Cephalopods and the Evolution of the Mind

Peter Godfrey-Smith

The Graduate Center
City University of New York

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In thinking about the nature of the mind and its evolutionary history, cephalopods – especially octopuses, cuttlefish, and squid – have a special importance. These animals are an *independent experiment* in the evolution of large and complex nervous systems – in the biological machinery of the mind. They evolved this machinery on a historical lineage distant from our own. Where their minds differ from ours, they show us another way of being a sentient organism. Where we are similar, this is due to the convergence of distinct evolutionary paths.

I introduced the topic just now as 'the mind.' This is a contentious term to use. What is it to have a mind? One option is that we are looking for something close to what humans have — something like reflective and conscious thought. This sets a high bar for having a mind. Another possible view is that whenever organisms adapt to their circumstances in real time by adjusting their behavior, taking in information and acting in response to it, there is some degree of mentality or intelligence there. To say this sets a low bar.

It is best not to set bars in either place. Roughly speaking, we are dealing with a matter of degree, though 'degree' is not quite the right term either. The evolution of a mind is the acquisition of a tool-kit for the control of behavior. The tool-kit includes some kind of perception, though different animals have very different ways of taking in information from the world. It includes some form of memory and learning, means by which past experiences can be brought to bear on the present. In some cases it includes problem-solving and planning. Some tool-kits are more elaborate and expensive than others, but they can be sophisticated in different ways, with different tools present and more investment in one technology than another. One animal might have better ways of tracking the environment through its senses, while another may have simpler senses but more sophisticated learning. Different tool kits go with different ways of making a living. The ordinary term 'mind' is awkwardly or misleadingly applied to an animal with a very simple behavioral repertoire, but it is parochial to apply it only to humans.

A submerged history

Now that cephalopods have us thinking about the evolution of the mind, why not go back further? In tracing this history, a good place is to start is with the evolution of the neuron. Neurons have long been taken to be the fundamental information-processing devices in animals. Some recent work has challenged this; it has challenged both the idea that all the smartness in a brain is due to the activity of neurons, and the idea that the smartness of an organism resides entirely in its brain (Halassa and Haydon 2010, Clark 1998, Noë 2009). But there is no doubt that the neuron was an evolutionary breakthrough. When did it occur?

Two familiar animals in the sea provide us with markers. Sponges do not have neurons, and jellyfish do. These facts, together with the overall shape of the historical tree of life, enable us to narrow down the date. If it is safe to assume that neurons arose just once in evolution, we can put a time-frame on the appearance of the neuron by looking at the relation between two branchings on the tree. (The *if* in the previous sentence may not be an entirely safe assumption (Moroz 2009), but I will work within it here.) One of these is the branching that leads on one side to animals like us and on the other side to sponges. This puts a no-earlier-than date on the evolution of the neuron. The other branching, further downstream, leads on one side to us and on the other side to jellyfish. This puts a no-later-than date on the evolution of the neuron. As we share neurons with jellyfish but not with sponges, then unless the sponge lineage once had neurons but lost them, neurons probably evolved between those two branching points. All the dates are very uncertain here, and there is ongoing debate about the branching sequence itself (Dunn et al. 2008), but this reasoning suggests that neurons probably evolved something like 700-800 million years ago.

This is early in the history of animal life, well before the Cambrian Explosion which produced the most of the basic designs of animals familiar to us now. Moving forward, the next landmark in the story is still probably before the Cambrian. This is the evolution of the *ancestral bilaterian*, the first animal with the bilateral body organization that we also share – an organization with left and right sides, along with a top and bottom or front and back. The first bilaterian lived perhaps 600 million years ago.

No one knows what this animal looked like, but a current guess is that it was a small flattened worm (Hejnol and Martindale 2008). It had neurons, might have had eyespots enabling simple vision, and may also have had some centralization of neurons at its front. I doubt if it was much to look at, but this nondescript creature had a body organization that seems to unlock possibilities, especially in the area of behavior. The bilaterian organization facilitates a mobile lifestyle – a life of wriggling, swimming, and crawling. Mobility puts a premium on the fine control of behavior, and hence on nervous systems.

