Octopus Motor Control

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Summary and Keywords

The octopus, with its eight long and flexible arms, is an excellent example of the independent evolution of highly efficient motor behavior in a soft-bodied animal. Studies will be summarized to show that the amazing behavioral motor abilities of the octopus are achieved through a special *embodied* organization of its flexible body, unusual morphology, and a unique central and peripheral distribution of its extremely large nervous system. This special embodied organization of brain–body–environment reciprocal interactions makes it possible to overcome the difficulties involved in generation and control of movement in an animal, which unlike vertebrates and arthropods lacks rigid skeletal appendages.

Keywords: mollusks, cephalopods, octopus, embodied organization, soft-body, motor control, motor program, goal-directed movements, locomotion

Introduction

The behavioral abilities of the *Octopus vulgaris* are achieved through a special *embodied* organization of its flexible body, unusual morphology, and a unique central and peripheral distribution of its extremely large nervous system. This organization enables this non-social, solitary hunter to survive well and compete successfully with vertebrates in the same ecological niche (Packard, 1972). This way of life is supported by a combination of good vision, excellent maneuverability, fast locomotion, and efficient defensive mechanisms such as camouflage (Hanlon & Messenger, 2018; Wells, 1978)—all coordinated by advanced cognitive abilities, supported by an efficient learning and memory system (Shomrat, Turchetti-Maia, Stern-Mentch, Basil, & Hochner, 2015; Turchetti-Maia, Shomrat, & Hochner, 2017). These active hunting and defensive behaviors, among others, require a motor control system that can efficiently integrate past experiences with the processing of a huge quantity of sensory information from the hundreds of millions of sensory cells in the highly evolved visual, tactile, and chemical senses.

Octopuses arouse curiosity because their body design differs from that of any other known large and highly active animal. The main external parts of the body of the common octopus (*Octopus vulgaris*) are shown in Figure 1. Less well known than their seemingly strange shape is the fact that *Octopus vulgaris* displays a rich behavioral repertoire. To give a sense of the richness to those unfamiliar with the behavior of the octopus, several examples are given (for a more comprehensive description, see Hanlon & Messenger, 2018; Huffard, 2007; Mather, 2008; Wells, 1978). Octopuses have two means of swimming, either by moving the arms to create rowing motions of the web of skin running between the arms, or by using the siphon to jet a strong stream of water, thereby creating propelled swimming. Apart from being used in swimming, the siphon, which usually serves for breathing, can also be used as a defensive tool; in moments of danger, the octopus emits a strong jet of water mixed with ink through the siphon in the direction of the predator to obscure its field of vision, thereby increasing the octopus's chances of successful escape. The syphon's controlled stream of water can also be used to clean the den or to remove sand from an object such as a coconut shell, making it easier for the octopus to carry and use it as a "portable house", as shown in a study on tool usage by octopuses (Finn, Tregenza, & Norman, 2009).

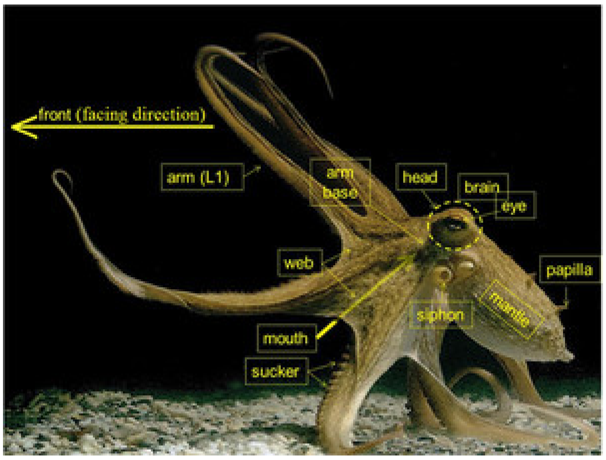

Figure 1. The unique morphology and body parts of *Octopus vulgaris*. The front side (facing direction) is shown by a thick arrow. The first left arm (L1) is labeled. Two suckers on one of the arms (L3) are shown by arrows. Part of the interbrachial web that runs between the proximal parts of the arms (L1+L2 and L2+L3) is labeled with arrows. The head that is positioned above the arm bases is labeled along with the left eye, and the location of the brain between the two eyes is also marked. The mantle is labeled along with the siphon, as is one of the skin papillae. The location of the mouth just below the head, surrounded by the arm bases, is marked by an arrow that is depicted as running below the web skin (adapted from Levy et al., 2017).

Octopus arms are a source of inspiration for the design of sophisticated flexible manipulators. In nature, the power of these arms can be seen when they open large clams. Their strength can also be seen in the laboratory, where they occasionally succeed in removing the heavy lids of their aquarium to escape, or when they open a jar plunger to obtain a crab from inside (Anderson & Mather, 2010; Fiorito, von Planta, & Scotto, 1990). Octopuses have several patterns of arm-propelled locomotion, such as walking, crawling, and climbing (see the section "***CONTROL OF ARM COORDINATION IN LOCOMOTION***"). Some species can use their arms for mimicry (Norman, Finn, & Tregenza, 2001), shaping them into algae-like branches, while using two arms for a rare bipedal form of walking (Huffard, Boneka, & Full, 2005). They can use one or several arms for stereotypical goal-directed movements, like reaching to a target and fetching food to their mouth (see the section "***CONTROL OF GOAL-DIRECTED ARM MOVEMENTS***"). Octopuses hunt by "netting" the prey with the interbrachial skin web that is stretched between the arms (Figure 1). Once collected in this net, the prey is held tightly and then paralyzed and undergoes external digestion by venom secreted from the octopus's salivary glands, before being slowly chewed by the hard beak of the mouth (Welsh, 1964). While consuming the prey, the octopus can continue hunting and collecting multiple food items in the interbrachial web. Octopuses can drill through clam shells to inject them with paralyzing and digesting materials secreted from their salivary glands (Fiorito & Gherardi, 1999).

