

How Nervous Systems Evolve in Relation to Their Embodiment: What We Can Learn from Octopuses and Other Molluscs

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Key Words

Embodiment · Self-organization · Motor control · Evolution · Molluscs · Cephalopod

Abstract

Cephalopods such as the octopus show the most advanced behavior among invertebrates, which they accomplish with an exceptionally flexible body plan. In this review I propose that the embodied organization approach, developed by roboticists to design efficient autonomous robots, is useful for understanding the evolution and development of the efficient adaptive interaction of animals with their environment, using the octopus as the leading example. The embodied organization approach explains adaptive behavior as emerging from the continuous dynamical and reciprocal physical and informational interactions between four elements: the controller, the mechanical and the sensory systems and the environment. In contrast to hierarchical organization, in embodied organization, self-organization processes can take part in the emergence of the adaptive properties. I first discuss how the embodiment concept explains covariation of body form, nervous system organization, and level of behavioral complexity using the Mollusca

as an example. This is an ideal phylum to test such a qualitative correlation between body/brain/behavior, because they show the greatest variations of body plan within a single phylum. In some cases the covariation of nervous system and body structure seems to arise independently of close phylogenetic relationships. Next, I dwell on the octopus as an ideal model to test the embodiment concept within a single biological system. Here, the unusual body morphology of the octopus exposes the uniqueness of the four components comprising the octopus' embodiment. Considering together the results from behavioral, physiological, anatomical, and motor control research suggests that these four elements mutually influence each other. It is this mutual interactions and self-organization which have led to their unique evolution and development to create the unique and highly efficient octopus embodiment.

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Introduction

The embodiment approach was developed for designing autonomous robots, which must be highly adaptive to their environment. Such robots need to process a tremen-

Embodied organization

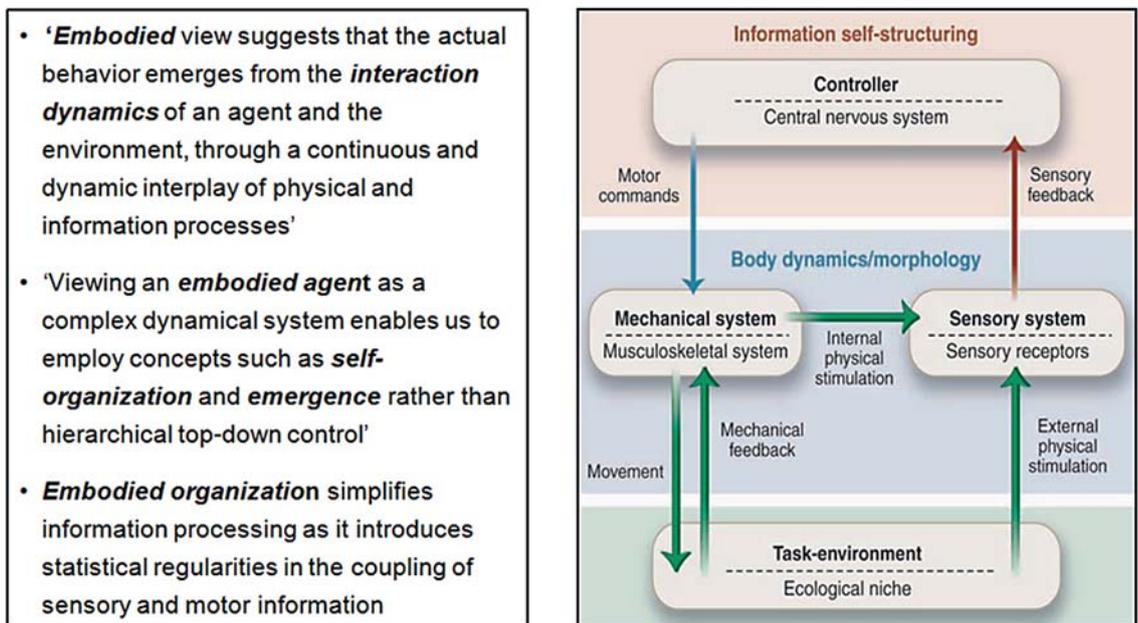


Fig. 1. Schema describing the embodied organization of behavior (from Pfeifer et al. [2007], reprinted with permission). Behavior emerges from the interaction of the agent and the environment through a continuous and dynamic interplay of physical and information processes. The main features of this organization are shown in the box. The first two bullets are cited from Pfeifer et al. [2007].

dous amount of internal and external physical information to generate adaptive behavior. Roboticists have found it important to design the robot as a whole, i.e. codesigning body and material properties with the control system in a specific environment. This approach is referred to as *embodied organization* (fig. 1). Although not derived directly from biological research, this approach was largely inspired by biology; for example, the concept of ‘embodied intelligence’ [Brooks, 1991; Pfeifer et al., 2007] was clearly inspired by the efficiency with which biological systems generate adaptive behavior.

Embodiment is seen as being created by the dynamic interplay of information and physical processes among the basic four parts making up an organism/agent – the controller, the mechanical system, the sensory system, and, importantly, the organism’s environment (fig. 1). In embodied organization, behavior arises from the system as a whole through reciprocal dynamic physical and information interactions among all of these components, embedding the organism in its environment in an optimal synergy. This dynamic organization allows self-organization processes to help shape efficient interactions among the four components of each embodiment. The

embodiment approach views global behavior as emerging solely through the information interactions among each of the embodiment’s components. The embodiment and self-organization may have an important implication for the nervous system function because they simplify sensory, motor, and control information processing. This is because the embodiment self-structuring property constrains the patterns of the relevant physical, sensory, and motor information flowing in the system (fig. 1).

