An Embodied View of Octopus Neurobiology   Minireview

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Octopuses have a unique flexible body and unusual morphology, but nevertheless they are undoubtedly a great evolutionary success. They compete successfully with vertebrates in their ecological niche using a rich behavioral repertoire more typical of an intelligent predator which includes extremely effective defensive behavior — fast escape swimming and an astonishing ability to adapt their shape and color to their environment. The most obvious characteristic feature of an octopus is its eight long and flexible arms, but these pose a great challenge for achieving the level of motor and sensory information processing necessary for their behaviors. First, coordinating motion is a formidable task because of the infinite degrees of freedom that have to be controlled; and second, it is hard to use body coordinates in this flexible animal to represent sensory information in a central control system. Here I will review experimental results suggesting that these difficulties, arising from the animal's morphology, have imposed the evolution of unique brain/body/behavior relationships best explained as intelligent behavior which emerges from the octopus's *embodied organization.* The term 'intelligent embodiment' comes from robotics and refers to an approach to designing autonomous robots in which the behavior emerges from the dynamic physical and sensory interactions of the agent's materials, morphology and environment. Consideration of the unusual neurobiology of the octopus in the light of its unique morphology suggests that similar *embodied principles* are instrumental for understanding the emergence of intelligent behavior in all biological systems.

Introduction

Cephalopods are unique amongst invertebrates, their extremely large nervous system containing as many neurons as in the dog brain (around half a billion [1]). They are intelligent, visually active hunters and compete successfully with vertebrates for the same ecological niche [2]. In the laboratory they readily learn to associate a visual or tactile stimulus with a negative or positive reward, they can learn by observation [3] and can decide into which compartment of a three-arm maze to push the tip of their arms [4]. Studies in natural habitats have shown the amazing abilities of these animals to disguise themselves, imitate poisonous species and to use tools [5–7].

Perhaps most astonishing is that they do all this with a soft, boneless body and with eight long, flexible arms. How have the muscular, neuronal and sensory systems of the octopus adapted to this unusual body plan to support its advanced behavior? Recent neurophysiological and behavioral studies on the species *Octopus vulgaris* have revealed an organization of the nervous system/body interactions that helps answer this question. In this review, I argue that the

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sophistication of the cephalopods' behavior emerges from its special *embodied intelligence*.

The embodied intelligence concept (see [8,9]), although not a direct outcome of biological studies, is definitely inspired by biological systems, which are amazingly efficient in generating adaptive behaviors with ease and elegance. The approach was developed for designing autonomous robots, which, unlike industrial robots, such as those used in car assembly, are highly adaptive to their environment. The first class of robots using this approach 'behave' without sensory input or feedback in a kind of an open-loop or feed-forward controlled system. The second class needs to process a tremendous amount of internal and external physical and sensory information to generate its adaptive autonomous behavior. Roboticists find it important to design such robots as a whole, with what they consequently refer to as an *embodied organization*.

The term 'embodiment' implies the dynamic interplay of information and physical processes between four components comprising the embodied creature: the controller, the mechanical system, the sensory system and the task-environment (see Figure 1, reproduced from Pfeiffer *et al.* [8], where additional information can be found). While in open-loop robotic systems behavior arises from more hierarchical top-down control, in an embodied organization the behavior arises from the system as a whole through dynamic physical and information interactions among all its components. These reciprocal, dynamical interconnections ensure that the system functions optimally in its ecological niche when each component is adapted (by evolution or self-organization) to the embodiment functionality; this ensures best adaptation in the bottom-up direction, where the morphology and the properties of the material are adapted for interaction with the ecological niche. Proper adjustment of the interactions between the morphology, the mechanical system and the environment achieves physical stability and energy efficiency; simplifying motor control as it leaves it to deal mainly with perturbations.

The materials and the physical interaction with the environment shape the pattern of the physical and sensory feedback. From the point of view of information processing such constrained interactions create statistical regularities in the sensory and motor information. That is, through its behavior, the robot structures its own sensory inputs (information self-structuring; Figure 1), reducing their dimensionalities and simplifying and speeding up information processing. In a robot, these dynamic interactions, together with the plastic processes at different levels, especially at the level of the controller [10], may lead via self-organizational processes to the emergence of an efficient adaptive behavior in a specific environment (Figure 1). This *embodied intelligence* approach has proved efficient for solving complex robotic problems. It does not seem unreasonable that biological evolution has followed similar principles [11].