About 300 suckers are aligned along each arm and function like sophisticated manipulating and sensing "fingers". The arms probe and search the environment aided by the millions of chemical and tactile receptors embedded all over the skin (most densely at the sucker rims). Using their suckers, octopuses collect stones for building or blocking their dens, passing them along their arms like along a "conveyor belt". The suckers are also used for grooming (see the documentary videos on the Octopus Group). There are no principle differences among the eight arms, except for the third right arm (hectocotylized arm) that the male octopus uses for introducing sperm into the mantle cavity of the female (Wells, 1978). Beyond the scope of this article are the separate chromatophore, iridophore, and subcutaneous musculature systems that are responsible for the fast and detailed changes in body color pattern and shape used by the modern cephalopods (Coleoidea) for frightening, "displaying mood", communication, and camouflage (see Chiao & Hanlon, 2019).

The Difficulty Involved in Motor Control of a Flexible Body

It is thought that the cognitive process of predicting the outcome of a specific behavioral action is computed by interfacing the sensory and motor information through some sort of internal *representation* of the two systems in the central controller. One prominent example of such organization is the somatotopic representation (i.e., in body-part coordinates) of sensory and motor information in the primary sensory and motor cortices of vertebrates. In humans, this creates representations in the forms of sensory and motor *homunculi* ("small human beings") (Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2012; Penfield & Rasmussen, 1950).

The soft and flexible body of the octopus poses major difficulties for basing motor control on sensory and motor representations of body parts. Topographical representation of the motor system is impractical because the long, slender arms are unsegmented and can deform at any point along their length. That is, at any point along its length each arm can bend in any direction, elongate, shorten, and twist either clockwise or counter-clockwise (see the section "***THE BIOMECHANICS OF THE OCTOPUS ARM***"). This requires the motor control system of the octopus to coordinate a virtually infinite number of variables. Topographical representation of the sensory system is similarly impractical, because the hyper-redundancy of the body and arms gives rise to a virtually endless number of spatial parameters that would be required to represent the source of sensory information with respect to the environment. In short, this hyper-redundancy of the octopus and the lack of limitation by the number of skeletal joints make the representation of information in body coordinates unrealistic.

Studies of octopus motor behavior have indicated that evolution has led to the emergence of unique strategies in the motor control system of the octopus, which are able to solve the difficulties involved in controlling its hyper-redundant, flexible body. These will be summarized in this article. These unique mechanisms, together with the unique morphology and organization of the octopus's nervous system, demonstrate an efficient *embodied* solution to the problem of motor control in soft-bodied animals (for review, see Chiel & Beer, 1997; Chiel, Ting, Ekeberg, & Hartmann, 2009; Hochner, 2012, 2013; Levy, Nesher, Zullo, & Hochner, 2017; Zullo & Hochner, 2011). The embodied organization has led to the selection of solutions that encompass tradeoff between the advantages provided by the high maneuverability of a soft hyper-redundant body and the limited computational resources that the relatively slow biological networks can provide. The embodied organization which was discussed (not always using explicitly this term) both in robotics and biological contexts (Brooks, 1991A, 1991B; Chiel & Beer, 1997; Chiel et al., 2009, Pfeifer, Lungarella, & Iida, 2007, 2014) demonstrates an important evolutionary principle and provides insights and inspiration for a distinct and prominent engineering approach—that control can be dramatically simplified by adapting the morphology to the task.

The Biomechanics of the Octopus Arm

The octopus arm, like other cephalopod tentacles, the elephant trunk, and the vertebrate tongue, lacks a rigid external or internal skeleton. In these organs, stiffening the muscles provides an alternative to skeletal support, against which contractions of other muscles can generate movement. Kier and Smith (1985) called this type of structure a "muscular hydrostat", because it is mainly composed of closely packed, incompressible muscle tissue, organized in different orientations—longitudinal, transverse, and in some cases, oblique (Figure 2A). Longitudinal and transverse muscles occupy, all along the longitudinal axis of the arm, the outer and an inner portion of the arm respectively, thus allowing transverse muscles to enclose the arm nerve cord running most centrally.

The incompressibility of the muscles constrains a muscular hydrostat to a constant volume. Due to this constraint (Figure 2B), the different muscle groups can work antagonistically against each other, because any change in the length of one group must be compensated by (passive) changes in the length of the others—a fundamental biomechanical principle. Muscle cells can produce active force only when shortening, and therefore elongate only when counteracting active shortening of other groups of muscles.

Reduction of arm diameter by contraction of the transverse muscles causes the arm to passively elongate, and shortening of the arm by contraction of the longitudinal muscles causes the arm to passively thicken. In both muscular-hydrostatic and skeletal systems, co-contraction of antagonistic muscle groups creates stiffening—a fundamental component in posture, locomotion, and movement. In cephalopods, particularly in the octopus, this characteristic seems to have developed to an unprecedented specialization. Stiffening can occur in the entire arm or in one or more of the two lateral, ventral, or dorsal longitudinal “muscular beams” (Feinstein, Nesher, & Hochner, 2011). Stiffening on one side of the arm is instrumental for producing forceful (to distinguish from passive) bending, because the stiffening of muscle groups on one side of the arm creates a dynamical beam that resists length changes on this side, thereby enabling the generation of inward/outward bending upon shortening/elongation of the other side of the arm. The bending point on the arm and the orientation of the bending depend on the variations of combinations between the locations of the stiffening and the length-changeling sections. Stiffening and bending can also occur in discrete, sometimes small, sections of the arm, enabling a vast variety of deformations at various locations along the arm (see Feinstein et al., 2011; Kier & Stella, 2007; Yekutieli, Flash, & Hochner, 2009, for more details).

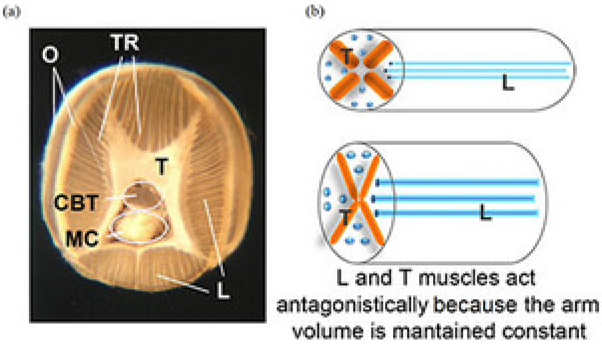

Figure 2. The intrinsic structure of octopus arm. (a) Transverse section of an arm showing the main components of the arm: arm nerve cord comprising cerebrobrachial tracts (CBT); medullary cord (MC); transverse muscles (T); trabeculae muscles (TR); longitudinal muscles (L); oblique muscles (O) (b) Constant volume constraint and antagonistic behavior of T and L muscles. Contraction of the transverse muscles causes the arm to become thinner (smaller diameter), and due to the constant volume constraint, this also causes it to elongate. Contraction of the longitudinal muscles causes the arm to shorten and, due to the constant volume constraint, also causes it to thicken.