The embodiment approach contrasts sharply with a hierarchical organization frequently used in motor physiology. Note, however, that the embodied organization may converge to a hierarchical top-down control organization if this type of organization is efficient for the system’s interaction with its environment.

Applying the Embodied Approach to the Functional Organization of Animal Body and Behavior

Molluscs offer a special opportunity to study the relationship between body, brain, and behavior, the essence of embodied organization. They form the second largest

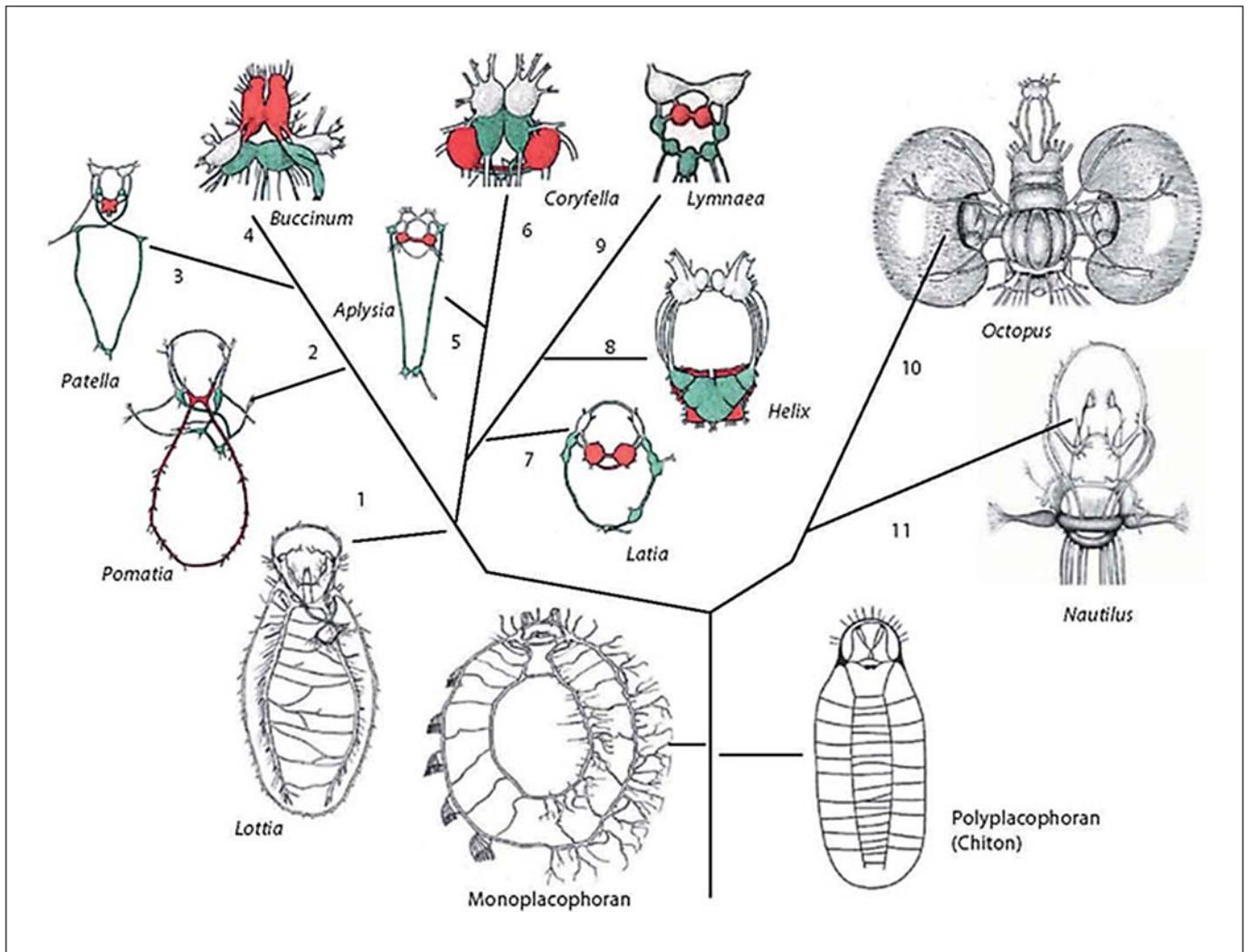


Fig. 2. Multiple occurrence of centralization of the nervous system in representatives of the phylum Mollusca. From Moroz [2009]. Examples of nervous system centralization are shown for two molluscan classes: Gastropoda (No. 1–9) and Cephalopoda (No. 10 and 11). Centralization of the nervous systems occurs independently in various groups of prosobranch (No. 2–4), opisthobranch (No. 5 and 6), pulmonate (No. 7–9), and cephalopod (No. 10 and

11) molluscs. Red – derivatives of the pedal cords (the pedal ganglia); green – components of the visceral loop (derivatives of pleural-parietal cords); the cerebral ganglia are uncolored. Color coding has not been applied to cephalopod molluscs due to the more complex 3-D organization of their brain. The diagrams of the various molluscan nervous systems are modified from Bullock and Horridge [1965, fig. 22.6a, 23.3, 23.8a, 25.2, 25.5a].

phylum (after Arthropoda) and are the phylum exhibiting the greatest morphological and behavioral diversity in the animal kingdom. Only recently has phylogenomics started to reveal deep molluscan relationships [Kocot et al., 2011]. The molecular data have confirmed that all molluscan classes are monophyletic and that they share a common ancestor with annelids, yet some of the phylogenetic relations among the various molluscan classes are still under debate [Haszprunar and Wanninger, 2012].

