

Cephalopod Intelligence

By John A. Catalani

I love cephalopods, particularly nautiloids (but you knew this). Cephalopods are certainly the most specialized members of the mollusks and, “in terms of speed, intelligence, and sensory ability, they represent the acme of invertebrate evolution” (Ward, 1988: 16). The class Cephalopoda consisted of three subclasses until the end of the Cretaceous Period when the Ammonoidea went extinct. The two extant subclasses, the Nautiloidea and the Coleoidea, differ greatly physiologically and ecologically. The Nautiloidea is represented by only two genera, *Nautilus* and *Allonautilus*, and a handful of species, whereas the Coleoidea is represented by 600-700 species of squids, cuttlefishes, and octopods. Although my research involves Ordovician nautiloids, I have an interest in all cephalopods, be they extinct or extant. The general perception is that the coleoids are sophisticated and “smart” whereas the nautiloids are primitive and “dim-witted.” Thankfully, as we shall see, new research is challenging this perception and has provided me with yet another topic concerning cephalopods.

Let me begin by briefly describing some of the characteristics of both groups of extant cephalopods. The major difference is immediately apparent: *Nautilus* and *Allonautilus* possess an external shell (“ectocochliate” in cephalopod speak) and coleoids do not. The external shell provides nautiluses with both protection and neutral buoyancy. This neutral (actually slightly negative) buoyancy is achieved through the removal of water from the chambers by osmosis and the diffusion of gas, which is at low pressures at normal *Nautilus* water depths, back into the chambers. Coleoids might or might not possess an internal shell. The internal shell of the squid provides support for the soft and streamlined body thus facilitating movement through the water. The internal shell of the cuttlefish aids in buoyancy (the cuttlebone is porous). Octopods contain no internal shell (the *Nautilus*-like shell secreted by *Argonauta* females is actually a brood chamber for their eggs). The loss of a protective external shell is more than compensated for by the speed

and maneuverability that coleoids possess. Interestingly, from what we have been able to infer from the fossil record and presumed taxonomic lineages, ammonoids possessed traits of both nautiloids (external shell) and coleoids (biology and lifestyle).

Arms and tentacles are another characteristic feature of cephalopods. All coleoids are equipped with eight muscular arms. Squids and cuttlefishes also possess two food-gathering tentacles that are usually much longer than the arms. The suction cups located on both the arms and the club-shaped end-process of the tentacles of squids and cuttlefishes often possess chitinous “teeth” that facilitate the grasping of food as well as provide the animal with some defense. The smooth

suction cups of octopods are able to hold onto objects and are equipped with chemoreceptors which allow them to “taste” what they are touching. Jet propulsion (accomplished by expelling water through the siphon), another classic feature of cephalopods, is the preferred method of horizontal movement for the coleoids (and nautiluses, although not nearly as efficiently). Movement over the substratum, particularly with octopuses, is facilitated with the eight arms. Some species of *Octopus* are even able to use

their arms to crawl out of the water for short forays onto land. Nautiluses are equipped with approximately 90 small tentacles, each consisting of a cirrus, with no suckers or arm hooks, and a sheath into which the cirrus can be withdrawn. The tentacles, which no longer contribute to the animal’s locomotion, serve many functions including food detection (using both chemosensory and tactile inputs), transportation of food to the mouth, and reproduction.

Much has been written about the large eyes of coleoids, particularly those of the squid. They are very similar in structure to vertebrate eyes, a classic example of convergent evolution (the presence of Pax-6 gene homologs, along with other genes, suggests some homology, although this has been contested). Coleoid eyes consist of a lens (with a pupil that ad-



Living Nautilus pompilius, photographed alive at the Berlin Zoo Aquarium. Photograph by J. Baecker via Wikimedia Commons.

justs by changing shape with differing light intensities) and a retina (with densely packed cells) providing excellent object resolution. Advanced musculature allows tracking of moving objects. Even though virtually all coleoids are color blind, they can detect polarized light due to the arrangement of photoreceptor cells. This allows the animal to detect both prey and predators against a reflective background. Although the eyes of nautiluses have an adjustable pupil as well as retinal characteristics and musculature similar to those of coleoids, the eye itself is a primitive pinhole type with no lens, thus allowing seawater into the eye chamber. The *Nautilus* eye structure permits only poor resolution and appears to be more adapted at detecting light intensity than discrete objects. This limitation, along with the low ambient light present in their deep-water habitat, suggests that sight is much less important to nautiluses as a sensory mechanism than either odor or tactile stimulation – more on this later.