The Unique Organization of the Neuromuscular System of the Octopus’s Arm

The neuromuscular system of the octopus arm differs dramatically from those of skeletal animals—both vertebrate and arthropod (Feinstein et al., 2011; Gutfreund, Matzner, Flash, & Hochner, 2006; Matzner, Gutfreund, & Hochner, 2000; Nesher, Maiole, Shomrat, Hochner, & Zullo, 2019; Rokni & Hochner, 2002; Zullo, Fossati, Imperadore, & Nodl, 2017). The neuromuscular system of the octopus arm includes the intrinsic musculature responsible for generating arm movements and an additional muscular system responsible for generating the sophisticated movements of the ~300 suckers per arm. These two muscular systems are innervated by ~3 million motor neurons distributed along the arm nerve cord. About 400,000 of these innervate the intrinsic muscles, and thus control arm movements.

The muscle cells of the arm musculature are small (~1,200 x 5 µm) and electrically compact and isopotential; that is, there is no voltage decrement along the cell (Matzner et al., 2000). Each muscle cell is innervated by three distinct types of excitatory cholinergic motor neurons converging at a single neuromuscular junction at the center of each muscle cell (Matzner et al., 2000; Nesher et al., 2019). Due to the electrical compactness of the muscle cells, these synaptic inputs control the membrane potential of the entire muscle cell, making the fast sodium action potentials that spread the electrical signal along the cell (as in vertebrate muscle cells) unnecessary. Indeed, the synaptic inputs to the muscle cells can activate the contractile machinery by activation of voltage-dependent L-type calcium channels. Uniquely to these muscle cells, at relatively high voltages, the L-type calcium channels can also generate fast calcium action potentials which likely participate in a vigorous activation of muscle contraction (Nesher et al., 2019; Rokni & Hochner, 2002).

The neuromuscular synaptic inputs lack both short-term synaptic plasticity (no short-term facilitation or depression) and postsynaptic inhibition (Matzner et al., 2000). The lack of these synaptic properties, which are frequently found in the neuromuscular systems of other invertebrates (Atwood & Karunanithi, 2002; Bullock & Horridge, 1965), suggests that the neuromuscular system of the octopus uses a more linear transformation of motor neuronal activity into muscular actions, more similar to the transformation found in vertebrate neuromuscular junctions. Such an organization may better fit a feedforward type of motor commands like those found in the octopus’s reaching movements (see the section “***CONTROL OF GOAL-DIRECTED ARM MOVEMENTS***”).

The muscle cells in the antagonistic longitudinal and transverse muscles show similar morphological and physiological properties (Feinstein et al., 2011; Matzner et al., 2000; Nesher et al., 2019). This unification of muscle cell properties in all muscle groups possibly simplifies the neural organization of motor programs. It also emphasizes the importance of the highly ordered morphological organization of the arm musculature and connective tissues in determining the biomechanics of the arm as a muscular hydrostat (see Figure 2A and Feinstein et al., 2011; Kier & Stella, 2007).

The intrinsic muscles of the arms, which generate both stiffness and movement, are innervated by ~400,000 motor neurons distributed along each arm nerve cord (Young, 1971). A rough calculation based on the average size of the muscle cells indicates that a motor unit (all 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’s total intrinsic musculature volume. This innervation pattern and density may achieve both highly localized and smooth, continuous neural control of this non-segmented arm musculature. This design is most likely optimized for generating the waves of muscle activation typically observed in octopus arm movements (Gutfreund, Flash, Fiorito, & Hochner, 1998; Sumbre, Fiorito, Flash, & Hochner, 2006).

Importantly, efferent axons from the brain do not directly innervate the arm muscles. Instead, they project to the arm nerve cord in the Peripheral Nervous System (PNS), where they activate motor neurons located at the level of the medullary cord (MC) that innervates the muscles through numerous lateral roots (Gutfreund et al., 2006).

The arm nerve cord contains a large group of low threshold axons running through the cerebrobrachial tracts (CBT) that functionally innervate long sections of the arm MC as they pass (*en passant*). These connections allow the axons to activate the motor neurons with signals passing in either direction along the arm (Zullo,Eichenstein,Maiole, & Hochner, 2019). Information from the CNS may also be transmitted to the arm via labeled lines in the CBT. However, no solid data have been provided to support the labeled line theory (Figure 3 and Zullo, Fossati, & Benfenati, 2011; Zullo et al., 2019).

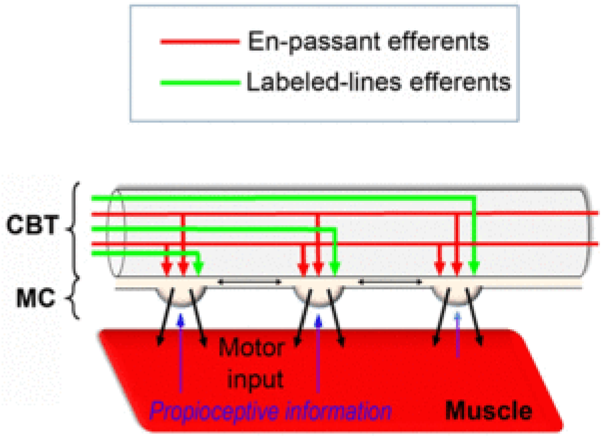

Figure 3. Scheme depicting the transmission pathway of the arm nerve cord. Two possible functional configurations of *en passant* (red) and labeled lines (green) are schematized in lateral view (adapted from Zullo et al., 2019).

These findings are not surprising in view of the organization of octopus arm motor control, in which the central brain sends efferent signals to activate the peripheral motor programs embedded in the elaborated neuromuscular system of the arm itself (Gutfreund et al., 2006; Zullo & Hochner, 2011; Zullo, Sumbre, Agnisola, Flash, & Hochner, 2009). The *en passant* distribution of the motor command represents a novel motor control mechanism that sets the point of motor action along the arm, based upon a unique interplay between global central commands and local sensory signals (Zullo et al., 2019). Such interplay between CNS and PNS may be involved in the morphological computation of the bending points along the arm during fetching movements (Sumbre, Fiorito, Flash, &

Hochner, 2005; Sumbre et al., 2006). This control mechanism functions without central representation of the long, flexible arms (Zullo et al., 2009).