The large diversity in body plan ranges from tusk shells (Scaphopoda) protected by their shells, through annelid-like glisten worms (Aplacophora) without shells, to freely moving, clever hunters like the octopus (Cephalopoda). These diverse body plans correlate with the different types of behaviors demonstrated by these animals. The tusk shell can only passively collect small food particles from the water. The modern cephalopods (Coleoidea), octopus, cuttlefish, and squid, have lost the heavy protective shell and

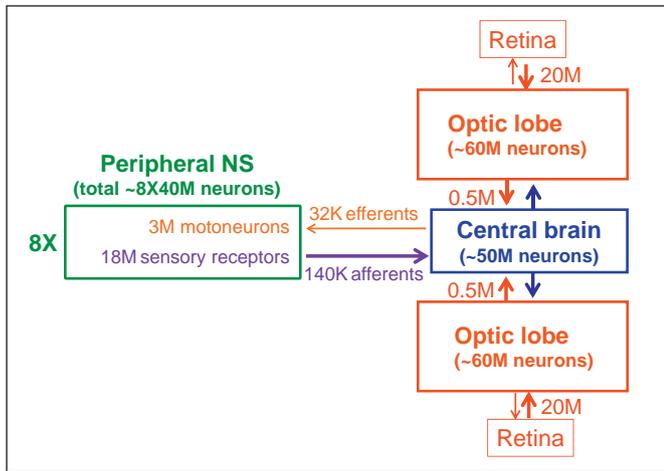


Fig. 3. The evolution of the octopus nervous system involves a unique ‘centralization’ into three separate compartments. The schema shows the distribution of the 500 million nerve cells of the octopus among these three main compartments, each shown in a different color. Note the relatively few efferent and afferent fibers connecting the peripheral compartments with the relatively small central brain. M = Million; K = thousand. From Hochner [2012] based on Young [1962, 1971].

their flexible body allows them to move fast and to compete with fish in the same ecological niche [Packard, 1972].

The relationship between the body and the nervous system can be demonstrated using the organization of the molluscan nervous system as shown in figure 2 [see also Bullock and Horridge, 1965, fig. 23.3]. The basal chiton mollusc (Polyplacophora) carries a distinct dorsal ‘shell’ formed by eight interlocking plates and segmental organization of the foot muscles. In the chiton nervous system (and those of other basal molluscs) the pedal ganglia form pedal nerve cords that show the segmental ladder-like organization typical of numerous segmented invertebrates (fig. 2). However, Friedrich et al. [2002] have shown that this segmental organization is not a true annelid-like segmentation but is secondary. Thus, it appears that the segmental organization in the chiton’s nervous system evolved independently of a true segmentation to match the body morphology. This suggests independent convergence to the same embodied organization at the level of the neuromuscular system.

According to Moroz [2009], several species in the phylum Mollusca also provide a good demonstration of the independent evolution of centralization in the nervous system. Parallel with the complexity of their behavior, the Gastropoda show a clear transition from the ladder-like organization of the nervous system, as for example in *Lot-*

tia in figure 2, in *Haliotis* and in Bullock and Horridge [1965, fig. 23.3], to a rather centralized ‘brain’ in *Aplysia* and even more so in *Lymnaea*. The other independent centralization according to Moroz [2009] occurred in Cephalopoda, which show a massive reorganization of the nervous system in addition to a huge increase in the number of nerve cells (several hundred millions).

However, the anatomy of the octopus nervous system, as described by Young [1971] and schematized in figure 3, tells us that centralization per se is not the sole way of evolving sophisticated behavior. The octopus nervous system is comprised of not one centralized brain but rather three main compartments, the largest of which is the peripheral nervous system of the arms. As we will see, locating the major part of the nervous system in the arms is an efficient solution to the complex problem of the motor control of eight long and flexible arms. The central brain has the duty of a controller and decision center that collects and distributes sensory and motor information from the arms and the optic lobes.

There are indications that cephalopods achieve their unusual body plan by different recruitment of genes involved in determining the morphological features of all bilateral animals [Lee et al., 2003]. The authors used the development of the bobtail squid *Euprymna scolopes* to study the involvement of the highly conserved *Hox* gene family. These genes determine the rostral-caudal axial patterning of all bilaterians. A very prominent conserved feature is the collinear pattern of expression of the *Hox* gene family where the anterior-class *Hox* genes are expressed more rostrally than posterior-class genes. Lee et al. [2003] found that in the bobtail squid the pattern expression of *Hox* genes lost its constrained collinearity. Thus, the morphological uniqueness of cephalopods may originate in the most fundamental genes that determine the body plan. This striking genetic finding is consistent with the idea that the morphology of the octopus has undergone profound evolutionary modification and thus the octopus should provide a favorable model to look for the interaction of morphology with the other components of its embodiment (fig. 4).