The unusual morphology of the octopus and its highly adaptive behavior is an excellent case in which to explore whether similar embodied organization principles play a constraining role in the evolution and self-organization of biological systems. Here, I review neurophysiological and behavioral findings from studies of motor control in the octopus as an inspiration for robotics, as well as relevant findings on the neural bases of learning and memory in
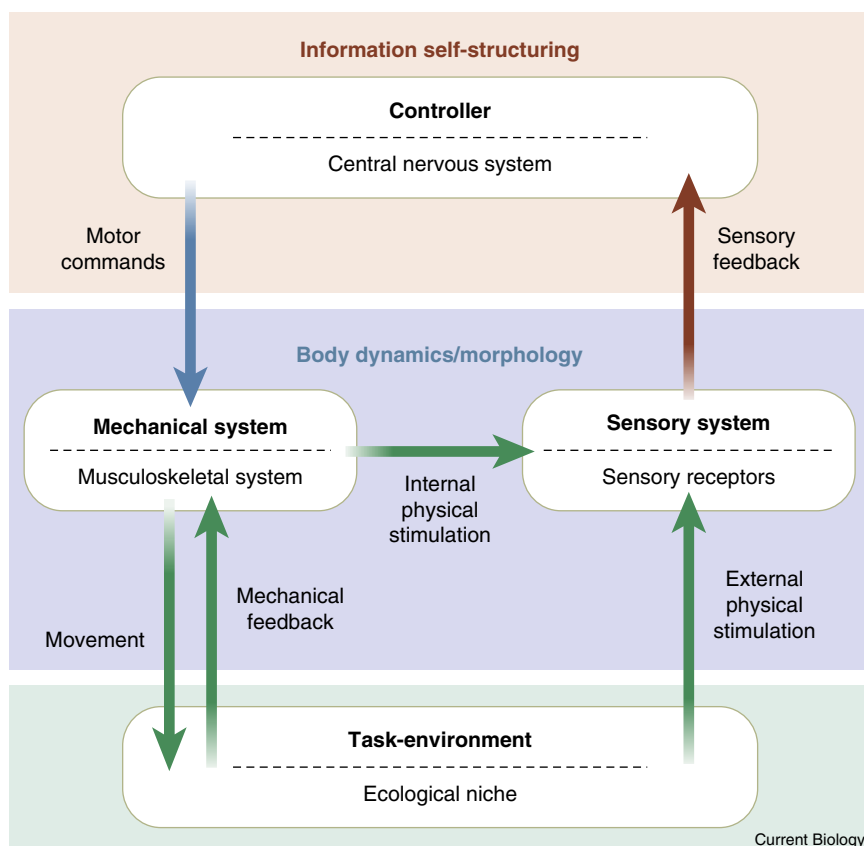
Figure 1. Schema describing the embodied organization of behavior.

Behavior emerges from the interaction of the agent and the environment through a continuous and dynamic interplay of physical and information processes rather than from a hierarchical organization. (Reproduced with permission from Pfeifer *et al*. [8].)

bend in any direction and at any point along their length, pose a great challenge for any motor control system because there are infinitely many ways to perform a specific task. That is, the control system must deal with an infinite number of degrees of freedom. It is not surprising, then, that roboticists are seeking inspiration from the octopus on how to solve this problem [15].

The second complex problem created by this high redundancy is the central representation of the huge amount of sensory information from the suckers, skin and intrinsic arm musculature — millions of tactile, chemical and proprioceptive sensory afferent fibers enter the peripheral nervous system. Representing the information gathered by a structure with no defined morphological constraints is a formidable challenge: it is much simpler to represent sensory information in the central nervous system of animals with limited degrees of freedom because of a limited numbers of joints. This raises the question of whether it is even possible to represent the body parts of the octopus somatotopically in the central nervous system, as in vertebrates (see below).

octopus and cuttlefish. I argue that the embodied organization approach indeed provides an interesting framework for understanding many of the unique features of the octopus nervous and muscular systems. Embodied organization thus appears a valid approach for further understanding the functioning of complex dynamical biological systems. I believe that it is a universal constraint in the evolution of adaptive behavior in animals, both simple and complex.