The advantage of the *en passant* configuration may be seen in actions such as stiffening. Generating stiffening requires the simultaneous contraction of a large part of the arm musculature to create a dynamic skeletal structure essential for generating movements in muscular hydrostats. Arm stiffening is important in a variety of motions from bend propagation to the creation of pseudo-articulated structures during fetching (see the section “***CONTROL OF GOAL-DIRECTED ARM MOVEMENTS***”). These movements are widely used in the behavioral repertoire of octopuses.

The Unique Organization of the Octopus’s Central and Peripheral Nervous Systems

The exceptional anatomical organization of the octopus’s nervous system has been described in Young (1971). As shown schematically in Figure 4, the nervous system of the octopus (and 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 via numerous nerve bundles; and the peripheral nervous system of the arms containing two thirds of the total ~500 million nerve cells of the octopus’s nervous system.

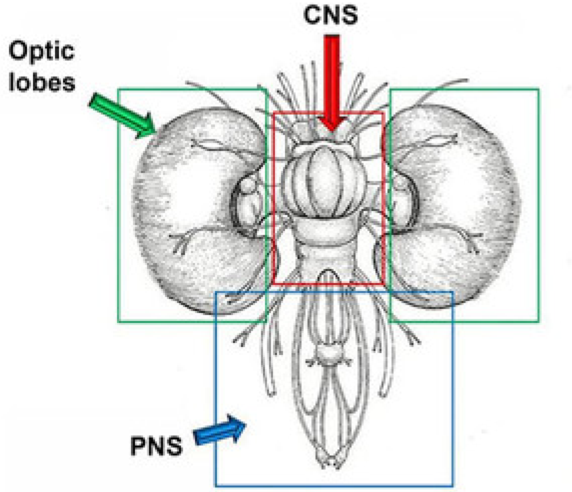

Figure 4. The octopus’s nervous system. The octopus central brain mass is composed of a central nervous system (CNS, red rectangle) occupying a central position between the eyes, two large optic lobes (green rectangles), and the peripheral nervous system of the arm (PNS, blue rectangle) that emerges from the central brain mass and passes through the arms via numerous nerve roots (adapted from Guglielmino et al., 2013).

These structures are all highly metabolically active, as in vertebrates, and their level of activation is linked to their physiological state (Zullo et al., 2018). Relatively few afferent and efferent fibers interconnect the peripheral nervous system of the arms with the central nervous system. This led Young (1971) to suggest that much of the processing of motor and sensory information required to generate movements, are performed in the peripheral nervous system of the arm. The higher centers of the central brain and the optic lobes fulfill more cognitive and executive functions like motor coordination, decision-making, and learning and memory.

The Unique Organization of Higher Motor Control Centers in the Octopus's Brain

A fundamental function of all central nervous systems is to interface the external and internal sensory information with preprogrammed motor programs and, based on stored information (experience), to orchestrate motor actions that can achieve a rewarding goal or avoid worthless targets. It is generally accepted that this interfacing involves some sort of *representation* of the sensory and motor information in dimensions that enable neural network algorithms to compute optimal decisions. The octopus is a special case (see the "**INTRODUCTION**"). Its unique body plan with its high redundancy poses many difficulties in representing the sensory and motor information in maps based on body-part coordinates, as is found universally in vertebrates.

In most animals, sensory information received peripherally is encoded and transmitted to the CNS, where this information is decoded, processed with the help of representation maps and past experience, and then encoded into motor commands output. These commands, in turn, are transmitted back to the PNS, where they are decoded into specific muscles or muscle synergy actions (d'Avella, Saltiel, & Bizzi, 2003; Flash & Hochner, 2005; Matheson, 2002). Very common in invertebrates, especially arthropods (see the octopus arm in the "***THE UNIQUE ORGANIZATION OF THE NEUROMUSCULAR SYSTEM OF THE OCTOPUS'S ARM***"), this decoding can take place even at the level of the neuromuscular junction, due to the polyneural innervation by excitatory and sometimes also inhibitory motor neurons, each with different short-term plasticity properties (Atwood & Karunanithi, 2002; Bullock & Horridge, 1965). These properties allow some degree of tuning of the motor commands from the CNS at the neuromuscular system level, which thus determines the final motor responses of the limbs. Therefore, in arthropods, for example, the neuromuscular system is part of the computational network that determines the motor output. In contrast, in vertebrates, as in octopus neuromuscular junction, the motor output is controlled more directly by the pattern of spiking activity of the motor neurons, each innervating a single group of muscle cells (i.e., a motor unit). It is interesting to note that a more linear relationship between motor neurons activity and muscle cells activation, that exist in vertebrates and octopus neuromuscular systems, may suit better a feedforward type of motor control where the neuronal output is centrally computed to achieve ballistically the final goal.

In the organization of the classical central control in vertebrates, motor planning is based on somatotopic representation of the body in the CNS, that is, spatial representation of the sensory and motor systems of the body in the central sensory and motor cortices in body-part coordinates. However, the octopus shows a quite different organization. The octopus has an active body with eight long and highly flexible arms (see the "**INTRODUCTION**"). Controlling these hyper-redundant limbs, which have a virtually unlimited number of degrees of freedom (DOFs), would be extremely challenging for any biological (or artificial) system, and somatotopic maps like those found in vertebrates cannot be practically implemented.

The octopus seems to have overcome this problem through the co-evolution of its unique body plan (Figure 1) together with the special organization of its higher motor control centers—these do not follow the classical somatotopic representation principles of vertebrates. Extensive micro-stimulation of the CNS by Zullo et al. (2009) showed that discrete electrical stimulation within the higher motor center in the basal lobes (see octopus brain anatomy in Figure 4 and in Turchetti-Maia et al., 2017) can initiate reproducible stereotypic motions belonging to the animal's behavioral repertoire (Zullo et al., 2019). In contrast, other natural movements of the octopus were impossible to elicit. For example, micro-stimulation never elicited the stereotypic fetching movement that the animal commonly uses to bring objects to its mouth (see the section "***CONTROL OF GOAL-DIRECTED ARM MOVEMENTS***"). This may be explained by the unique nature of the control of this movement, which depends on peripheral sensory input arising in the arm from the grasped object. It is this sensory input that initiates the central command triggering the peripheral motor program for reshaping the arm into a *quasi*-articulated structure to bring the object to the mouth (Sumbre et al., 2006).