Explaining the Approach: A Robot Provides an Example of Embodied Organization

It is relatively easy to show in skeletal animals that their morphology alone can support and simplify the control of motion. Borrowing the notion of ‘morphological intelligence’ from robotics helps explain how. There are a num-

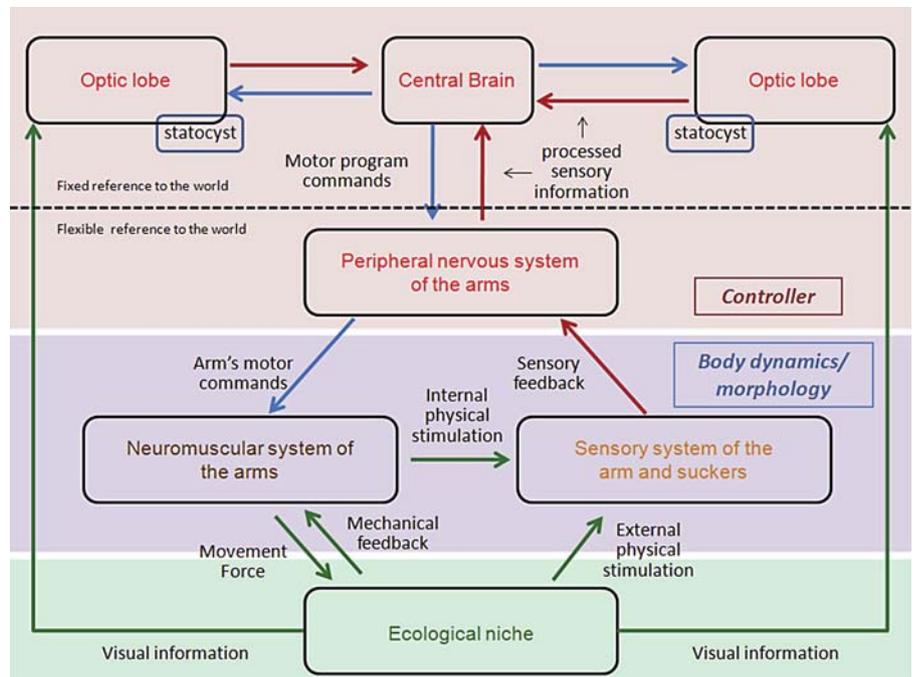


Fig. 4. Embodied organization of octopus behavior. The main modification of the generic embodiment (fig. 1) is the separation of the controller (the nervous system) into central and peripheral nervous systems. The central nervous system lies in the head, which is in fixed reference to the world due to the visual and vestibular system attached to the cartilaginous brain capsule. The peripheral nervous system is located in the flexible arms and thus lacks a rigid physical reference to the world.

ber of astonishing examples where passive robots can be built by appropriate morphological design [Collins et al., 2001, 2005]. These robots can perform meaningful tasks without using any supervising control system such as an external computer. It is not surprising that the structures of several of these passive robots converge to the form of the human skeleton and that they can generate passive, bipedal, self-stabilized, human-like walking with only a slightly negative slope to supply sufficient gravitational energy [Collins et al., 2005]. That is, appropriate organization of the structure and materials creates an embodied dynamics, where physical interaction with the environment generates the mechanical feedback allowing the embodied creature to self-organize and generate intelligent behavior. In biological organisms, such embodied organization, like the mechanical part of human walking, has obvious evolutionary advantages. It reduces energy costs and the dynamic stability simplifies neural motor control, which can now deal mainly with perturbations.

Examples of Biological Self-Organization

Cephalopod Chromatophores

The above example of robot bipedal walking shows the importance of physical parameters in the embodied organization of behavior. There are cases where an isolated

component of the embodiment cannot generate a coherent behavior. However, due to internal interactions within this isolated component, it may generate 'self-organized' dynamic behavior of some kind. This capacity is demonstrated by the chromatophore system of the octopus, squid, and cuttlefish. Its self-organized behavior is reminiscent of case V of the traveling wave predicted by Allen Turing's famous reaction-diffusion model to explain the self-regulated formation of biological patterns [reviewed by Kondo and Miura, 2010]. Packard [2006] already used the chromatophore system to demonstrate what he has termed 'horizontal control', a very similar idea to what I am suggesting here, i.e. the self-control property of a system when separated from the higher control.

This chromatophore system, an image-generating motor system separate from the neuromuscular motor system, is unique to the modern cephalopods [Hanlon and Messenger, 1996; Packard, 2006]. Skin colors can change rapidly due to neural signals, which cause radial muscle cells to contract. This contraction expands a membranous sack containing one of several pigments (red, black, brown, yellow, etc.). The expansion of the pigment sack exposes its color near the skin's surface. The cephalopods use these neurally controlled color changes to adapt their body color to the environment, imitating poisonous fish, signaling conspecifics, etc. [Norman et al., 2001; Hanlon et al., 2005; Huffard et al., 2005; Hanlon, 2007].