This animal also stands near another historical branching point. As always, it is only after the fact that these branchings can be recognized as important. But something like this animal, an early bilaterian, stands (or swims) at a fork on the tree of life from which one side leads to vertebrate animals like us, and the other leads to a range of invertebrate groups. Those include arthropods like insects and crabs, annelids like earthworms, and molluscs, among which are the cephalopods. The most recent common ancestor of ourselves and octopuses, then, lived something like 600 million years ago, round the time of early, small bilaterian animals. The two histories run separately from there.

On our vertebrate side of this branch, we see the eventual evolution of large nervous systems in some groups, especially in mammals and birds. On the other side, many different kinds of invertebrates arise, many of them small animals and most without large and complex nervous systems, but with an exception. The exception is a group of cephalopods, the *coleoids*, which include octopuses, cuttlefish, and squid. These evolved brains that are comparable in size, in both absolute and relative terms, to those of vertebrates. Andrew Packard, in 1972, mapped brain weight as a function of body weight in a range of different groups. His chart put cephalopod brain sizes, especially those of octopus and cuttlefish, roughly between the ranges for what were then called 'higher' vertebrates (mammals and birds) and 'lower' vertebrates (reptiles and fish). The significance of simple measures of brain-to-body weight may be doubted. The idea that cephalopods are the exception to the rule of simple nervous systems and behavior in invertebrates also encounters challenges, especially from stomatopods or mantis shrimp, which are long-lived, monogamous, and fearsomely-armed shrimp who have formed their own unusual evolutionary lineage for hundreds of millions of years (Cronin *et al.* 2006). But in this paper I will work within the view that cephalopods have indeed done something unusual among invertebrates. They have made a huge investment in nervous machinery – something like 500 million neurons in the common octopus, for example (Hochner, Shomrat, and Fiorito 2006). Given this, and given that the common ancestor of vertebrates and cephalopods was a simple flatworm-like animal, there have been two independent experiments in the evolution of large and complex nervous systems from small and simple ones. We are among the products of one of these experiments and cephalopods are the products of the other.

To speak of a single vertebrate experiment is to take a coarse-grained view. Within the vertebrates, mammals and birds have been separate for about 300 million years. But all vertebrates share a general body-plan, and their nervous systems show a common inheritance (Edelman and Seth 2009). Cephalopods have an entirely different organization, both in body in brain. The vertebrate plan features a head and spinal cord, with the peripheral nervous system coming off it. This is a rather centralized design. Molluscs, along with several other invertebrate groups, developed what is sometimes called a 'ladder-like' nervous system. In many molluscs there are knots of neurons, or ganglia, spread along the body, linked by two kinds of connections – 'vertical' ones along the body and 'horizontal' ones across it, like a ladder. Though this was the likely molluscan starting point, in the evolution of coleoid cephalopods there was both expansion and partial centralization of this nervous system (Budelmann 1995, Nixon and Young 2003, Zullo and Hochner 2011). Neurons were packed together up front between the eyes, and many of the ganglia were fused. So there was a partial submerging of the invertebrate neural plan – but only a partial one. I said earlier that a common octopus has about 500 million neurons. Two thirds of those are not in the brain at all, but in the arms themselves (Hochner, Shomrat, and Fiorito 2006). Their nervous system remains much more 'distributed,' more spread through the body, than ours.

How smart?