Growth and reproduction differ greatly between coleoids and nautiluses. Most coleoids live only one year, spawn only once (some species lay several batches of eggs but always during a single spawning cycle), and quickly die after mating (males) or after egg laying (females). In contrast, nautiluses grow slowly and can live for 10-20 years or more (there is a lot of uncertainty when dealing with nautiluses). After sexual maturity is reached, breeding, which occurs during a single, annual breeding season that can last several months, occurs many times during the animal's life span. The eggs laid by coleoids are small but are produced in the hundreds to thousands by individual females. Although most coleoids simply deposit the eggs with no further involvement, the females of many species of *Octopus* deposit their eggs in a den and care for the eggs not only by guarding them but also, for example, by passing water over them so that they remain aerated. During this time, the females do not eat and essentially waste away until they die, usually just after the eggs hatch. By contrast, the dozen-or-so eggs laid by female nautiluses are usually 25-35 mm in diameter – the largest eggs laid by any invertebrate. Although no nautilus eggs have ever been observed in the field, studies of the oxygen isotopes present in different parts of the shell indicate that the eggs are deposited in warm, shallow water and that the animal assumes a normal deep-water lifestyle immediately after hatching. If the eggs are indeed laid in shallow water, odds are that there is no subsequent parental care.

Possibly the most spectacular adaptation of coleoids is the ability to create and alter skin colors, patterns, and textures with blinding speed. The colors and patterns are generated mainly by chromatophores, which are cells that contain sacs of pigment and are located just below the surface of the skin, but are assisted by other cells called iridophores and leucophores. Each chromatophore is controlled by a nerve fiber that either contracts the surrounding muscles expanding the sacs and making the color visible or relaxes the muscles contracting the sacs thereby muting the color. Because each

chromatophore is controlled individually, a large repertoire of patterns and signals can be generated and modified very quickly. Some species are also equipped with photophores that produce luminescent colors thus enhancing their displays. Octopuses and cuttlefishes can also achieve various skin textures by contracting muscles to form various protuberances and tubercles. These color, pattern, and texture displays are not only useful in warning or intimidating predators but also essential to mating challenges, courtship rituals, and general monospecific communication. In addition, when texture changes are coupled with color and pattern displays, coleoids, particularly octopuses, can virtually disappear against a background, the ultimate in creature camouflage, to either avoid predators or assist in stalking prey. The *Nautilus* shell provides the animal with limited camouflage – the dorsal surface has reddish-brown patterns to blend with the substratum when viewed from above and the ventral surface is white to blend with the bright surface waters when viewed from below.

Field observations of both the remarkable range of colors and patterns that coleoids are able to generate and the interactions of these animals with each other, led scientists to speculate that they were observing not only same-species communication but also some degree of intelligence. When discussing intelligence, however, it must be understood that researchers were attempting to correctly identify (for example coleoids are, nautiloids are not) and measure intelligence in other species – a difficult task given the problems we have defining and quantifying human intelligence. For coleoid researchers, the next logical step was to conduct various field observations and laboratory experiments to explore this presumed intelligence. Experiments on a variety of coleoids have been conducted for 60-or-so years but the most common subject of these studies has been various species of *Octopus*. Experiments range from simple observations in the field to classical conditioning in the laboratory.