The behavior of the millions of chromatophores can be static (when camouflaging) or very dynamic as they create complex moving patterns along the body that may be termed ‘traveling waves’ (see online suppl. video provided by Andrew Packard; for all online suppl. material, see www.karger.com/doi/10.1159/000353419). The existence of such waves indicates that the individual chromatophores are not independent. Rather, such waves can be seen as an example of biologically generated ‘dynamic attractors’. This term is used here because the stereotypical spatial and temporal patterns of chromatophore flashing are analogous to an important property of neuronal networks, viz. their activity converges into ‘attractors’, theoretically defined as stable states in network dynamics [Cossart et al., 2003]. The emergent stable states may represent an important computational property of the nervous system [Hopfield, 1982].

The stereotypical activity patterns of the chromatophores are generated independently of the higher control centers, demonstrating self-organization within this system. The interactions between the chromatophores leading to this self-organized behavior are not entirely understood, but they may be mediated by electrical coupling between the muscles [Packard, 2006]. It is conceivable that, as suggested by the concept of embodied organization, these internal self-organization properties of the chromatophore system simplify its motor control, since the central commands may make use of these basic patterns of behavior. These may be similar to the motion primitives for bending that are instrumental in the motor control of octopus reaching and fetching movements (see below) [Flash and Hochner, 2005].

Examples of Self-Organization in Nervous Systems

The scope of this paper does not allow describing in detail several reports, where the involvement of self-organization properties could be implicated in the functional organization of central pattern generators. An interesting example is the pyloric circuit of the stomatogastric ganglion of the crab [Prinz et al., 2004; Goaillard et al., 2009]. In these studies a substantial variability in the level of expression of different ionic channels and the strengths of the synaptic connections was demonstrated in identified cells in different animals. However, this heterogeneity has little effect on the dynamics of the network output. Such homeostatic regulation that converges neural activity to the same target may be achieved by self-organization.

Self-organization based on simple interaction rules was suggested to explain the developmental pattern of connectivity leading to the unique ‘pinwheel’-shaped ori-

entation columns of the mammalian visual cortex. The lack of close phylogenetic relationships among mammals possessing this pinwheel organization [Kaschube et al., 2010; Miller, 2010] suggests that it evolved several times independently. Because self-organization can explain pattern formation independently of genetic instructions [e.g. see Sasai, 2013], this finding is easy to explain if self-organization, rather than genetic instructions, is involved in the development of the visual cortex. Self-organization mechanisms have also been implicated in forming the neural connections in the olfactory bulb of rodents [Nowotny et al., 2005].

A Detailed Example from the Cephalopod Nervous System

Octopuses and cuttlefish show extremely sophisticated behavior on par with that of lower vertebrates [Hochner et al., 2006]. The vertical lobe (VL) of the central brain plays a major role in their learning and memory, an essential component of this sophisticated behavior. The network in the VL is simple and has been characterized as a ‘fan-out fan-in’ neural network (fig. 5a) [Shomrat et al., 2011]. In the octopus, 1.8 million axons enter the VL from the superior frontal lobe (SFL). These fan out to innervate en passant tens of millions of small amacrine interneurons (AM) in the intermediate neuron layer. The dendrites of the amacrine interneurons converge (fan-in) to innervate only about 65,000 large neurons (LN), which are the sole output of the VL [Young, 1971]. Their targets outside the VL are still unknown.

Cuttlefish and octopus VL share the same electrophysiology and connectivity but show great differences in synaptic properties. In both the octopus and the cuttlefish the synaptic input to the amacrine interneurons is glutamatergic, but only in the octopus is this synaptic connection endowed with a robust activity-dependent long-term potentiation (LTP) [Shomrat et al., 2011]. This LTP is important for the acquisition of long-term memory [Shomrat et al., 2008]. Only in the octopus does this glutamatergic connection demonstrate short-term synaptic plasticity and short-term serotonin-mediated presynaptic facilitation, similar to that found in learning and memory of the defensive reflex in the simpler mollusc *Aplysia* [Kandel, 2001; Glanzman, 2010]. In both species the synapses onto the large efferent neurons (fan-in) are cholinergic. These synapses show a robust LTP in the cuttlefish but not in the octopus [Shomrat et al., 2011]. That is, the two networks have the same architecture, but the synaptic plasticity is located in a different layer of the network in each species.