Invertebrates, especially mollusks, show an enormous range of behavioral complexity [12] that I suggest emerges from each animal's unique embodiment. It would be interesting to test the hypothesis that mollusks which have a very simple behavior, like the shell tusk, which lies barely moving buried in sea sand, filtering microscopic food particles and lacking any major sensory organ, are organized more like industrial robots in a framework of open-loop organization, such as that based on a central pattern generator, driven mainly by mechanical feedback from the environment (Figure 1).

Flexible Arms: a Challenge to Sensory Representation and Motor Control

The neuromuscular system of the octopus arm combines extreme flexibility with the ability to make precise goal-directed movements and carry out highly sophisticated tasks [4,5,13]. Kier and Smith [14] were the first to explain the biomechanics of motion and stiffness generation in cephalopod arms and tentacles. They termed these structures 'muscular hydrostats' as they are characteristically built entirely of incompressible muscle cells.

Such flexible structures, especially the long and flexible arms of the octopus, which can elongate, shorten and

The Unique Neuromuscular System of the Octopus Arm

The neuromuscular system of the octopus arm and other mollusks differs dramatically from those of skeletal animals, vertebrates and arthropods [16–19], suggesting adaptation of the mechanical system (Figure 1) to a flexible embodiment. The muscle cells of the arm are small and electrically compact. Most likely because of their electrical compactness, each muscle cell is innervated by three distinct excitatory cholinergic motoneurons at a discrete synaptic junction near the center of each cell [20]. In contrast to other invertebrates, the neuromuscular junction lacks short-term synaptic plasticity with no short-term facilitation and/or depression, and there is no postsynaptic inhibition. These synaptic properties, which are not commonly found in invertebrates, suggest that there is a more linear transformation of neuronal activity into muscular action, as in vertebrates. Furthermore, the muscle cells in the antagonistic longitudinal and transverse muscles show similar properties, possibly also simplifying neural motor control.

The arrangement of the neuromuscular system appears specifically suited to a flexible motor system. The intrinsic muscles of the arms, which generate the arms' motion and stiffness, are innervated by a very large number of motoneurons distributed along the arm nerve cord ($\sim 4 \times 10^5$ motor

Figure 2. The unique distribution of the 500 million nerve cells of the octopus nervous system between its three main compartments.
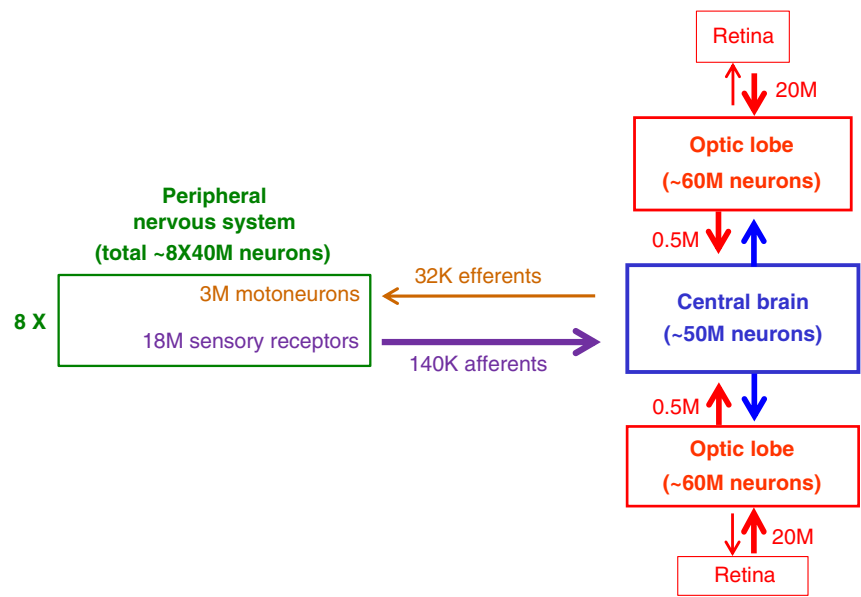
Each is shown in a different color. Note the relatively few fibers connecting the compartments. (Based on data in [21,36].)

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neurons per arm [21]). With the small dimensions of the muscle cells [16], this leads to an estimate of a motor unit size of about 3300 muscle cells innervated by a single motor neuron. Because of the small dimensions of the muscle cells, the motor unit occupies a volume of only about 0.2 mm^3 of the arm musculature. This innervation pattern may achieve both a highly localized and continuous neural control of this non-segmented arm structure. This would be ideal for generating the waves of muscle activation typically observed in octopus arm movements [22]. The pattern of innervation and the properties of the neuromuscular transmission may simplify transformation of neural information into muscular action and fit the feed-forward type of motor command prevailing in the octopus [23].