Various other forms of motor behavior were elicited by stimulating the basal lobes. They could be discrete action components or complex motor behavior, which could be divided into four main types—arm extension, crawling, jetting, and inking. Each complex pattern was composed of several of the discrete components recruited in a specific way for each motor behavior (Zullo et al., 2009).

Both the discrete action components and complex behaviors had no central somatotopic organization as they could be elicited over wide regions of the brain's higher motor areas. Significantly, no stimulation site for eliciting movements of only a single arm or body part could be found, even though it was possible to demonstrate a certain degree of lateralization. These findings fit the morphological data which suggest a lack of somatotopic organization of afferent and efferent neurons, traced by labeling axons in the arm nerve cord (Budelmann & Young, 1985; Robertson, Schwartz, & Lee, 1993).

The stimulation experiments by Zullo et al. (2009) suggest that motor programs, rather than body parts, are represented in the higher motor centers in the octopus's brain in intermingled and distributed neural networks. This points to a unique organization, wherein single cells or groups of cells can be recruited into different pathways to generate a variety of behaviors according to the animal's ethological requirements. These overlapping circuits are consistent with a motor program representation in the form of motor primitives (as described by Flash & Hochner, 2005) that does not require representation of actions in body-part coordinates. Such mechanisms could be compared to what Graziano (2016) described as "ethological action maps". While Graziano's definition is based on the coexistence of action maps together with a standard, blurred body map along the motor cortex, Zullo et al. (2009) showed that the responses elicited from the octopus's higher motor centers are similar in nature to responses obtained by stimulating vertebrate multisensory integrative areas (Cooke, Taylor,Moore, & Graziano, 2003). These areas in vertebrates tend to be morphologically distinct from the primary motor area.

Thus, higher motor centers of the octopus appear to function as higher-order integrative areas. This conclusion is supported by an investigation of the central sensory representation in which the basal lobe was activated in response to sensory stimulation of various body parts. In other words, the sensory inputs, like the motor responses, do not appear to be somatotopically organized. The recordings in the basal lobes showed multimodal sensory responses (e.g., visual, tactile), further suggesting that cross-modal sensory integration occurs at the higher motor centers of the octopus brain.

Behavioral Assessment of How Sensory Information from the Arms Is Processed in the Brain

Behavioral learning and memory experiments can assess how octopuses perceive sensory information from their arms. Octopuses use their arms differently for different behavioral tasks, preferring certain arms for specific actions (Byrne, Kuba, Meisel, Griebel, & Mather, 2006), and they can use both visual and tactile information to control their arms. Touching the arms evokes robust electrical activity in the central brain (e.g., basal lobes; Zullo, 2004; Zullo, Sumbre, Agnisola, Flash, & Hochner, 2005). Thus, the statement that "octopuses are not aware of their arms" (Wells, 1978) is most likely untrue. However, it may be not entirely false; recent results, that are described in the section below ("***CONTROL OF GOAL-DIRECTED ARM MOVEMENTS***"), suggest that the octopus uses the information gathered by its arms in a special way that may superfluous the need for central somatotopic sensory representation of arm identities or spatial coordinates.

Wells (1978) showed that octopuses can learn by touch, using their arms as chemical or tactile sensors, and that this learning is generalized from one arm to all arms (Wells, 1978). Indeed, it has not proven possible to train octopuses to learn different tasks for different arms (or perhaps it is only because no one has been persistent enough). These findings together suggest that perhaps octopuses simplify chemo-tactile learning by generalizing the learned task and memorizing it in the CNS in the context of all arms, in the same way octopuses generalize visual learning to the two eyes (Muntz, 1961).

A set of experiments was designed to clarify how tactile, chemical, and visual information are processed and integrated into higher cognitive abilities such as operant tasks, solving mazes, and arm skill learning. The experiments showed that octopuses do not have clear skill learning at the level of the arms; they cannot learn how to use an arm to more quickly solve an operant task (Gutnick, Byrne, Hochner, & Kuba, 2011; Richter, Hochner, & Kuba, 2015, 2016). Indeed, they learned relatively slowly to adopt a more successful strategy (or to abandon a less successful one). For example, an octopus can learn to solve a three-choice maze, requiring it to use a single arm to reach a visually cued goal compartment (Gutnick et al., 2011), but as it learns the task, it takes longer for the arm to reach the goal compartment. This is presumably because the octopus learns to employ a slower but more successful strategy of watching its arm tip searching among the compartment entrances before deciding to push the bend of the arm tip into the visually cued goal compartment. Although this visually guided searching strategy seems both a simple and logical explanation, it is still possible that the octopus learns to interpret and use some proprioceptive information arriving from its arm tip to direct it to the visually cued compartment (Gutnick et al., 2011).

Control of Goal-Directed Arm Movements

In goal-directed arm movements the octopus needs to precisely move an end-point of its arm from point to point. The typical visually guided reaching movement (see Octopus Group), in which the octopus extends one or several arms toward a target, exemplifies the strategies it uses to simplify control in a motor system with a potentially infinite number of DOFs. The octopus simplifies the control of goal-directed movements by propagating a stereotypical bend from the base of the arm to its tip. This strategy radically simplifies motor control because the stereotypical propagation of the bend is controlled by a local motor program embedded in the neuromuscular system of the arm. This program requires minimal central computation because only one parameter (one DOF), the velocity with which the bend moves along the arm, needs to be computed. This control strategy thus reduces the virtually infinite number of DOFs needed to be controlled during the reaching movement to effectively just three DOFs: two for the direction of the base of the arm in space, and one for scaling the velocity of the bend propagation along the arm (Gutfreundet al., 1996).

The reaching movement also involves different levels of elongation of the segment between the base of the arm and the bend (Hanassy, Botvinnik, Flash, & Hochner, 2015), and it is still unknown if the bend propagation and arm elongation are controlled by the same or by separate motor programs. For example, the level of elongation may be correlated with the distance of the octopus’s eyes from the target, in which case arm elongation may be controlled independently from bend propagation (Hanassy et al., 2015).