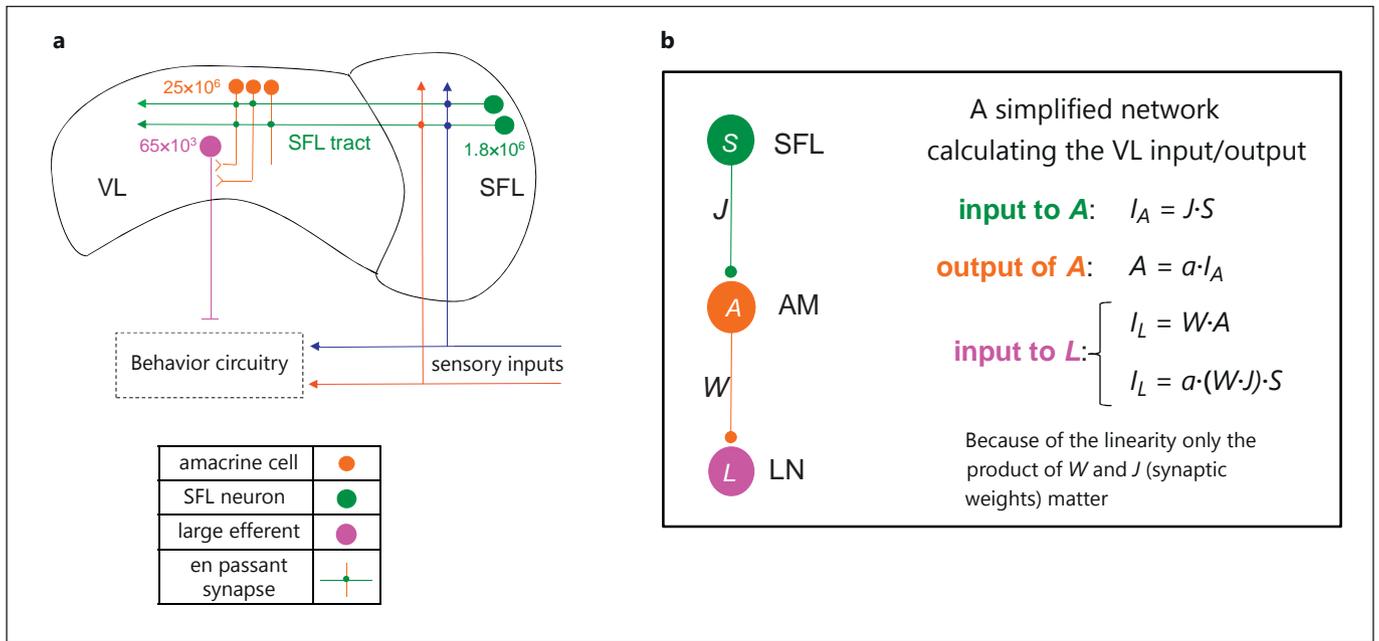


Fig. 5. The learning and memory networks of octopus and cuttlefish vertical lobe (VL) systems have similar ‘fan-out fan-in’ architecture. **a** The main connectivity and cell numbers of the learning and memory system of the octopus. From Shomrat et al. [2011]. **b** A simplified three-cell network to demonstrate the dependence

of the input/output relationship on the synaptic properties. See text for details. a is a constant, and S and A denote the activity of the superior frontal lobe (SFL) and AM neurons, respectively. From Hochner [2012].

This difference is surprising considering that these species are closely related. The computational analysis shown in figure 5b provides a possible explanation. This suggests that the VL networks in each of the respective species perform the same computation if there is a linear input/output relationship at the intermediate synaptic layer between the amacrine and the large cells [Shomrat et al., 2011]. The input/output relation has been simplified in figure 5b to a network containing only one cell in each layer. The network equation shows how the input to the large neuron (LN) depends on the activity of the input neurons (SFL). If the input/output relationship of the amacrine interneurons (AM) is linear, then the input to the large neuron is given by the product of the synaptic weights (strength) of the first (J) and second (W) synaptic layers. That is, the input/output relationship can be equally modified by changing either the first or the second synaptic connections. This means that the computational capabilities of the two networks are similar. Physiological recordings have confirmed that this relationship is linear in both the octopus and the cuttlefish [Shomrat et al., 2011].

If the networks of the two species carry out similar computations, why have they evolved diametrically dif-

ferent synaptic properties? A possible answer is that neural networks converge to specific computational properties similarly to the stomatogastric networks of crabs which converge to a similar motor output (see above). If the computational properties of the vertical lobe network are self-organized, like the orientation pinwheel in the vertebrate visual cortex (see above), then the properties of the neurons can be selected so that, with self-organization, they give rise to a specific computation. In this scenario natural selection selects for the self-organized computational properties rather than for the particular properties of each neuron in the network. Therefore self-organization and natural selection may work together to select for global properties [see discussions of this issue in Weber and Depew, 1996; Batten et al., 2008; Swenson, 2010].

The Octopus as an Example of a Unique Biological Embodiment

The special morphology of the octopus illustrates how embodied organization involves not only morphological adaptation of the body plan together with the anatomical

organization of the nervous system (discussed above), but also the functional organization of the nervous and muscular systems (schematized in fig. 4).

Eight Long, Flexible Arms: A Challenge to Sensory Representation and Motor Control

Octopuses can elongate, shorten, and bend their arms in any direction and at any point along their length. There are virtually unlimited ways of performing a specific task, posing a great challenge to their motor control system which must theoretically deal with a practically infinite number of degrees of freedom.

A further complexity resulting from this high redundancy is the representation of the sensory information gathered by a structure with no defined morphological constraints. The octopus nervous system must in some way represent the spatial information from millions of tactile, chemical, and proprioceptive afferent fibers distributed along the arms and suckers to make this information available for movement planning. This problem is much simpler for animals with limited degrees of freedom due to a limited number of stiffened joints, because a fixed body plan allows representation of the spatial information in body and joint space coordinates. Somatotopic representation in the vertebrate cortex is therefore an efficient way to represent the spatial parameters of sensory information in the brain. In an animal like the octopus, where only the head has a fixed relation to the outer world (fig. 4) and the rest of the body is hyper-redundant with no defined morphological constraints, a huge number of parameters would be needed to define a spatial relation between different body parts. This would make somatotopic representation an inefficient mechanism for representing sensory information in the motor control system, because additional, probably very complex, mechanisms, like a dynamical internal model of the flexible body, would be needed to use somatotopically represented information for generating motor commands. Indeed, the octopus uses the arm itself for representing the spatial information needed for the computation (see octopus fetching behavior below).

