

# A new perspective on the organization of an invertebrate brain

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The concept of 'embodiment' and its implications for the evolution of cognitive capacities is emerging as a major issue in biology. Invertebrates have immensely diverse nervous structures and body plans, revealing the variety of solutions evolved by animals living successfully in all kinds of niches. Among invertebrates, the octopus is a special case because of its high cognitive abilities and a uniquely flexible body and manoeuvrable arms with virtually infinite degrees of freedom. Here we discuss how the octopus embodiment may be considered a 'key' to the development of its neural organisation and cognitive abilities.

The parallel evolution of vertebrates and invertebrates has resulted in both many homologies and differences in their brain structures and functions.<sup>1</sup> In contrast to the greater similarity among vertebrates, the invertebrates show an enormous diversity of species with profound differences in their body plan, nervous organization and cognitive capacity. The most advanced class among the invertebrates is the Cephalopoda, which possess the largest invertebrate nervous system. Amongst the cephalopods, the octopus shows the highest cognitive abilities and a unique 'embodiment' comprising a flexible body and maneuverable arms with virtually infinite degrees of freedom. We suggest that this body structure is a key to the emergence of its neural organisation and cognitive abilities.

The octopus has a relatively small central brain which integrates a huge amount of visual and tactile information from the large optic lobes and the peripheral nervous system (PNS) of the arms. The brain also sends commands to the elaborate neuromuscular system of the arms.<sup>2-4</sup> To follow the transformation of sensory input into motor output both during initiation and control of behaviors we need to understand the basic sensory-motor organization of the brain. That is, we need to determine whether this immense quantity of sensory and motor information is represented in the brain and, if so, how? How is this rich sensory information treated and integrated to generate the octopus' complex behavioral repertoire?

Sensory-motor interactions may be easier to achieve where the sensory and motor systems are somatotopically organized in

well defined areas,<sup>5</sup> as in the vertebrate cortex, where sensory and motor systems of the whole body converge somatotopically. This configuration is one possibility for simplifying the generation of motor commands in the central nervous system (CNS). The octopus, in contrast, appears not to use somatotopic representation of movements and body parts in higher levels of the CNS. Rather, recent results suggest an organization of overlapping circuits, possibly each representing a motor function.<sup>6,7</sup>

## Vertebrate Somatotopic Sensory-Motor Representation

A fundamental organizational principle of the vertebrate brain is the topographic sensory and motor representation of different body parts, i.e., "somatotopic organization", which was first postulated in the late 19<sup>th</sup> century. In 1950 the concept was summarized by the two well known drawings by Penfield, Woolsey and Rasmussen: the homunculus and the simiusculus. These are topographic maps for humans and monkeys displaying the relative areas of primary sensory and motor cortices where activity is related to a specific body part.<sup>5,8</sup> More recently it has been shown that this somatotopy applies only to the major body parts and at a gross scale. In fact, most of the sensory and motor activity related to specific body regions is distributed throughout the cortex, generating what is called "multifocal representation".<sup>5,9-11</sup> This means that following the motor or sensory activation for, say, a finger or a joint reveals a wide mosaic distribution of activation within the cortex.<sup>5</sup>

In addition, the clearest representation seems to be that of the function of a body part rather than the representation of the body part itself; that is, there appears to be a 'functional somatotopy'.<sup>12,13</sup> Motor output is achieved by the activation of neural stations spatially distributed but functionally connected across parallel pathways within the brain.<sup>14</sup> This 'somatotopy with overlap', where neurons may be specifically recruited into different pathways and brain networks results in a greater serial and parallel processing of information, which most likely contributes to a qualitative leap in behavioral performance.<sup>15</sup>

## A Brief Sketch of Invertebrate Sensory-Motor Organization

The structures and functions of invertebrate nervous systems reveal the diverse solutions evolved by animals living successfully

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in all kind of niches. Invertebrates have immensely diverse nervous systems.<sup>16</sup> As invertebrate ‘embodiment’ (nervous structure and body plan) becomes more complex, two major trends can be observed in the nervous system. Firstly, there is a tendency toward centralization, manifested by morphological changes, such as shortening of the commissures and connectives and formation of a structured cephalic ganglion. The second trend is ganglionic swelling, where a ganglion or even groups of ganglia tend to form several semi-autonomous systems for sensory-motor control. The large diversity in nervous organization is reflected in profound differences in the level of behavioral complexity.