The method(s) used by octopuses to find their way back to their dens after foraging for food was one behavior that puzzled researchers. One possibility was that the animals used their chemotactile ability to retrace their outgoing path back to their dens. Another possibility was that the animals remembered landmarks in their foraging area and used these to find their way home. One study, reported by Mather (1991), used both field and laboratory experiments in an attempt to determine the method used in navigation. In the field, several individual *Octopus vulgaris* were observed during foraging. Maps were constructed of the ocean floor and the foraging paths taken by the animals were drawn on these maps. Several years later, a more experimental approach was taken in the field when the animals were presented with artificial landmarks amid the natural ones. These artificial landmarks were changed once the animals became accustomed to them and, once again, maps were made of their paths. Analysis of both sets of foraging maps revealed that not only was the amount

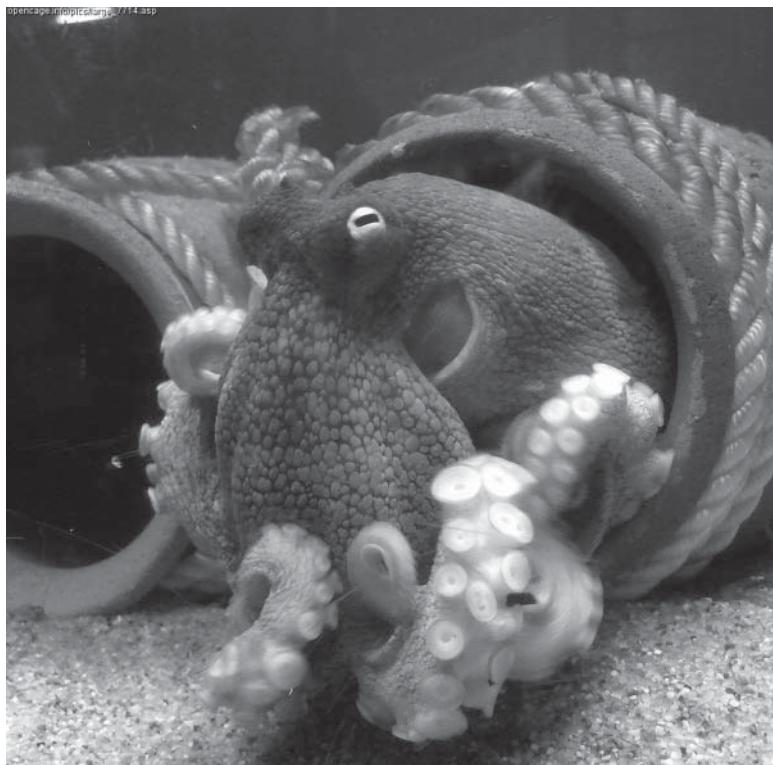
of outgoing-path/return-path overlap small but also the angle of return path averaged 30° from the outgoing path. On longer forays, the animals would jet out and jet back without making contact with the substratum, thus reinforcing the scenario of landmark-memory recognition. Additionally, when the artificial landmarks were moved, the animals were still able to return to their dens, suggesting that “they were ignoring the conspicuous but smaller artificial landmark because stable larger natural landmarks were more salient” (Mather, 1991: 494). The laboratory experiments, too involved to describe here, reinforced the importance of landmarks to navigation. This study “suggests strongly that octopuses use visual spatial information for navigation within their home ranges and to guide their returns from hunting trips” (p. 496). It is as if the animals constructed a mental map of their immediate vicinity and stored it in their long-term memory. Because the animals foraged in different areas, returned by different paths, and did not remain on the ocean floor while foraging, the chemotactile scenario was rejected.

More familiar to most of us are the classical-conditioning experiments performed on coleoids in the laboratory. It has been determined that octopuses can distinguish between shapes and patterns when conditioned by a reward-punishment technique. Problem solving experiments in which, for example, the animal is presented with food enclosed in a jar and must “learn” to open the container has also been observed and studied (Fiorito *et al.*, 1990). Not only did the time required to “solve” the jar problem decrease with practice but the animals were able to repeat this task months after the initial conditioning, indicating the presence of long-term memory. In another experiment (Fiorito & Scotto, 1992), the possibility of one octopus learning by observing another octopus was investigated. An unconditioned *Octopus vulgaris* was allowed to observe, from a separate but adjacent tank, a previously conditioned individual performing object recognition behavior. The observing animals selected the correct object around 80% of the time even when no reward was presented. A similar experiment was shown on an episode of *Scientific American Frontiers*

(PBS) in which one octopus observed another who had been previously conditioned to open a jar containing food. The observer octopus displayed an intense interest in the activity of the conditioned octopus. When presented with a jar, which the animal had not previously been able to open, the observer was successful in opening the jar to obtain the food.