The Organization of the Higher Motor Centers

As in other modern cephalopods, the higher motor centers in the octopus lie in the basal lobes in the supraesophageal part of the central brain [Boycott, 1961]. These centers are not organized somatotopically [Zullo et al., 2009]. Unlike vertebrate motor cortex, local electrical stimulation within the basal lobes does not activate localized movements but only complex behavior whose com-

plexity increases with stimulus intensity [Zullo et al., 2009]. With a somatotopic organization, one would expect local stimulation to activate only a single arm, but stimulation evoking arm extensions, for example, always activates several arms together. These results suggest that motor programs are represented in the higher motor centers rather than body parts [Zullo et al., 2009]. Note that local stimulation in the vertebrate motor cortex may also evoke complex motor actions [Todorov, 2000; Graziano and Aflalo, 2007], suggesting that under the right conditions the somatotopically represented information can be integrated into motor actions. In the octopus, on the other hand, only complex motor actions are represented, suggesting a different way of processing motor commands in the higher motor centers.

Sensory representation also does not appear to be somatotopically organized. Tactile and visual responses recorded in the motor areas show no somatotopy; a site responding to local tactile stimulation of an arm responds equally well to stimulation all along the arm and of different arms [Zullo and Hochner, unpubl. data]. Both the sensory and the motor representations are thus distributed throughout the basal lobes. Experiments with natural behavior and with isolated arms demonstrate that motor commands and even computations are generated or performed within the arm itself (see below) [Zullo and Hochner, 2011; Hochner, 2012]. All of these findings fit the octopus higher motor centers being organized to command complex peripheral motor programs.

The Unique Neuromuscular System of the Octopus Arm

The neuromuscular system of the octopus arm (and most likely of other molluscs) differs dramatically from those of skeletal animals, vertebrates, and arthropods [Matzner et al., 2000; Rokni and Hochner, 2002; Gutfreund et al., 2006; Feinstein et al., 2011]. The differences can be viewed as an adaptation of the 'mechanical system' (fig. 1) to a flexible embodiment (fig. 4).

The muscle cells of the arm are small ($\sim 1,200 \times 10 \mu\text{m}$) and electrically compact (isopotential). Each muscle cell is innervated by three excitatory cholinergic motoneurons at a discrete synaptic junction near the center of each cell. This synaptic input can control the membrane potential of the entire cell, most likely due to its electrical compactness [Matzner et al., 2000; Neshet et al., 2011]. Fast sodium spikes are thus unnecessary for spreading the electrical signal along the cell, as in vertebrate muscle cells. Only calcium action potentials acti-

vate the contractile machinery. 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 uncommon in invertebrates, suggest that the octopus neuromuscular system uses a more linear transformation of neuronal activity into muscular action. The muscle cells in the antagonistic longitudinal and transverse muscles all show similar properties, possibly also simplifying neural motor control [Matzner et al., 2000; Feinstein et al., 2011].

In contrast to the octopus, arthropods have a skeletal muscle system more like the vertebrates (although the skeleton is external rather than internal as in vertebrates). Also in contrast to the octopus muscular system, the arthropod external skeleton is operated by a relatively small number of large muscle cells, each controlled by polyneuronal and multiterminal innervation. The membrane potential of the large muscle cells is controlled by synaptic inputs from the nerve terminals distributed over their surface and no regenerative action potential is required for spreading the activity. Arthropod neuromuscular junctions show short-term synaptic plasticity with short-term facilitation and/or depression and postsynaptic inhibition and, thus, part of the computation of the motor output is performed at the level of the neuromuscular junction [Bullock and Horridge, 1965].

The special properties of the octopus muscle cells appear specifically suited to a flexible movement system. The intrinsic muscles of the arms, which generate both the arms' stiffness and their movements, are innervated by an extremely large number of motoneurons distributed along the arm nerve cord ($\sim 4 \times 10^5$ motor neurons per arm) [Young, 1971]. Based on the muscle cell size, a motor unit (the muscle cells innervated by a single motor neuron) comprises about 3,300 muscle cells [Feinstein et al., 2011], occupying a volume of only about 0.2 mm^3 of the arm musculature. This innervation pattern may achieve a highly localized and continuous neural control of this nonsegmented arm structure and is ideal for generating the waves of muscle activation typically observed in octopus arm movements [Gutfreund et al., 1998; Sumbre et al., 2006].

The Organization of Arm Motor Control: Managing the Degrees of Freedom

The typical reaching movement, in which the octopus extends one or several arms toward a target, exemplifies the strategies used by the octopus to simplify control in a motor system with a potentially infinite number of de-

grees of freedom. The octopus simplifies the control of goal-directed movements by propagating a stereotypical bend along the arm from base to tip. This bend can be viewed as a motor primitive out of which more complex movements can be generated by combining it with other motor primitives [Flash and Hochner, 2005]. This strategy of using a bend propagating along the arm as a motor primitive radically simplifies the motor control because the propagating bend is controlled by just one parameter (one degree of freedom). This control strategy thus collapses the infinitely large number degrees of freedom to be controlled during reaching into just three: two for the direction of the base of the arm and the third for scaling the propagation velocity of the bend along the arm [Gutfreund et al., 1996]. Electromyography (EMG) during reaching in freely behaving animals was used to test the relationship between muscle activity and the kinematics. The recordings suggested that reaching is controlled by a feed-forward (ballistic) motor program [Gutfreund et al., 1998].

