Quick guide

Octopuses

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What are they? Octopuses and their relatives, the cuttlefish and squids, form the class of modern cephalopods (coleoids). These are soft-bodied molluscan invertebrates like garden snails or sea hares (*Aplysia*). The modern cephalopods appeared in the sea at the same time as bony fish; more than 200 million years ago. The old cephalopods are virtually extinct — their only living representative is the shell-bearing *Nautilus.* Modern and old cephalopods separated about 450 million years ago and the modern cephalopods have evolved into highly effective hunters which compete with fish in their marine habitat.

The cleverest invertebrate? There is no easy way of comparing intelligence between different species. We intuitively classify animal intelligence using three criteria. How rich is the animal's behavioral repertoire? Is the behavior complex and adaptive, or is it more stereotypic/reflexive? How well and fast can animals learn and remember?

The octopus's eight arms and soft body endow it with an amazingly large repertoire of behaviors. Octopuses can squeeze through tiny holes. They use their eight arms, each equipped with a row of sophisticated active suckers, for standing, walking, crawling, swimming, catching prey, opening clams, reaching towards a target, grasping, fetching, probing the environment, grooming, collecting stones, digging to build a den, and more. The mantle and siphon, used in breathing, allow fast, jet-propelled swimming and can squirt streams of water at intruders to deter them. In severe danger, octopuses add ink to the water stream for cover. Their unique chromatophore system generates rich skin color patterns, adding additional complexity to all these behaviors. Octopuses process huge amounts of sensory information through their highly developed eyes, the only invertebrate eyes that are camera-like (as are vertebrate eyes), and from millions of tactile and chemical sensory cells distributed all over the body, arms and suckers.

Learning and memory provide a basis for quantitatively assessing intelligence and comparing the octopus with other species. The octopus shows operant and associative learning and long-term memory in both visual and tactile tasks. Especially revealing is the octopus' ability to learn by observation: if an octopus watches a trained octopus perform a discrimination task, it will learn the discrimination much more quickly than the trained octopus did.

One demonstration of behavioral flexibility, which anybody who keeps octopuses can readily observe, is the very clear acclimatization process that octopuses undergo when brought from the sea to the laboratory. After about a week, the octopus stops hiding and starts moving around curiously, watching what is happening around its tank. In this aspect octopuses differ completely from *Aplysia*, garden snails, cockroaches, fruit flies or even honey bees. There are even reports that octopuses have personalities, different temperaments, that they like to play, and have eye and arm preferences.

How do its nervous system and intelligence compare with those of other animals? Nervous systems differ dramatically in size and organization. It is still an open question which brain parameters — such as volume or weight, the number of neurons in relation to body weight or length, and so on — co-vary with the complexity of behavior and intelligence.

Perhaps not surprisingly, the size of the modern cephalopod nervous system normalized to body weight lies within the same range as vertebrate nervous systems — smaller than those of birds and mammals, but larger than those of fish and reptiles. Comparing the total number of neurons, a variable that may be more relevant to neural processing, the octopus nervous system contains about 500 million nerve cells, more than four orders of magnitude greater than in other molluscs (garden snails, for example, have around 10,000 neurons) and more than two orders of magnitude more than in advanced insects (cockroach and bee, for example, have around a million neurons), which probably rank next to cephalopods in invertebrate behavioral complexity. The number of neurons in the octopus is well into the range of amphibians such as the frog (~16 million) and small mammals such as the mouse (~50 million) and rat (~100 million), and not much fewer than in the dog (~600 million), cat (~1000 million) and rhesus monkey (~2000 million).

Neuron density varies much more between different brain areas in the octopus than it does in vertebrate brains. The vertical lobes of the octopus brain contain ~25 million cells, about half the cells of the central brain. This high density arises because 99% of the cells in the vertical lobe are tiny interneurons. The tightly packed vertical lobes somewhat resemble the mushroom bodies of the insect brain.

Do these exceptional brain structures have special functions? Indeed they do! The vertical lobe is involved in long-term memory acquisition (insect mushroom bodies are similarly involved in odor discrimination learning and memory). It has a matrix-like structure similar to that of the mammalian hippocampus and, like the hippocampus, it shows long-term potentiation of synaptic connections that is activity-dependent. It is a puzzle that the octopus vertical lobe contains roughly 10 times the number of cells in the rat hippocampus.

All these numerical data certainly support the view that octopuses are the smartest invertebrates. The comparison with mammals is more intriguing, however: on one hand, the comparable number of neurons may explain the comparable behavioral repertoire and learning and memory abilities of octopuses and lower mammals; on the other hand, most of us would feel that octopuses show less behavioral flexibility and learning ability than dogs and cats. Does this mean that the difference between vertebrates and invertebrates is more than just in the number of neurons?