Electromyograph (EMG) recordings during reaching in freely behaving animals were used to test the relationship between muscle activity and kinematic parameters. The recordings suggested that reaching is controlled by a feedforward (ballistic) motor program, as the level of muscle activity detected by the EMG predicted global parameters like peak velocity, even though the level of activity was measured at the initial stages of the extension before the arm reached its peak velocity (Gutfreund, Flash, Fiorito, & Hochner, 1998).

Movements with the natural kinematic characteristics could be elicited in an amputated arm by tactile stimulation of the skin or by electrical stimulation of the arm nerve cord at the arm base (Sumbre, Gutfreund, Fiorito, Flash, & Hochner, 2001). This shows that the circuitry for generating the movement is embedded in the neuromuscular system of the arm itself. If the detailed movement programs are embedded in 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 behaviors, as indeed found by Zullo et al. (2009) (also see the "***THE UNIQUE ORGANIZATION OF HIGHER MOTOR CONTROL CENTERS IN THE OCTOPUS'S BRAIN***"). In reaching or extension movements by multiple arms, either synchronously or consecutively, the velocity profiles of all the arms are similar. That is, the higher motor centers may generate only one motor command to multiple arms if they are activated in the same behavioral context (Gutfreund et al., 1996). This conclusion is supported by a later study by Zullo et al. (2009) (also see the "***THE UNIQUE ORGANIZATION OF HIGHER MOTOR CONTROL CENTERS IN THE OCTOPUS'S BRAIN***") showing that stimulation of a site in the basal lobes triggers arm extension with similar kinematic parameters in several arms simultaneously.

Kinematic (motion) and dynamic (muscle action) analysis of the fetching behavior (Figure 5) provides an even more striking demonstration of how the arm flexibility is exploited to simplify not only motor programs like reaching, but also more complex computational processes, such as the fetching movement (Sumbre et al., 2006).

The octopus usually uses a stereotypical fetching movement for bringing an object to the mouth after successfully reaching for it and grasping it with a few arbitrary suckers after they contact it. The arm is then reshaped into a dynamic *quasi*-articulated structure by dividing the part of the arm between its base and the object into three segments—proximal, medial, and distal (light blue, green and yellow, respectively, in Figure 5). The distal segment grasps the object and serves as a "hand", while the proximal and the medial segments, which have similar lengths, reshape to resemble our upper arm and forearm. Then, as in the fetching movement of humans and many other skeletal animals, the octopus brings the object precisely to the mouth mainly by rotating the medial joint ("elbow") in a stereotypical movement that requires only three controllable DOFs (Sumbre et al., 2005).

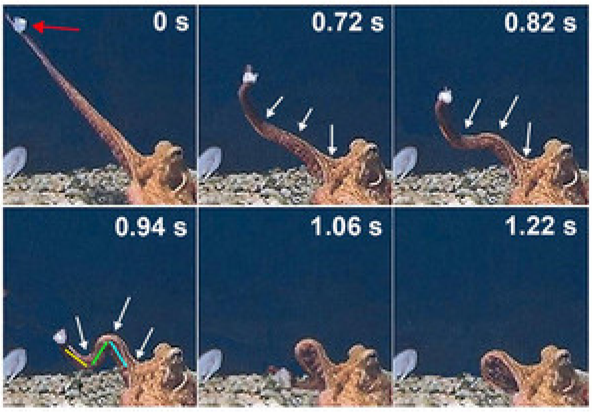

Figure 5. Fetching by an octopus arm. Time lapse video of a fetching movement by which the octopus brings a piece of food (red arrow) to its mouth. The arm is gradually reconfigured into a *quasi*-articulated structure through the formation of joints (white arrows) dividing the part of the arm between its base and the object into three segments (marked in light blue, green, and yellow, respectively, in time = 0.94 s frame) (adapted from Sumbre et al., 2006).

By correlating kinematic features of the octopus fetching movement with arm muscle activity recorded at various locations along the arm, Sumbre et al. (2006) showed that grasping a piece of fish elicits two waves of muscle activation that propagate toward each other: one propagates proximally starting from the part of the arm grasping the target, and the other propagates distally from the base of the arm. It was proposed that the medial joint is formed where the two waves meet. 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).

This strategy provides an elegant example of how reshaping the arm into an articulated structure can be achieved without central intervention, since it requires no central representation, and the computation is all done in the periphery. In other words, the control system uses the arm itself as a representation. The fetching movement is thus a striking demonstration of biological “morphological computation”, a notion tightly associated with embodied organization in robotics (Pfeifer et al., 2007).

The octopus also can fetch objects by conveying them along the suckers (as when collecting stones; see Octopus Group) or simply by pulling the object by shortening and curving the arm (Richter et al., 2015). These last two forms of fetching are associated with finding the target during arm searching or arm waving behaviors, especially when vision is obscured or a direct path between the body and target is unavailable, or when arm movement is physically constrained (Richter et al., 2015).

Control of Interactions Among the Arms

The long and flexible arms of the octopus raise the major difficulty of avoiding interference between arms and between arms and other body parts. Preventing appendage interactions in articulated animals can rely on central computations, which can be based on central representation of the limited number of appendage joints. In some articulated animals the configuration of the body prevents such interference simply because body parts physically cannot touch each other (e.g., fish fins). In other cases, central pattern generators (CPGs) in the motor control system produce rhythmical sequences of alternating stereotypical stepping movements of the appendages, preventing them from stepping on each other. The octopus’s morphology and flexibility do not permit using these strategies for controlling the interactions between body parts.

The problem arising from potential interference among octopus arms is intensified by the instinctive tendency of the suckers to attach to anything they contact (Grasso, 2008; Kier & Smith, 1990; Rowell, 1966; Wells, 1962). The neuromuscular system of each of these sucking rings, which are an integral part of the octopus’s object manipulation system and are densely aligned on the ventral side of the arm, can generate a huge negative pressure to firmly adhere the arm to a substrate by vacuum (Grasso, 2008; Kier & Smith, 1990). This tendency to hold on to any substrate could pose a significant problem for inter-arm coordination if not appropriately regulated.