Many additional observations and experiments of octopuses have revealed that they exhibit rudimentary tool use by utilizing rocks to block their den openings or water jets from their siphons to clean debris from their dens, engage in “play” behavior, and appear to have distinctive personalities because they tend to react individually to the same stimuli – all evidence for some level of reasoning power.

Based on the amount of evidence acquired during these observations and experiments (and I have mentioned only a few examples), it would seem illogical not to refer to these animals, particularly octopuses, as intelligent. They are able to input visual and tactile stimuli, store it in what appears to be long-term memory, and then recall it for use when needed, particularly for navigation. From observations in the wild and laboratory experiments, it has been demonstrated that “they evaluate sensory input and choose actions based on consideration of such input” and, although much of how data is actually processed remains unknown, what we do know about their abilities suggests that “we should add cephalopods to the groups of animals that might have primary



Living Octopus vulgaris, photographed alive at Suma Aqualife Park, Kobe, Japan.
Photograph by OpenCage via Wikimedia Commons.

consciousness” (Mather, 2008: 45).

Now, with all due respect, these researchers and authors might state that their conclusions relate to the behavior and learning in “cephalopods” but they are in reality referring only to coleoids. To some extent this is understandable – because they inhabit deep-water habitats, observing nautiluses in the field presents researchers with innumerable challenges and it is very difficult to maintain these animals in aquaria. Recently, however, there has been an upsurge in published research detailing experiments involving nautiluses.

Much of this research has concentrated on the sensory ability, mainly odor detection, of nautiluses. In an early ex-

periment (Basal *et al.*, 2000), it was determined that nautiluses could detect and track odors at a distance of 10 meters (33 feet). However, when the rhinophores (olfactory organs located below each eye) of test animals were blocked, it was discovered that odors could be detected but not tracked. A more comprehensive investigation (Basil *et al.*, 2005) identified four odor-detecting structures: the rhinophores, digital tentacles, preocular tentacles, and postocular tentacles. Ciliated epithelial cells on these structures act as chemoreceptors allowing for both remote and contact odor detection. When odor stimuli were presented directly (within 1 cm) to test animals, several behaviors were elicited. Stimulation of the rhinophores resulted in the digital tentacles spreading out into the “cone-of-search” odor-detection behavior used by nautiluses to track distant odors. Stimulation of the digital tentacles resulted in the extension of the lateral digital tentacles, movement toward the substratum (or food source), and contact with the substratum with the medial digital tentacles. This behavior is used by the animals as they near the food source. Stimulation of the preocular tentacles elicited similar reactions although not as intensely for either behavior whereas the other odor-detecting structures were of lesser importance. Non-odor control stimuli elicited no reactions. It appears that chemotactile sensory mechanisms are indeed much more important to nautiluses than vision for food detection and, probably, predator detection and avoidance. Additionally, although the eyes of nautiluses are inferior to those of other cephalopods, the rhinophores, as well as the olfactory lobes in the brain, are similar to, but larger than, those possessed by coleoids and represent another adaptation for living in a low-light deep-water habitat.

Another study (Soucier & Basil, 2008) investigated the ability of nautiluses to detect mechanical and acoustical stimuli underwater. As in some experiments with coleoids, changes in ventilation (respiratory) rates were used as a measure of response to stimuli. The test animals responded to vibratory stimuli in the water by lowering their ventilation rates. The ability to sense vibrations would obviously be advantageous in detecting potential predators and lower respiratory rates would be an effective strategy for predator avoidance.

These experiments have given us a clearer picture of how nautiluses interact with their environment in terms of food acquisition as well as possible predator detection and avoidance. However, classical conditioning experiments similar to those performed on coleoids described above have been lacking for the Chambered Nautilus. Why? Crook & Basil (2008, and the article that provided me with the incentive to write this essay) reasoned that, because nautiluses lack coleoid-like regions of the brain that are dedicated to learning, memory, and recall, “it is assumed that the absence of these regions should limit memory storage and recall in nautilus, but,” they continued, “this assumption has never been tested” (p. 1992). The authors further reasoned that, because *Nautilus* is the last representative of the lineage ancestral to

all extant cephalopods (either directly or indirectly) and possesses a primitive brain when compared to coleoids, experiments on nautiluses “may provide important insights into the evolution of complexity in invertebrate nervous systems” (p. 1992).