Movements with the natural kinematic characteristics can be elicited in an amputated arm by tactile stimulation of the skin or by electrical stimulation of the arm nerve cord [Sumbre et al., 2001]. This shows that the circuits for generating the movement are embedded in the neuromuscular system of the arm itself. If the detailed movement programs are embedded within the peripheral nervous system, somatotopic arm representation in the higher motor centers may no longer be necessary. Rather, the higher control centers may represent more complex and multi-limb behavioral programs, as indeed was found (see above) [Zullo et al., 2009].

Kinematic and dynamic (muscle action) analysis of fetching behavior provides an even more striking demonstration of how the arm's flexibility is exploited to simplify not only motor programs, as in reaching, but also more complicated computational processes [Sumbre et al., 2006]. In the fetching movement, the octopus grasps food with its suckers anywhere along the length of the arm and brings it precisely to its mouth. To do this, it reshapes its arm into a quasi-articulated structure by dividing the section of the arm from the base to the food into three segments – proximal, medial, and distal. The distal segment grasps the food and serves as a 'hand', while the proximal and the medial segments are of similar length, like our upper arm and forearm. Like humans, the octopus can bring food precisely to the mouth mainly by rotating the medial joint ('elbow') [Sumbre et al., 2005].

How does the octopus compute the shape of this stiffened structure to fit the changing grasping location along the arm? Correlating muscle activity and kinematic features of the octopus fetching movement revealed the mechanism for calculating the structure of the quasi-articulated arm for each grasping location [Sumbre et al., 2006]. EMG recordings at various locations along the arm showed that grasping the food elicits two waves of muscle activation that propagate one toward the other; one propagates from the grasped food toward the base of the arm, while the other propagates from the base of the arm toward the food. The medial joint is formed where the two waves collide. This simple mechanism explains how the articulated structure can be dynamically computed at the level of the arm for each fetching movement [Sumbre et al., 2006]. Note that this mechanism does not require central representation of the arm because the computation is done at the periphery (see above).

The fetching movement is thus a striking demonstration of biological '*morphological computation*', a notion tightly associated with embodied organization [Pfeifer et al., 2006], where dynamical changes in the morphology may take part in setting the temporal and spatial parameters of a computation algorithm.

Conclusions

Using octopus biology as an inspiration for robotics [Walker et al., 2005; Calisti et al., 2011; Li et al., 2011; Hochner, 2012] has led to the application of the robotics embodiment concept to the octopus and likely to animals in general. Here it was shown that all components of the octopus embodiment have special properties due to the need to adapt to the octopus' unique morphology and flexibility (fig. 4). The concept of embodied organization also explains the vast covariation of the body plan with the size and organization of the nervous system and with the complexity of behavior generally in the phylum Mollusca.

A very important property of embodiment in robotics is that the components of the embodiment (fig. 1) have self-organizational properties. That is, the embodiment itself shapes some of its properties. Therefore, when trying to adopt the term embodiment in biology, we appear to be entering into a conflict with natural selection as the driving force for evolution [see Weber and Depew, 1996; Batten et al., 2008; Swenson, 2010], because self-organization and natural selection both may converge to similar solutions. It is therefore not easy to explicitly point out

self-organizational processes in biological systems. Self-organization in the nervous system, for example, may make use of many plastic processes like short- and long-term synaptic plasticity, neuromodulation, and hormonal modulators. All of these processes may lead to what may be defined as 'biological self-organization', i.e. biological regulation mechanisms that determine to what dynamical state the system will converge. This self-organization has more complex properties than the simpler direct physical and chemical interactions that may be implicated, for example, in 'self-regulated' biological pattern formation [Kondo and Miura, 2010].

In the main text I highlighted findings that offer support for 'biological self-organization'. These suggest that, due to self-organizational properties, the embodiment dynamically collaborates with genes to determine the properties of the embodiment's components. This means that self-organization properties of the components may lead to the emergence of different global properties when the interactions of a component with the embodiment are manipulated (e.g. the self-organized behavior of the isolated chromatophores) or where internal interactions within a structure lead to the emergence of a global morphological property like the optic cup [Sasai, 2013]. Self-organization mechanisms as part of the embodied organization may explain why phylogenetically close species evolved systems carrying out the same function using elements with different properties as in octopus versus cuttlefish VL (fig. 5) and the crab central pattern generators [Goaillard et al., 2009]. In other cases, systems may evolve different functional organization using elements with similar properties (e.g. the pinwheel organization of orientation columns that evolved independently several times in visual cortex of mammals) [Kaschube et al., 2010].

In conclusion, I think that embodiment and self-organization may explain that not every property has been developed by natural selection. They also suggest how evolutionarily selected properties can account for a very large repertoire of emerging global properties despite the surprisingly limited repertoire of genes (a few tens of thousands) that are largely shared by all living organisms. I find the analysis of the genetic source for the convergent evolution of camera-like eyes of octopuses and humans [Ogura et al., 2004] to be supportive of this conclusion.

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