The unique solution that has evolved in the octopus is based on a mechanism that controls arm and body interactions at the peripheral level of the arm itself. Nesher, Levy, Grasso, and Hochner (2014) showed that freshly amputated *Octopus vulgaris* arms have a strong tendency to use their suckers to grab and hold on to any object they touch, except other amputated arms (or other body parts of the octopus) as long as the skin of these body parts is intact (see the documentary videos on the Octopus Group). This avoidance mechanism is mediated by the skin itself, as the suckers of amputated arms did grab skinned arms and avoided grabbing skin that was stretched over plastic Petri dishes. Amputated arms also avoided, almost entirely, grasping plastic Petri dishes coated with gel soaked in a crude hexane extract of octopus skin. The grabbing forces toward these plates were approximately 10-fold weaker than those applied to Petri dishes coated with gel containing only hexane and 20-fold weaker than those applied to dishes coated with gel containing hexane extract of fish skin. It appears that molecules in the skin trigger a local inhibition mechanism, thereby preventing the suckers from activating their touch-induced attachment mechanism. The fact that the intensity of the attachment response is adjusted to the nature of the stimulus suggests a complex computation mechanism at the arm level with some behavioral flexibility.

In contrast to the deterministic behavior of amputated arms, the behavior of animals toward amputated arms was not unequivocal (see Nesher et al., 2014). The results suggest that octopuses can distinguish between their own and another conspecific’s amputated arms, as in about 94% of the trials octopuses attached their suckers to the skin of amputated arms taken from another conspecific, versus less than 40% of the trials in which octopuses attached their suckers to the skin of their own amputated arms. Sometimes octopuses grabbed amputated arms even by the skin and treated them as prey, while in other cases, octopuses refrained from grabbing amputated arms and would, instead, only “pet” them. An interesting behavioral consequence would sometime occur when presenting an amputated octopus arm to a behaving octopus. The octopus would, sometimes, detect the exposed flesh at the amputation site, and would grab the amputated arm at this location and bring it to its mouth. It would then hold the amputated arm only by its beak and avoid grabbing the part of the amputated arm still covered with skin (see the Octopus Group). This shows how peripheral control mechanisms can contribute to the behavior of the animal as a whole.

This peripheral self-recognition mechanism that constrains interactions between arms at the periphery is a simple and elegant solution to a potentially very complicated control problem in the hyper-redundant flexible body of the octopus. These findings show an embodied control organization where the body itself contributes to the emergent behavior that does not rely on central processing.

Control of Arm Coordination in Locomotion

Efficient locomotion with appendages like the long and flexible arm of *Octopus vulgaris*, which lacks any structural constraint, requires a completely different control strategy from that in locomotion with skeletal appendages. In the latter case the small number of joints reduces the number of DOFs involved in the movement. This allows the control of locomotion with repeated rhythmical patterns of motor output generated by rather simple neural networks defined as central pattern generators (CPGs). This is a universal control mechanism—it is found in all types of locomotion throughout the animal kingdom.

The first indication that the octopus is a unique exception, appearing to lack CPGs in locomotion control, was obtained by studying arm coordination during crawling (Levy, Flash, & Hochner, 2015). The octopus crawls by making moment-to-moment (ad hoc) decisions about which of its arms to recruit for pushing the body. The proximal part of the active arm shortens and then adheres to the substrate with a group of suckers. These form an anchoring point for a stereotypical elongation of the proximal segment that generates the thrust to move the body. The moment-to-moment direction of crawling is determined by a vector sum of the pushing directions of the active arms; each arm has a single predefined pushing direction that is determined by its position around the body. This calculation of direction is simple because the arms are organized in a radial symmetry around the body. No apparent order in the stepping records of the octopus arm were found, nor did fast Fourier transform (FFT) analysis of instantaneous crawling velocity reveal any characteristic frequencies indicating the presence of a rhythmical CPG (Figure 6C; Levy et al., 2015) as clearly evident in similar analyses of locomotion by skeletal animals (Figures 6A and 6B; Graham, 1972; Mendes, Bartos, Akay, Marka, & Mann, 2013).

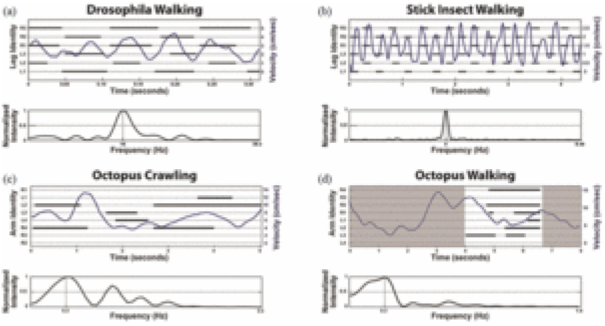

Figure 6. In contrast to the universal role of CPGs in vertebrate and arthropod locomotion, octopus locomotion involves ad hoc recruitment of the arms interacting with the environment. Upper panels are stepping records (black) with the body's instantaneous velocity superimposed (blue), lower panels give the spectrum of frequencies of the respective velocity extracted by fast Fourier transform (FFT). In the upper panel of d only the time interval between 4 seconds and about 6.6 seconds was analyzed (white area) because in the remaining time the position of some of the arms was obscured. (a) *Drosophila* walking; adapted from Mendes et al. (2013). (b) Stick insect (*Carausius morosus*) walking; adapted from Graham (1972). (c) Octopus crawling. (d) Octopus walking. Note the lack of temporal pattern in c and d. The extracted frequencies of octopus crawling and walking merely reflect the window sizes (for example, the frequency of 0.3 Hz in c means a cycle every 3.3 seconds, but the entire movement lasts only 6 seconds). In contrast, the extracted frequencies of *Drosophila* and stick insect walking each show a single prominent characteristic frequency reflecting the underlying CPG rhythmicity (adapted from Levy et al., 2015).

Investigation of the mechanism of arm coordination during several forms of octopus locomotion further supported the existence of unique locomotion control mechanisms (Levy & Hochner, 2017). During their various forms of locomotion octopuses keep their head constantly horizontal (Figures 7 and 8; the Octopus Group). This is not surprising because, as in many animals, especially those living outside water, keeping the head in fixed orientation to the external world and gravitation simplifies the planning of locomotion commands. Indeed, even the simplest creatures possess mechanisms for sensing gravity, and cephalopods are known for their highly evolved vestibular system, with a pair of statocysts embedded within the rigid cartilaginous brain capsule (Barber, 1966; Wells, 1978; Young, 1971). The location of the statocysts enables octopuses to directly gauge the orientation of the head and, thus, even with its soft body, to keep the head at a fixed orientation to the external world and simplify motor control.