The authors used Pavlovian conditioning to test learning, memory, and recall in *Nautilus pompilius*. Briefly, the experiment involved 12 individual nautiluses that were conditioned in an experimental arena (separate from their home tank) using a pulse of blue light of a wavelength visible to nautiluses, which elicited no unconditioned response, and a solution (no solids) of home-tank water and food substances thus producing a food-odor stimulus. A preliminary test verified that this solution elicited the normal food-detection responses from the animals – extension of the tentacles and elevated ventilation rates. Throughout the conditioning phase of the experiment, each training episode consisted of 10 trials with three minutes between each trial. During training, either the food-odor solution or the control solution of home-tank water without food was released directly onto the rhinophores and tentacles while, simultaneously, a single pulse of the blue light was flashed. Retention testing, performed randomly at time intervals of 3 minutes, 30 minutes, 1 hour, 6 hours, 12 hours, and 24 hours, consisted of an unrewarded presentation of the blue-light with test-subject responses recorded on video tape.

Analysis revealed that food-detection responses to the unrewarded blue light were higher with animals conditioned with the food-odor solution than those receiving just water when tested 3 minutes and 30 minutes after training and then again 6 hours and 12 hours after training thus identifying two distinct memory peaks. At 1 hour and 24 hours after training, there was little difference in response between the experimental and the control groups. Although, as stated above, the brains of coleoids and nautiluses are structurally different, the two distinct memory peaks (termed biphasic) in nautiluses are similar to those exhibited by coleoids and can be tentatively described as short-term memory storage and long-term memory storage although, as the authors stated, “this awaits confirmation in future physiological studies” (p. 1996). It was also discovered that short-term storage duration for nautiluses was similar to coleoids but that long-term storage duration was significantly shorter. In octopuses, for example, long-term memory can extend several months after conditioning. A possible explanation for the difference in long-term retention between nautiluses and coleoids centers on the structural differences in their brains – coleoids have a vertical-lobe complex whereas nautiluses do not. In coleoids, it has been determined experimentally that the vertical-lobe complex is necessary for visual-stimulus memory but, because nautiluses as well as some noncephalopod mollusks also exhibit long-term memory, it appears that “the presence of a vertical lobe is not a necessity for long-term storage and recall of conditioned behaviours” (p. 1997).

Differences in the brain structure of these two groups of cephalopods have been linked to differences in their lifestyles. Nautiluses, with their more primitive brains, are for the most part scavengers that inhabit low-light water depths where chemotactile sensory inputs are more important than visual inputs when foraging for food items. Coleoids, on the other hand, have adopted a fast, active, visual, and predatory lifestyle. The more complex brain of coleoids appears to have been essential to their adopting this aggressive lifestyle. Therefore, divergence in *Nautilus* and coleoid lifestyles appears to account, at least in part, for the differences in their brain structures. Clearly, further investigation of these structural differences has the potential to “provide us with unique insights into the competing roles that a close evolutionary relationship and widely divergent ecology have played in shaping neuroanatomy of modern cephalopods” (p. 1997).

So, it appears that the “primitive” Chambered Nautilus has acquired new respect among researchers investigating cephalopod intelligence. There is no question that coleoids are the most neurologically advanced invertebrates on the planet, but don’t ignore nautiloids – they have been around a lot longer. And to those who say nautiluses are on the way out, I hasten to remind them that several times in Earth history nautiloids have been down but have not yet been counted out (as opposed to the obviously inferior ammonoids). In fact, several studies have revealed that the populations of nautiluses are genetically viable and appear to be diversifying.

I am in awe of these marvelously engineered animals. They are a testament to evolution’s ability to solve a structural problem, in this case neutral buoyancy of an externally shelled animal, with a design so successful not even the vagaries of deep time could toll their doom. And we are the beneficiaries of this success because scientists are just beginning to appreciate what this “living fossil” can teach us.

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