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Primer

Cephalopod behaviour

Tamar Gutnick[1], Daniel S. Rokhsar[2,3,4], and Michael J. Kuba[1,*]

> *“Of molluscs the sepia is the most cunning, and is the only species that employs its dark liquid for the sake of concealment as well as from fear: the octopus and calamary make the discharge solely from fear. … The sepia, as has been said, often uses its colouring pigment for concealment; it shows itself in front of the pigment and then retreats back into it; it also hunts with its long tentacles not only little fishes, but oftentimes even mullets. The octopus is a stupid creature, for it will approach a man’s hand if it be lowered in the water; but it is neat and thrifty in its habits: that is, it lays up stores in its nest, and, after eating up all that is eatable, it ejects the shells and sheaths of crabs and shell-fish, and the skeletons of little fishes. It seeks its prey by so changing its colour as to render it like the colour of the stones adjacent to it; it does so also when alarmed. By some the sepia is said to perform the same trick; that is, they say it can change its colour so as to make it resemble the colour of its habitat.”*
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> — Aristotle, The History of Animals, Book IX. Translated by D’Arcy Wentworth Thompson

Underlying all animal behaviors, from the simplest reflexive reactions to the more complex cognitive reasoning and social interaction, are nervous systems uniquely adapted to bodies, environments, and challenges of different animal species. Coleoid cephalopods — octopuses, squid, and cuttlefish — are widely recognized as the most behaviorally complex invertebrates and provide exciting opportunities for studying the neural control of behaviour. These unusual molluscs evolved over 400 million years ago from slow-moving armored forms to active predators of coastal and open ocean ecosystems. In this primer we will discuss how, during cephalopod evolution, the relatively simple ganglion-based molluscan nervous system has been extensively transformed to control the complex bodies and process extensive visual, tactile, and chemical sensory inputs, and summarize some recent findings about their fascinating behaviors.