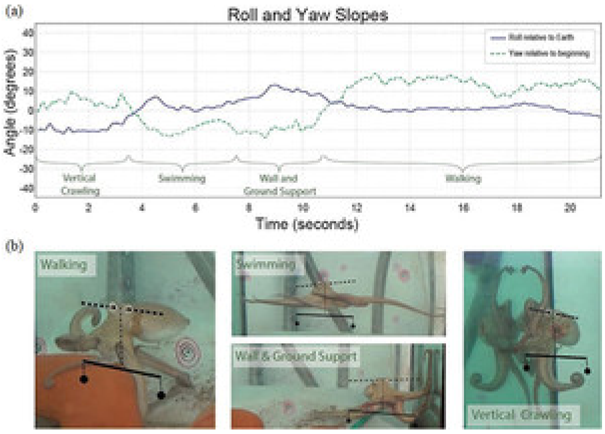

Figure 7. The octopus keeps its head in a horizontal posture. (a) The slope between the eyes during behavior (roll—blue). The yaw slope (green dashed line) was added for comparison. The time during which the octopus showed each type of locomotion is marked on the plot. (b) Video images of octopuses during different types of behavior. The slope of the axis that runs between the eyes (dashed line) and the scale below it (continuous line) are shown on the video images. The scale shows zero-degree orientation relative to Earth. The concentric black and red circles were marks made on the aquarium to calibrate the three cameras in order to reconstruct the 3D position of the eyes (adapted from Levy & Hochner, 2017).

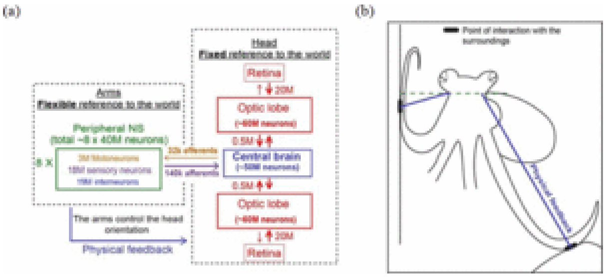

Figure 8. Physical feedback from the arm to the head simplify the control of the arms' interaction with the world. (a) The distribution of the 500 million nerve cells of the octopus's nervous system among its three main compartments (peripheral nervous system, central brain, and paired optic lobes). Each is shown in a different color. Note the relatively few fibers connecting the compartments. (Based on Hochner, 2012). Numbers are taken from Young (1963, 1965). (b) The interaction of the arms with the surroundings provides the physical feedback that determines the fixed horizontal orientation of the head (explained schematically with the blue lines marked "Physical feedback" in a and b) (adapted from Levy & Hochner, 2017).

Keeping the body in a stable posture relative to the force of gravity seems fundamental and simple for animals with a rigid skeleton, but it is a much greater challenge for an animal with flexible appendages. The evolved solution for this difficulty is based on "morphing" (shaping) the soft body instead of controlling joint angles as in skeletal animals. As indicated by the name of their class "Cephalopoda", octopus arms emerge directly from the base of the head (see Figure 1) around which they are radially distributed. During locomotion, the imaginary axis that runs between the eyes remains close to horizontal (Figures 7 and 8; the Octopus Group), implying an active adjustment of the eyes' height by controlling the distance between the contact points of the active arms with the environment and the base of the head. This simplifies the controlling of the head orientation, because it is achieved by a straightforward mechanism that only controls the stiffness of the arms (Figure 8B). Such stiffness control may involve only one DOF per interacting arm.

Using the shape of the interacting arms as *physical feedback* in the control of arm-propelled locomotion (Figure 8) implies that octopus locomotion is unlikely to be based on a motor program involving a robust feedforward deterministic components like the rhythmical patterns in the CPG-driven locomotion of skeletal animals. Indeed, kinematic analysis of octopus crawling and walking (Figure 6) suggest that both these locomotion maneuvers are controlled by what would be suggested as a "probabilistic" strategy—moment-to-moment changes in the probability of recruiting the arms that have better chances of moving the body in the desired direction. It is clearly understandable why probabilistic control can better suit locomotion with hyper-redundant limbs that change their structure with each step, while CPGs better suit locomotion with highly structured jointed appendages with only a limited number of DOFs. Note that the lack of involvement of a CPG in walking is functionally more significant than the lack of a CPG in crawling. In crawling, on the one hand, there is no need to care for body stability as the body essentially rests on the substrate. In walking, on the other hand, arm coordination must deal with stability as well as with locomotion, as the center of body mass is above the ground; walking control must take into consideration that the arms that are in contact with external support must also stabilize the body above the ground.

The octopus's probabilistic control strategy, together with the radial organization of the arms around the body, creates yet another unique feature in the control of octopus locomotion. In contrast to all bilaterian animals (animals with bilateral body symmetry), the octopus can locomote in any direction relative to its facing direction and, as shown for crawling, at the same time it can independently control the orientation in which its body faces (Levy et al., 2015).

These findings further support the theory that *embodied organization* of behavior has led to the evolution of a unique body plan that enables the existence of efficient (i.e., simplified) motor control mechanisms that overcome the huge complexity involved in the control of hyper-redundancy of the soft-bodied animal. In other words, the special morphology of the octopus enabled the evolutionary selection of control strategies, reducing the number of controlled variables that the nervous system must deal with.

Conclusion: Unique Features in Octopus Motor Control

The results presented here were gathered in a search for biologically based inspiration for a better design of soft robots and flexible manipulators (Calisti et al., 2011, 2012; Pfeifer et al., 2014; Walker et al., 2005). Taken together, these data clearly demonstrate how the octopus uses unique strategies to cope with the complexity arising from its hyper-redundant body and appendages and the consequent inability to use representation maps based on body-part coordinates. These strategies are present at all levels—from the neuromuscular system to higher motor control centers. These mechanisms collectively shaped the octopus into an efficient functional and morphological soft *embodiment*. The concept of embodied organization was described in a biological context (although without using this term) by Chiel and Beer (1997) and Chiel et al. (2009). Earlier works in the field of autonomous robotics described this approach (e.g., Brooks, 1991A, 1991B) and also in the context of biologically inspired robotics (e.g., Pfeifer et al., 2007, 2014). The octopus is an outstanding example of the concept, and a useful tool for understanding the co-evolution of animal morphology and its control systems to enable the emergence of adaptive behavior in the specific functional and behavioral niche.

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Website

The octopus group

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