Is its nervous system more vertebrate-like or invertebrate-like? The nervous system of vertebrates is composed of a large central brain connected to a relatively small spinal cord. In contrast, the octopus nervous system is divided into three parts, with the two largest parts, the optic lobes and the nervous system of the arms, lying outside the central brain capsule.

The optic lobes and arm nervous systems are connected to the brain by a relatively small number of nerve fibers. This suggests that they each send highly processed information to the brain and receive high-order commands and inputs from it. That is, much of the planning, computation and execution of stereotypic arm movements are conducted within the arm neural system itself. Accordingly, natural-looking arm extension movements can be generated in amputated arms. This organization may be an optimal solution for the motor control of highly redundant flexible appendages and for processing sensory information gathered by millions of receptors distributed on the arm's skin and suckers. Similarly, much of the visual processing may be performed in the optic lobes, which may also store long-term memories.

As a result of intensive encephalization, the octopus brain superficially resembles the centralized vertebrate brain more than the distributed nervous system of other invertebrates — but it still maintains typical invertebrate features. It still shows clear boundaries between discrete lobes, indicative of fusion of individual invertebrate ganglia, and their organization within the brain is much simpler than in vertebrate brains. This lobed structure is advantageous for experimentally deciphering the brain's functional organization.

Each lobe in the octopus brain still maintains the typical anatomical organization of invertebrate ganglia, with the cell bodies arranged in an outer layer. The neurons are of the typical invertebrate monopolar type, with a single neurite extending from the cell body into the deeper neuropil, where it ramifies into the dendritic tree and the axon. Cell bodies of vertebrate neurons, in contrast, lie deeper in the brain tissue and both the axon(s) and dendrites emerge from the cell body. The electrical properties of the octopus central neurons, where examined, are also typical for invertebrates; the cell bodies, and probably the dendrites too, are inexcitable and action potentials are generated only at the transition to the axon.

Are there convergences with mammalian brain organization?

Some parts of cephalopod brains show a strikingly similar morphological organization to areas of the vertebrate brain mediating similar functions. For example, the three outer layers of the cephalopod optic lobe are organized similarly to the deeper layers in the vertebrate retina, a similarity all the more striking as the octopus's typically invertebrate mechanisms of transduction and physiological responses to light are quite different from those of vertebrates.

In the peduncle lobe, small granular-like cells give rise to arrays of thin parallel fibers, strongly resembling the arrangement in the folia of the vertebrate cerebellum. The parallel and linear organization of small diameter fibers in the vertebrate and octopus systems suggests the importance of this type of organization for possible timing computations.

Finally, the vertical lobe, as already mentioned, resembles the vertebrate hippocampus, both in its involvement in learning and memory and in its morphological organization. This area possesses a robust activity-dependent long-term synaptic potentiation (LTP) very similar to that in the mammalian hippocampus, even though it differs in mechanism of induction. The octopus LTP was shown to be involved in long-term memory.

From the point of view of evolutionary convergence, the mammalian-like anatomical organization of these higher brain areas in the octopus, highlight the importance of network connectivity rather than the properties of single cells in achieving certain behavioral function. In other words, if there is a hierarchy of constraints in the evolution of neural systems, it seems that anatomical connectivity lies at the top.

Where can I find out more?

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Primer

The planar polarity pathway

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Research in the area of developmental biology has historically focused on the key question of how different cell fates are determined in different regions of the body. From the point of view of producing a functioning organism, however, an equally important question is how cells acquire the appropriate polarities. Indeed, it is the polarisation of the single-cell embryo that underlies the diversification of cell fates that follows. One particular problem in this area is how groups of cells of the same or different fates coordinate their polarity with that of their neighbours and the axes of the tissue and organism as a whole. Over the last 15 years considerable progress has been made in understanding the mechanisms underlying coordinated cell polarisation, with attention focusing on its genetic control by genes acting in the so-called 'planar polarity pathway'. As I shall discuss here, however, there is still considerable disagreement and uncertainty regarding the definition of this pathway and the functional relationships of its different components.

The term 'planar polarity' was first used by Katharina Nübler-Jung in the 1980s to refer to the patterned polarisation of cells in the plane of an epithelium. The studies of Nübler-Jung and other workers in the preceding decades were carried out on the cuticles of various insects, which were both amenable to experimental manipulation and showed obvious cellular polarity as manifested by the ordered orientation of hairs, bristles or scales. More recently the focus of planar polarity research has shifted to a different insect: the fruitfly *Drosophila melanogaster*, which also exhibits many beautiful manifestations of planar polarity on its cuticle (Figure 1A–F), such as the ordered arrangement of trichomes produced by cells in the wing and the polarised