Unique Organization of the Cephalopod Nervous System
The exceptional anatomical organization of the octopus nervous system was described by J.Z. Young, M.J. Wells, E.G. Gray and colleagues in the mid-twentieth century [21]. As shown schematically in Figure 2, the nervous system of the octopus, like that of other modern cephalopods, is divided into three main parts: a central brain surrounded by a cartilaginous capsule; two large optic lobes connected to the retinae of the highly developed, camera-like eyes; and a third and numerically the most prominent part, the peripheral nervous system of the arms that contains two-thirds of the octopus's total 500 million nerve cells. These pioneering researchers deduced from the relatively few afferent and efferent fibers interconnecting the three main parts (Figure 2) that much of the processing of motor and sensory information is performed in the peripheral nervous system and in the optic lobes, with the central brain acting more as a coordination and decision-making unit. Recent physiological results (see below) have highlighted the tight relationship between the special distributed anatomy of the nervous system and its function and, by and large, have confirmed the deductions from the anatomy. The bulk of the nervous system is thus located in the periphery, close to the site of greatest motor and sensory information flow. This is a striking demonstration of an organization that fits the special octopus embodiment, which, as we discuss below, lacks central representation of the arms.

As mentioned earlier, octopuses and dogs have similar numbers of neurons. According to the prevailing top-down dogma, one may challenge this comparison, claiming that the number of neurons in the central nervous system of the octopus is 'only' about a third of the total 0.5 billion (Figure 2) and counting the central and peripheral neurons together is misleading. However, the embodiment concept teaches us that each embodiment may develop a different organization of the control system. I would argue that, in the octopus, the nerve cells are distributed specifically to implement the animal's special embodied intelligence (this is true generally for invertebrates which show great diversity in the distribution of their nervous system, most likely correlating with body plan and behavioral complexity). Indeed, as explained below, the peripheral nervous system performs computations usually attributed to the central nervous system of vertebrates.

Organization of the Higher Motor Centers
The central brain of the octopus is arranged quite differently from the vertebrate brain. It is composed of about 40 interconnected lobes which are arranged, typically for invertebrate ganglia, with the cell bodies of the monopolar neurons forming an outer cortex. The dendrites of these cells constitute the neuropile in the center of the lobes [21].

The higher motor centers in the octopus brain show a different functional organization from that of the motor cortex of vertebrates. The higher motor centers in the basal lobes of the supraesophageal part of the central brain are not organized somatotopically [24]. Stimulation of single neurons in the basal lobes does not activate localized movements but rather a complex behavior, the complexity of which increases with stimulus intensity. Moreover, stimulation in the higher motor centers that evokes arm extensions always activates several arms: it is not possible to activate only a single arm, as would be expected were each arm represented at a specific location. These results suggest that the higher motor centers contain representations of motor programs rather than of body parts.

Tactile and visual responses recorded in these motor areas are also not somatotopically organized; a site that responds to a local tactile stimulation of an arm responds equally well to stimulation all along the arm and of different arms (my and L. Zullo groups' unpublished data). These sensory-motor areas thus also appear to have an integrative

function. The lack of sensory-motor somatotopy supports the suggestion that the higher motor centers make decisions about the type of behavior and combination of motor programs to be executed and activate the peripheral motor centers accordingly.

These results show how the octopus's redundant body morphology may have imposed a new organization of the internal sensory-motor representations and that these are not based on body part-coordinates. Discussing self-organization in the embodied approach, Brooks [9] has suggested that intelligent creatures or robots can be evolved without localized representations of sensory information. As I explain next, the special distribution of the load of motor control between the central and the peripheral nervous systems may explain the lack of a need for central motor and sensory representation of the arms.

Special Organization of Arm Motor Control

The allocation of motor control between peripheral and central nervous systems is exemplified by the reaching movement in which the octopus extends one or several arms toward a target. The octopus simplifies the control of this goal-directed movement by using a stereotypical bend propagating from the base to the tip of the arm. This collapses the infinitely large degrees of freedom into just three: two for the direction of the base of the arm, and the third for scaling the propagation velocity profile of the bend along the arm [25]. This strategy radically simplifies the motor control.