Lower invertebrates have simple nervous systems such as a circular nerve net or a chain of segmentally organized ganglia. Such anatomical organization may represent a more distributed form of control, where sensory-motor integration occurs closer to the body part involved. This may increase efficiency by restricting central nervous control to limited fast responses to specific external stimuli (i.e., reflexes), which requires only limited information processing. More developed invertebrates, with their highly developed sensory structures, show a more complex nervous system and the development of brains in the animals’ rostral part. This more advanced nervous system allows them to receive, process, and respond in greater variety to distant stimuli in the animal’s direction of travel. Here interneurons become a major neuroarchitectural element within the CNS and are a key element in processing and integrating information.<sup>17</sup>

A further important increase in complexity above a completely reflexive organization is the formation of central pattern generators (CPGs) by groups of electrically and synaptically connected neurons. CPGs are motor control stations which can autonomously produce specific patterns of motor output, such as those underlying various rhythmical actions like cardiac function, feeding, walking, flight and swimming. CPGs producing rhythmic outputs have been extensively studied in the somatogastric and cardiac system of crabs, as well as in many other invertebrate and vertebrate systems. While they can be viewed as a primitive system for organizing “fixed actions”,<sup>18,19</sup> CPGs tend to be regulated by external and internal sensory signals, frequently by neuromodulators.

A higher level of integration of sensory information can be achieved by specialized brain areas and similar specialization has developed in animals as different as insects and cephalopods. Parallels can be drawn between areas involved in memory formation and storage and in the higher motor centers. Insect mushroom bodies and the cephalopod vertical lobe system are the main invertebrate areas involved in learning and memory. Consisting of a rich interneuronal net, both systems are unique in that a large proportion of their neurons are intrinsic interneurons.

Another parallel can be drawn between the areas where complex behaviors are elaborated, the insect central complex and the cephalopod basal lobe system. The insect motor control system consists of a number of richly interconnected and overlapping loops that operate co-operatively to determine the motor output.<sup>14,20,21</sup> In cephalopods the final generation of efficient behavioral responses is determined by the dynamic recruitment of single cells or groups of cells organized in overlapping networks.

In addition, this center for higher motor control may play a major role in the integration of sensory inputs from various body parts.<sup>6</sup>

In spite of the parallels, the prominent differences in the organization of the higher nervous system among the invertebrates raise the questions of how the higher sensory and motor levels are organized. A further question is whether new features emerged with increasing complexity of embodiment. For example, many invertebrate motor systems are distributed throughout a semi-autonomous PNS, yielding ‘distributed’ low level motor representations. Within the higher nervous system of most invertebrates, sensory feedback areas tend to be topographically organized, central ganglia receive projections from various body parts and show a general somatotomy.<sup>22-24</sup> Exceptions appear among the cephalopods.

### Cephalopods—An Exceptional Invertebrate Class

The cephalopods are a diverse class of highly derived mollusks. Although the morphological plan of the cephalopod nervous system derives from that of other molluscs, it shows much more centralization.<sup>4</sup> Cephalopods have the largest of all invertebrate nervous systems, with a brain weight-body weight ratio exceeding that of most fish and reptiles.<sup>25</sup> In addition, their evolution from a monoplacophoran-like ancestor entailed several key morphological body modifications that have contributed to their impressive evolutionary success.<sup>26</sup> The three main features of the phylum Mollusca, shell, mantle and ventral foot, evolved new functions—locomotion, respiration and manipulative abilities (development of prehensile arms). These changes were accompanied by many sensory and neural innovations.<sup>26</sup>

The cephalopod nervous system comprises a CNS and a PNS. The large PNS includes the nervous system of the body and of the arms. The CNS consists of the brain and the two optic lobes. The brain is divided into a around 30–40 lobes interconnected by commissures and tracts. These connections create a high degree of cross-talk between the lobes but the interconnections appear much less elaborate than those in vertebrate brains.<sup>3</sup>

The high level of centralization, together with the division of labor at different levels of the nervous system, raises the question whether and how movements and body parts are represented in this distributed system. In contrast to vertebrate and insect brains, morphological studies have shown that there is no obvious somatotopic arrangement in motor areas in the cephalopod CNS. Instead, the motor neurons seem to be equally scattered throughout the relevant brain lobes. Similarly, retrograde cobalt filling and retrograde labeling with lipophilic fluorescent dyes (DiI) applied to the areas carrying sensory information from the arm to the CNS reveals a widespread distribution of the sensory areas within the higher nervous centres.<sup>2,27</sup>

The modern cephalopod nervous system thus shows an organization different from the somatotomy of other mollusks, other invertebrates and vertebrates. The special features of their nervous system most likely co-evolved with their highly dynamic embodiment, which created new physical interactions with the environment, all these changes allowing complex behavior to emerge. The cephalopod CNS represents a further step in the organization of a complex nervous system.

## A Special Case—The Octopus

The central octopus brain contains ~50 million neurons. It integrates processed information from the huge visual system (~120 million neurons) and controls the large, complex and highly autonomous PNS of the arms (~300 million neurons). The brain shows a high cognitive capacity and its vertical lobe is dedicated to learning and memory.