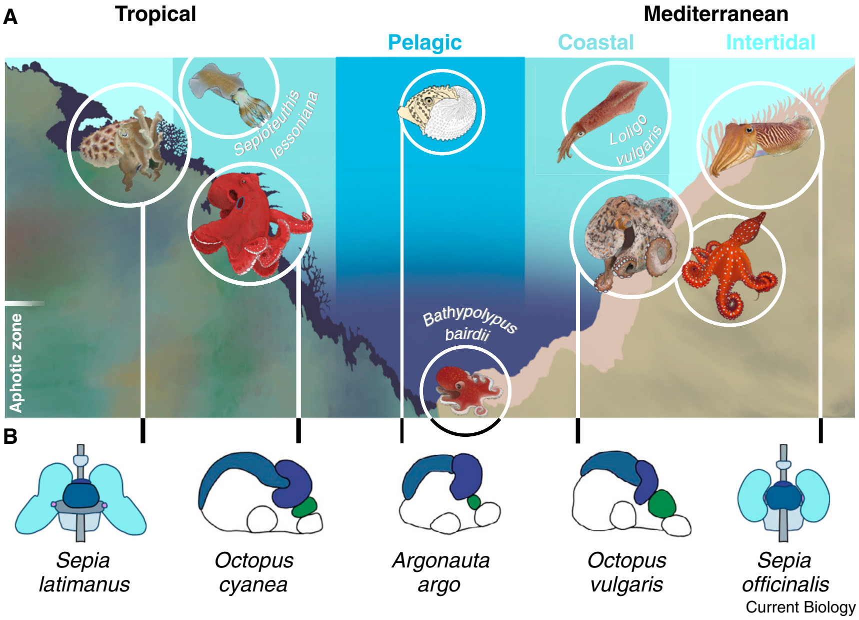

Figure 1. Habitat, life-style and central nervous system adaptations.
(A) Cephalopods are strictly marine animals but inhabit all oceans encompassing a wide variety of habitats, from deep sea to coastal and intertidal. These diverse habitats provide different environmental stimuli: for example, tropical seas are highly structured and more visually complex than temperate coastal areas. Among decapods, cuttlefish are benthic and live in more coastal areas, whereas the majority of squid are pelagic. In contrast, octopuses can be found in many habitats from intertidal to pelagic. On many coasts, the temperate-water, diurnal *O. vulgaris* and nocturnal *Callistoctopus macropus* share an ecological niche. The cuttlefish *Sepia officinalis* is found in the same temperate oceans but prefers sand or soft ground habitats over rocky coastal areas. The pelagic squid *Loligo vulgaris* lives in the same temperate oceans. Stemming from a benthic octopus, *Argonauta argo* is a fully pelagic octopus species. *Bathypolypus bairdii* is one of several species of deep-sea benthic octopuses. In the tropical seas, the diurnal *Octopus cyanea* is a high-order predator observed to cooperate with fish species when foraging. Sharing some of the same coastal areas are the cuttlefish *S. latimanus* and the reef squid *S. lessoniana*. Both species are visual predators that live in groups or aggregations of animals. Members of the *Sepiotheuthis* genus are known to school, and have a complex social life with conspecific communication through body patterns. While species from extreme environments can be sensitive to even the smallest changes, several species that are generalist predators are known to be extremely adaptable to environmental changes (Chun *et al.* 2022, Gutnick *et al.* 2022). (B) The relative sizes of visual and tactile processing areas in the octopus and cuttlefish brain. The inferior frontal lobe (IFL, green) is part of the tactile information processing circuitry. The medial superior frontal lobe (MSF, dark blue), vertical lobe (VL, blue) and the optic lobes (OL, light blue) are part of the visual information processing circuitry. Comparison of sagittal sections of the supraesophageal brain in octopuses shows that the MSF-VL of the tropical water *O. cyanea* is larger than that of the temperate water *O. vulgaris*. The marked difference in the IFL of *Argonauta argo* is likely a secondary adaptation to a pelagic lifestyle. A top-down view of the CNS of cuttlefish reveals a remarkable difference in size and complexity of the OL between the tropical, diurnal and social *S. latimanus* and the temperate water, nocturnal *S. officinalis* (Chun *et al.* (2022), Gutnick *et al.* (2022)).

Coleoid cephalopods

The soft-bodied coleoid body plan is characterized by eight flexible and independently controllable fleshy ‘arms’ which have extensive tactile and chemosensory capabilities. The octopus and squid/cuttlefish lineages diverged ~240 million years ago, roughly the time that the mammalian lineage was diverging from the bird/dinosaur lineage on land — the ancestral armored cephalopods, which once ruled the seas, are today represented only by the endangered nautiluses. Squid and cuttlefish, known collectively as decapods, also have two extensible tentacles used in prey capture and mating.

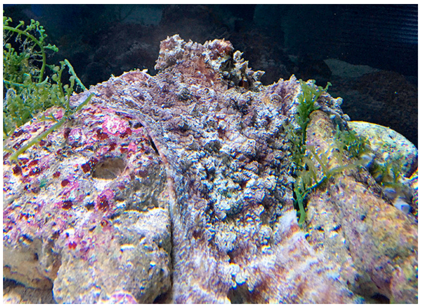

Figure 2. Hide by adjusting the color and the texture of your skin.
Camouflaged *O. cyanea* imitating both the coloration and the tactile structure of the surface close to the animal (photo: Tamar Gutnick).

All coleoids can propel themselves by squirting jets of water through a flexible funnel, and octopuses can also ‘walk’ on their arms along the sea floor. Coleoids have sophisticated visual systems with large camera eyes that superficially resemble the eyes of vertebrates but evolved independently, with distinct structure and completely different retinal and post-retinal processing (Figure 1). The skin of coleoids contains millions of individually controlled chromatophores and iridophores, and is capable of elaborate visual and tactile camouflage to protect these soft-bodied animals from vertebrate and crustacean predators (Figure 2).

The nervous systems of the common octopus, *Octopus vulgaris*, has an estimated 500 million neurons, comparable to the brain of a dog, distributed unequally over three principal components, with enormous variation across species. The smallest component is the central ‘brain’, which is formed by an elaborate network of more than two dozen interconnected lobes surrounding the oesophagus, a ‘design flaw’ inherited from the ancestral molluscan ganglionic ring. Various lobes of the central brain can be associated with specific aspects of sensory perception and behavior. The optic lobes behind each eye process visual signals and are somewhat larger than the central brain. Lastly, more than half of the neurons are typically found in the brachial or axial nervous system that runs along each arm and serves the arm musculature and numerous individually innervated suckers, driving complex coordinated movements and supporting tactile and chemosensory inputs.

Central versus distributed nervous systems

The complex nervous systems of coleoid cephalopods are therefore organized in a completely different manner to the comparably sized nervous systems of small vertebrates and underlie a correspondingly unique and complex behavioral repertoire. The neuro-ecological study of coleoid behavior is in its early stages and requires the integration of prior and new knowledge of many aspects of brain morphology, connectivity and functional organization, as well as the study of survival and reproductive strategies in diverse habitats. Because coleoids process the sensory world very differently from the vertebrate and crustacean species with which they share their environment, they are an important subject for comparative studies in psychophysiology, perception, eco-morphology and learning.