Testing the relationship between muscle activity and the kinematics using electromyography (EMG) during reaching in freely behaving animals suggested that this movement is controlled by a feed-forward (ballistic, open-loop) motor program [22]. The detailed neural information for the execution of this movement is embedded in the neuromuscular system of the arm itself, as movements with natural kinematic characteristics can be elicited in an amputated arm by either tactile sensory stimulation of the arm or by electrically stimulating the nerve cord running along the arm [26].

If the detailed movement programs are embedded within the peripheral nervous system, one would not expect to find arm representation in the higher motor centers, but rather more complex behavioral programs, as indeed has been found (see above, [24]). For reaching, the brain must issue the command triggering the extension and the scaling factor for determining the speed by which the bend should propagate along the arm.

Kinematic and dynamic (muscle action) analysis of fetching behavior provides an even more striking demonstration that not only motor programs but also rather complicated computational processes employ the arm's flexible morphology [27]. In the fetching movement, the octopus brings a target (food) precisely to its mouth. To do this it reshapes its arm into a quasi-articulated structure. The octopus can grasp food with its suckers anywhere along the length of the arm. To form the quasi-articulated structure, the octopus divides the section of the arm from the base to the target into three segments; proximal, medial and distal. The distal segment serves as a hand, while the proximal and the medial segments are of similar length, exactly like the arm and forearm in our skeletal upper limb. This allows both us and the octopus to bring food precisely to the mouth by mainly rotating the medial joint (elbow) [28].

How does the octopus compute the shape of this stiffened structure for each movement? In humans, the rigidity of our skeletal structure simplifies the representation of the arm in our motor cortex and an internal model of our arm aids central control of the arm movement. In contrast, as discussed above, it is hard to envisage how to represent the infinitely large degrees of freedom of the dynamically articulated structures that the octopus uses in its fetching movement.

Studies of the dynamic aspects of this movement — correlating muscle activity and kinematic features of the movement — once again revealed an ingenious mechanism for calculating the structure of the quasi-articulated arm for each target location [27]. Correlating EMG recordings at various locations along the arm showed that grasping the target elicits two waves of muscle activation which propagate one toward the other; one propagates from the target toward the base of the arm, while the other propagates from the base of the arm toward the target. When the electrodes were located on either side of the medial joint there was no delay between these two waves, suggesting that the medial joint is formed where the two waves collide. It is conceivable that the back-propagating wave is initiated at the site grasping the target, while the forward-propagating wave is initiated at the central brain in a response to a faster sensory signal. Such a mechanism is very attractive as it explains how the articulated structure is dynamically computed at the level of the arm for each fetching movement. This result is a striking biological demonstration of '*morphological computation*', a notion tightly associated with embodied organization of intelligence [29].

Self-organization in the Cephalopod Central Nervous System

As explained by Pfeiffer *et al* [8], self-organization in robotics is an important property of the embodiment organization. Self-organization of this kind has not been considered to be broadly important in biology, so it is perhaps surprising that a recent comparative neurobiological study in the phylogenetically close species *Octopus vulgaris* and the cuttlefish *Sepia officinalis* indicated that self-organizing processes may participate in shaping the cephalopod central nervous system [30]. Self-organization may thus be a biological process contributing to establishing octopus embodiment.
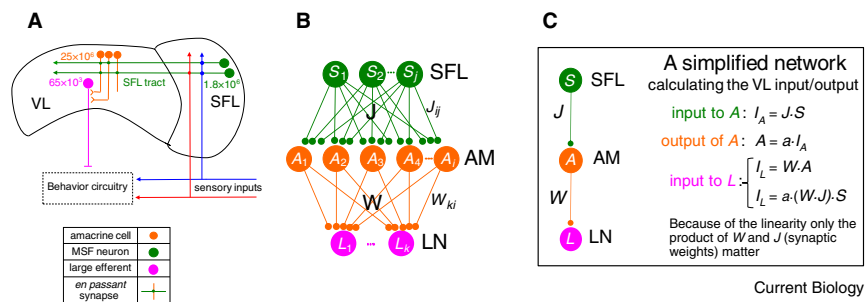
In both octopus and cuttlefish, the vertical lobe plays a central role in learning and memory, important components of the sophisticated behavior of these animals. Figure 3A,B schematically illustrates the 'fan-out fan-in' neural network in their vertical lobe systems. The tens of millions of amacrine interneurons in the intermediate neuron layer are innervated *en passant* by the 'fan-out' (diverging) input from the superior frontal lobe. The neurons of the superior frontal lobe are assumed to integrate sensory information [21]. The amacrine interneuron dendrites then 'fan-in', converging onto only several thousand efferent large neurons, which are the sole output of the vertical lobe.

