead, exhibit a much higher constitutive complexity (compared to the other examples) but a quite poor interactive complexity. In eumetazoa, instead, we see a high complexity at—and strong interdependence between—both the constitutive and interactive dimensions.

In a trivial sense, in all the MC systems that we have analyzed, there is some collective interaction that induces changes in the environment that contribute to the system's maintenance. But in many cases this fact does not fit with what we usually mean by an agent, which implies that the action could be attributed in some sense to the agent as a 'whole'. And in fact, the critical difference between eumetazoa and all other MC 'agents' is that in the former, the action not only contributes to the energetic maintenance (by getting food) of the constitutive identity, but to the very organizational maintenance and even to the development of such constitutive identity. Conversely, the animal's action requires a highly specific developmental process leading to an entire body plan, in which a subsystem–the NS–organizes the interactions. By contrast, in the non-eumetazoan cases, the way in which agency maintains the identity of the agent is comparatively weak; the constitutive identity can be developed independently of the interactive activity (or even be reversed towards a previous stage where the parts live autonomously). In case the agent was externally provided with what the MC system requires (energy, food, etc.), the constitutive identity can be maintained even without the activity of the agent. For example, isolated germ cells in *V. carteri* will grow and divide under euphotic conditions (Koufopanou and Bell 1993). Furthermore, due to its colonial nature, the interactive dimension is not fully integrated into the constitutive dynamics. The somatic cells of the daughter colonies are ready to swim after the parental spheroid disintegrates. So, in a way, the movement acts for the development of the new generation, which on the contrary, contributes neither to the development nor to the maintenance of the source of the swimming.

Instead, in the case of eumetazoa, agency is strongly embodied and causally entangled in the constitutive identity of the agent, to the point that the ongoing maintenance of the constitutive identity requires the activity of the agent. In case the agent was prevented from acting, its nervous system would be damaged and ultimately, organizationally destroyed, and with it, the whole entity, including its cells (regardless of whether the agent is externally provided with food). Even the development of the constitutive identity is itself dependent on the motile activity of the developing agent. Actually, the significance of the actions exerted from the animal on its environment goes beyond the concept of sensorimotor loop (i.e., a guidance and harnessing of what the organism perceives). The animal's actions not only provide it with food and allow it to avoid predators and find sexual mates, they also operationally maintain the activity of the NS itself, and furthermore, they maintain the whole constitutive identity of the animal.

Summing up, a functionally complex form of agency requires also a functionally complex constitutive identity, and the maintenance of the latter depends on the former. But this can only be done in an organismically integrated way, because of the high number of constraints the internal organization of the MC system needs to generate in order to drive complex behavior. Ultimately, this means that in MC systems with such type of organization (i.e., eumetazoa) a global regulatory (sub)system should ensure the integration of the diverse and complex functionality of its interactive dynamics. Moreover, it should ensure that this integration is functionally compatible with the set of the related complex constitutive processes. The MC behavior contributes to the maintenance of the constitutive identity of an integrated MC agent. This is because the behavior supports the constitutive processes, which in turn contribute to the maintenance of a (sub)system that exerts a higher-level control on the global constitutive identity of the MC system. This is important, because otherwise we could say that any form of collective collaboration between agents (leading to a benefit of the collectivity) would itself be an agent. Without such a 'central self' the action of the MC system is non-integrated and functionally simple, because the role of this regulatory 'center' is precisely to hierarchically organize the constitutive structure of the MC system allowing plastic and complex functional interactions with its environment.

MC agency provides a new way to understand multicellularity. Elsewhere, we have argued that MC systems can be considered integrated organisms if and only if the cells that constitute them generate a complex organization, "which plays a key causal role in the generation of the material structures that actually make it possible:

i.e., the production of those regulatory control mechanisms that will guide the development of the functional relations among its autonomous unicellular parts, turning the whole system into a self-maintaining and self-reproducing integrated organization that becomes, itself, autonomous, but at a different hierarchical level" (Arnellos et al. 2014). MC agency is, as we have shown, a masterpiece in the construction of this integrated organization, because it is only through the causal action of complex behavior that a highly integrated MC organization can be maintained and, consequently, be re-produced in evolution.

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