Morphological differences in nervous system anatomy among animals reflect differences in habitat, lifestyle, and associated changes in general body morphology and distinctive sensory systems, which are evolutionarily contingent on the history of each lineage. While gross morphology can give some insights into interspecies differences in behavior, these may also reflect changes in the underlying neural circuitry. For example, until recently many higher cognitive behaviors were linked to mammals and their specific brain structure. But from comparative research we now know that problem solving and tool use can be performed by some bird species at a level similar to that of a primate, using distinct circuits. With the growing diversity of cephalopod species in research, both similarities as well as the many distinctive differences between species are furthering our understanding of what shapes the behaviors and nervous systems of these remarkable animals. These comparisons are made over a wide range of spatiotemporal scales, from observations in the field, and testing of specific sensory abilities to describing detailed morphological, cellular and molecular features of their nervous systems.

Even though the arms of all coleoids are muscular hydrostats lined with suckers, in most cases the manipulation abilities of the arms and their use in active chemotactile search are much more limited in decapods than in octopuses. Correspondingly, volumetric studies of the relative sizes of visual processing areas in the central nervous system, including the optic lobes and lobes of the supraesophageal brain, suggest that in comparison with octopuses, cuttlefish and squid rely more heavily on the visual system than on chemical and tactile sensing. Indeed, in decapods, vision is an essential part of prey localization and the subsequent attack sequence which ends with a rapid tentacle strike.

The visual systems of several species of tropical diurnal cuttlefish, such as *Sepia lessoniana* and *Sepia plangon*, show increased complexity relative to other coleoids, which might be associated with their enriched visual environment, but may also be related to their more social lifestyle, given the active pattern-based communication that has been observed in these species. Although the nervous systems of pelagic and deep sea squid have been less studied, their brains are considered the simplest among the decapods, with optic lobes more than twice as large as the less-well-structured central brain, with more limited lobe structure. Yet even the mesopelagic squid *Dosidicus giganteus*, which vertically migrate hundreds of meters daily and are often naturally found in shoals, uses chromatophore patterns and specific arm postures in the presence of conspecifics, presumably for communication.

Social interactions and personality

Over the past few years, researchers have discovered that various species of octopuses, squid, and cuttlefish exhibit different levels of socialization and interaction both within and between species. While octopuses are typically solitary, other coleoids are social animals with correspondingly complex social behaviors (Figures 1 and 3).The difficulty in conducting long-term underwater field observations on the behavior of well-camouflaged cephalopods in the wild, however, has limited our understanding of the social behavior of many cephalopod species. The best-studied species are the more social decapods. In field studies of schooling Caribbean and Pacific reef squid, researchers subdivided observed body patterns and body postures into a series of components, and found that specific co-expressed behavioral components make up a distinct signal aimed at a conspecific (Figure 4A). Thus, in a matter of seconds, a Caribbean reef squid can switch from signaling aggression to one individual in the school to sexual communication with another (Figure 4B).

Even more solitary animals have behavioral traits that may be considered as cephalopod ‘personality’. These include tendencies towards avoidance versus aggression (‘shy’ versus ‘bold’), or varying degrees of persistence and reactivity in various situations, which have been measured in bobtail squid (*Eupryma* spp.) and octopus, and were found to be context dependent and to change with sexual maturity and size. Although these traits appear to be heritable, their neural correlates are presently unknown.

Controlling a soft and sensitive body

The octopus provides one of the most exciting examples of coordinated motion and control, with eight flexible appendages that can interchangeably serve as arms, legs, and fins utilizing a myriad of movements and locomotion patterns (see supplemental Videos S1 and S2). A central aim of cephalopod research is to investigate how these boneless animals manage the complex control of arms that have a practically infinite number of degrees of freedom. As such, the study of peripheral motor control in cephalopods provides an animal model, with a body plan and behavior more complex than that of a simple worm, for research that should inform the development of soft-bodied robots with complex motions.

Researchers have recently developed experimental setups that allow them to investigate the role of the octopus brain in controlling octopus arms. They used mazes and other behavioral experiments to determine what octopuses can detect with their peripheral nervous system and soft bodies. The unique system of camouflage based on actively controlled chromatophores in the skin provides an opportunity to delineate the relationship between visual input and motor output by relating statistically defined visual images to the output on the skin of the animal (Figure 2).

Behavioral studies showed that the octopus can direct its arm at a visually identified target, thus dispelling the old myth that the behavior of the arm is entirely independent of the central nervous system. Still, it is important to recognize that more than half of the octopus’s nervous system and thousands of sensory cells are located in the arms. Recent investigations which describe variability in brain structures between cephalopods suggest that interspecies differences in nervous system morphology are related to habitat and life-style. In addition to the adaptations of the nervous system, the entire body plan is adapted for the different ecological niches that species live in. Nocturnal octopuses have different brain areas enlarged and some nocturnal species also have elongated arms which have more suckers which provide the central nervous system with more input from the sensory systems located on the suckers/arms of octopuses.