Intracellular recordings of membrane potential and local field potential recordings reveal that the two species have the same vertical lobe electrophysiology and connectivity. Yet, there are differences in the synaptic properties. In both octopus and cuttlefish the synaptic input to the amacrine interneurons is glutamatergic. Surprisingly, however, only in the octopus is this synaptic connection endowed with a robust activity-dependent long-term potentiation (LTP). This LTP is important for the acquisition of long-term memory, most likely outside the vertical lobe [31].

Figure 3. The learning and memory networks of octopus and cuttlefish vertical lobe systems have similar 'fan-out fan-in' architecture.

(A) The main connectivity and cell numbers of the learning and memory system of the octopus (from [30]). (B) The feed-forward network connections of the ventral lobe system (from [30]). (C) A simplified three cell network to demonstrate the dependence of the input/output relationship of on the synaptic properties (courtesy of Y. Loewenstein).

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Furthermore, in the octopus, but not in the cuttlefish, this glutamatergic connection demonstrates short-term synaptic plasticity and short-term serotonin-mediated presynaptic facilitation, similar to that operating in learning and memory of the defensive reflex in the simpler mollusk *Aplysia* [32,33].

In both species, the fan-in synaptic connections to the large efferent neurons are cholinergic. But in the octopus, these cholinergic synapses show no LTP, while in the cuttlefish these synapses do show a robust LTP [30]. That is, the fan-out fan-in nature of the synaptic connections is similar in the two networks, but the synaptic plasticity is located in a different layer of the network in the two species. Why is there such a difference in two closely related species? One exciting explanation may be that, despite the different sites of plasticity, the computational capabilities of the two networks are similar. Computational analysis suggests that the two networks perform the same computation if there is a linear input/output relationship at the intermediate synaptic layer between the amacrine and the large cells [30].

The fan-out fan-in network organization is shown in the panel in Figure 3B; for simplicity, the input/output relation is represented in Figure 3C in a network containing only one cell in each layer (*S, A* and *L*). The equation describes how the input to the large neuron (*L*) depends on the activity of the input neurons (*S*). If the input/output relationship of the amacrine interneurons (*A*) is linear, then the input to the large neuron is given by the product of the synaptic weights (synaptic strength) of the first (*J*) and the second (*W*) synaptic layer. That is, the input/output relationship can be equally modified by changing either the first or the second synaptic connections.

Physiological studies have confirmed that the input/output relationship of the amacrine interneurons in both the octopus and the cuttlefish vertical lobes is linear [30]. It thus appears likely that the two systems are computationally similar in spite of the different location of their synaptic plasticity. Developmental processes like self-organization may therefore select for computational constraints rather than for specific neuronal properties. Recent biological results suggest that self-organization may be important for establishing the connectivity of the visual cortex [34,35]. As suggested by Pfeifer *et al.* [8], therefore, this property can contribute to 'self-structuring' of information processing in the controller (Figure 1). These results suggest that self-organization is likely a biological phenomenon and thus support embodied organization as a feasible biological constraint.

Conclusions

It should be clear that each system of the octopus reviewed above has some special or unusual properties. The unique functional organization of each of the bottom-up control levels has been interpreted as reflecting adaptation to the octopus's unusual morphology and flexibility. I have exploited this special constellation of behavioral complexity, together with the unusual morphology of the octopus, to explain the principles of embodied organization in a complex biological system. The organization of motor behavior in the octopus appears to support the concept of embodied intelligence that the intelligent behavior is the outcome of adaptation of all the systems and that the animal as a whole in its environment — its embodiment — is what determines its survival. Thus, this approach, which has been instrumental in building robots with high adaptability to their task environment, is possibly also applicable to the evolution and self-organization of complex biological systems. Note that embodied principles may also apply to simple systems, in which simple but successful adaptive behaviors (but maybe less 'intelligent') may emerge from a less complex embodiment where the level of complexity and dynamics is determined by the reduced amount of sensory and motor information involved in the interaction with the ecological niche.

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