Most of our knowledge of the organization of the octopus brain derives from morphological and lesion studies.<sup>28-30</sup> Such studies have shown that both motor and sensory ‘centres’ are distributed over the higher parts of the CNS.<sup>2,27</sup> Recently developed electrophysiological techniques together with careful kinematic analysis now allow investigating whether and how movements and body parts are represented within the octopus’ higher motor centers (the basal lobe system).

Gross brain stimulation in restrained or anesthetized animals revealed that motor control in the octopus nervous system is hierarchically organized into three functional levels: higher motor centers, intermediate motor centers and lower motor centers.<sup>31,32</sup> Microstimulation of the higher motor centers can evoke discrete and complex responses, movements and behavioral responses which are characteristic of the animal’s behavioral repertoire.<sup>6</sup> No evidence was found for a somatotopic motor representation, the same discrete behavior could be induced by local stimulation throughout the basal lobe system. Furthermore, a complex behavioral response was elicited by increasing stimulus strength and increasing the area stimulated. This gradually recruited each movement component. These results suggested that movements are not somatotopically represented in the higher motor centers but rather that they are controlled by a number of parallel overlapping circuits representing individual motor programs.

These physiological results fit the morphological data which also do not indicate a somatotopic motor organization in the basal lobes.<sup>2,4,33,34</sup> Recordings from the basal lobe system in a freely behaving animal have shown that sensory afferents from the mantle and arms are also not somatotopically organized (Zullo L, et al. unpublished). As several major pathways from the optic lobes and other sensory centers input to the higher motor centers,<sup>3</sup> the basal lobes, together with the peduncle lobes, may be a major area for the integration of visual, vestibular and proprioceptive inputs.<sup>30,32,35-37</sup> That is, this area appears somewhat to resemble the vertebrate parietal cortex, an important multisensory association area.<sup>38</sup> Stimulation of parietal cortex can similarly elicit complex movements. This contrasts with multi-joint movements evoked by microstimulation of the motor cortex,<sup>39,40</sup> where movements and body parts are coarsely somatotopically represented.<sup>41</sup> While there appears to be an overall similarity, vertebrates differ from the octopus in that the areas devoted to motor control and to integrative processes tend to be more morphologically distinct.<sup>41</sup>

### What are the Advantages of a Non-Somatotopic, Distributed Representation?

Has a distributed sensory-motor representation evolved in the octopus as part of its special embodiment? We now present a

scenario in which such a representation reduces the complexity of controlling the octopus’ complex behavioral output.

The octopus’ unique embodiment comprises a very large and complex peripheral sensory and motor system which is dynamically interconnected with several layers of higher control in the brain. Overall, this hierarchical functional organisation appears basically similar to that of vertebrates and arthropods. Yet unlike them, in the octopus much of the control of the highly unconstrained neuromuscular arm system lies in the PNS. Building a set of peripherally controlled stereotypical motion primitives helps solve the lack of mechanical constraints (virtually infinite degrees of freedom). Yet the PNS transfers sufficient sensory-motor information to the CNS so that PNS and CNS can cooperate closely to generate a complete set of elaborated motions. This integration leads to a reduction in both the complexity of the movement command and in the control of movement execution, the central brain mainly deals with global control parameters and with coordination. It is still quite unknown how the vast amount of visual, chemical and tactile information is used to coordinate the arm movement responses to external stimuli.

Given the absence of an orderly somatotopic representation in the octopus brain, motor output results from the activation of various areas distributed across parallel pathways. These distributed and intermingling neural networks appear to be a unique organization where single cells or groups of cells are dynamically recruited into functionally quite different networks. The body, with its motor and sensory systems, does not need to be represented centrally because its information is processed peripherally. Therefore, a somatotopic organization is not required in the higher motor centres. Instead, the distributed and overlapping sets of motor areas in the higher centre may represent motor programs which may be integrated with multimodal sensory information.

Octopuses use their arms differently in various behavioral tasks and have preferred arms.<sup>42-44</sup> This raises us a further question. If there is no somatotopic representation of the body, how can the animal determine which arm/s to move during natural behavior? We suggest that an additional mechanism may have evolved to overcome this problem. We suggest that the brain may use a gating mechanism to tonically inhibit the PNS and that the gating is released by a higher command or a sensory input. Such a central command could trigger a stereotyped movement embedded in the PNS of the arms (generalized arm movements), while tactile or visual inputs<sup>42,43,45-47</sup> are used to direct the higher or global command to a specific arm (few or single arm movement). Our hypothesis is supported by the observation that octopuses frequently use a few arms together rather than a single arm for most tasks. In particular, during the execution of stereotyped movements such as reaching, several arms extend together toward a target and show a similar kinematics. This suggests that a single motor command is sent from the brain and distributed to the periphery.<sup>6</sup>

In summary, the absence of somatotopic motor representations in the octopus may have evolved together with its unique body plan—its active body with eight long, highly flexible and maneuverable arms—to ensure both appropriate information processing and reactions to the external world. We consider the octopus’ embodiment the key to its neural and cognitive features.

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