Sleep

Sleep, or sleep-like states, have been observed in all animal species that have been investigated to date, suggesting that it is essential for survival. Behavioral sleep, fulfilling several criteria such as loss of locomotion, distinct posture, enhanced arousal thresholds and rapid reversibility, has been characterized in several species of octopus and in the common cuttlefish. Among invertebrates, only cephalopods have been shown to clearly exhibit multiple sleep stages. Video analysis has revealed at least two stages of sleep based on chromatophore patterns and body motions. The first stage is quiet sleep, with a uniform or pale body colour, closed eyes, and little to no motion. Quiet sleep alternates with the spectacular active sleep state, in which the skin flashes different patterns and textures, muscles twitch, and arms and suckers move around rapidly. These displays may include coherent patterns, such as a completely half-dark/half-light animal; since patterning is coordinated by the central brain, active sleep likely reflects changes in brain activity (see supplemental Video S3).

Figure 3. Cuttlefish aggregation.
Aggregation of hatchling *S. latimanus* in a stone coral structure for protection (photo: Tamar Gutnick).

While studies on octopuses have included both nocturnal and diurnal species, thus far sleep has only been studied in one species of decapod (squids and cuttlefish). The importance of decapod species to our understanding of the organization and importance of sleep in cephalopods is directly related to their marked diversity of habitats. For example, most squid species are pelagic or semi-pelagic, meaning that the majority of their lives are spent in the water column. Vertebrate species such as dolphins and various migrating birds whose life-style requires constant swimming, flying, or semi alertness have developed unihemispheric sleep, in which one half of the brain generates slow waves, whereas the other half retains a low level of alertness. Whether similar patterns arise in continuously moving cephalopods remains to be determined.

A soft body and a sharp mind

New genomic and molecular tools are enabling the exploration of cephalopod nervous systems and behavior at the level of genes, cells, networks and systems. Coleoid cephalopods make extensive use of mRNA editing, allowing individuals with constant genomes to produce diverse neuronal proteomes that may be responsive

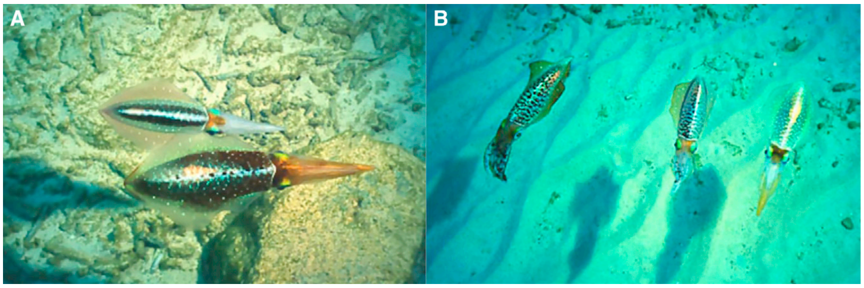

Figure 4. Signal using your skin.
(A) Mating signals between a male and a female *S. sepioidea*. Both individuals show the typical male and female patterns in the mating season (photo: James B. Wood). (B) Three individuals of *S. sepioidea*. The central positioned animal shows a split pattern to the individuals on the left and right side (photo: James B. Wood).

to cellular and environmental cues. The degree to which this flexibility is involved in regulating behaviors is an exciting area of research. Methods for genome editing in cephalopods promise to bring forward genetics to cephalopod biology, coming full circle from the classic use of the squid giant axon to explore the basic phenomenon of signal transmission in neurons. Understanding the molecular underpinnings of the nervous systems of a range of species facing diverse challenges will in turn help elucidate the general principles underlying complex behavior.

In the present often fast-changing environments, animals might on one hand be an invasive species or on the other hand be hunted by new competitors or predators. For example, in the Mediterranean Sea we can observe several tropical cephalopod species entering the sea while the local species are struggling with the high temperatures of the water and the better adapted competing predators from the Red Sea. Investigating responses of cephalopods to changing climate and habitat will help us to see how these animals are impacted. Cephalopod fisheries play an important role in food webs and human consumption, with extensive interest in aquaculture and conservation. In addition to exploring the unique neurobiology of these creatures, future research will also focus on how changes in the environment and overfishing endanger these populations.

SUPPLEMENTAL INFORMATION

Supplemental Information includes three videos and can be found with this article online at https://doi.org/10.1016/j.cub.2023.08.094.

DECLARATION OF INTERESTS

The authors declare no competing interests.

FURTHER READING

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[1]Department of Biology, University of Naples Federico II, Via Cintia 26, 80126 Naples, Italy. [2]Department of Molecular and Cell Biology, University of California, Berkeley, CA 94720, USA. [3]Molecular Genetics Unit, Okinawa Institute of Science and Technology, Onna, Okinawa 904-0412, Japan. [4]Chan-Zuckerberg BioHub, San Francisco, CA 94158, USA.
*E-mail: michi.kuba@mac.com