I'll return to the distinctive organization of the cephalopod nervous system later, but first I will turn to behavior. How smart are the smartest cephalopods? The question is hard to even address, in part for reasons outlined at the start of this paper. When one animal has a different tool-kit from another, comparison is difficult and often looks arbitrary. It is probably fair to say that when octopuses – the best-studied cephalopods – have been tested using standard experiments designed for vertebrate animals, they have done fairly well, without showing themselves to be Einsteins (Hanlon and Messenger 1996, Mather 2008, Grasso and Basil 2009). Octopuses in experimental situations can learn to use visual cues to determine which of two possible environments they might be in, and take the correct route to a goal (Hvorecny *et al.*, 2007). Octopuses are good navigators in the wild, too, often taking long loops that reliably lead back to their den (Mather 1991). Here it must be added that animals with much smaller brains, such as bees, are able to perform quite uncanny acts of navigation (Gallistel and King 2009), so these spatial skills are not distinctive to octopuses. A group of researchers in Indonesia were recently surprised to see octopus carrying around pairs of half coconut shells, to use as portable shelters (Finn *et al.* 2009). One half-shell would be nested inside another, and the octopus would carry the pair beneath its body as it stilt-walked across the sea bottom. The octopus would then assemble the half-shells into a sphere and climb inside. Many animals use found objects for shelters (hermit crabs are an example), but to assemble and disassemble a compound tool like this is rare. One experiment in the 1990s suggested that octopuses can also learn by imitating the behavior of other octopuses (Fiorito and Scotto 1992), though this finding has remained enigmatic as it has not yet been replicated.

Against a background of mixed experimental results, there are anecdotes suggesting very complex cognitive abilities. Some of these anecdotes are becoming used as the basis for experiments. For example, it has long seemed likely that captive octopuses recognize and behave differently towards individual human keepers. Stories of this kind have come out of different labs for years (Boal 2006, Mather *et al.* 2010). In 2010, an experiment was done to test this, and confirmed that Giant Pacific Octopuses *Enteroctopus dofleini* can indeed recognize individual humans, even when they are wearing identical uniforms (Anderson *et al.* 2010). Given this, it was not surprising when a study in 2011 found that, in another species, octopuses could recognize other individual octopuses (Tricarico *et al.* 2011).

The internet is full of stories of octopus escapes and thievery, and at least some of these stories are true (Jean McKinnon, University of Otago, pers. comm). Octopuses climb out of their home tanks at night to raid neighboring tanks for food, returning to their home tanks by morning. The need for intelligence in these escapades sometimes seems to be over-stated, as neighboring tanks are perhaps not so different from tide-pools. Octopuses have also learned to turn off the lights in aquariums when no one is watching, by squirting jets of water at them (also confirmed by Jean McKinnon). This is an apparently impressive behavior, but one that is still open to several interpretations. It might be a smart piece of learning, but it might instead be just a consequence of a general aversion to light; octopuses squirt water at many things they do not like, and are probably more likely to be far enough out of their dens to squirt at this target when no humans are around. Resolving different interpretations of the "lights out!" behavior might be the basis of another good experiment.

Evolution and neural complexity

If cephalopods are unusually intelligent animals, a further question is why they evolved to be this way. Nervous systems are expensive machinery for any animal. Signaling between neurons requires the continual pumping of chemicals back and forth to concentrate electrical charges. So when an organism has a brain that is large in relation to its body size, that is probably because it is doing something useful for the animal that makes it worth the cost.

Cephalopods are predators, and many of them live active and exploratory lifestyles. This seems to be relevant. On the other hand, all animals have to find food and avoid being eaten in the process. What is it about cephalopods that might make the costs of a large nervous system worth paying?

In 1986 Kathleen Gibson, writing about vertebrates, distinguished styles of foraging for food that correlate with smaller and larger brains. She distinguished inflexible foraging programs that include little manipulation of food, from "extractive" foraging, the kind that involves adapting food choices to circumstances, removing food from protective shells and nut casings, and doing so in a flexible and context-sensitive way (Gibson 1986). Compare the foraging of a frog, lashing out at flying insects, to that of a chimp. In the frog there is no significant flexibility in strategy, and no manipulation of food once caught. Chimps, in contrast, wander about and seek out a variety of foods, many of which require extraction and processing. Gibson argued that extractive foraging is seen in animals with larger and more complex brains.

Although her discussion was entirely focused on vertebrates, some of Gibson's description of cognitively demanding styles of foraging fit octopuses quite well. They are exploratory animals – as many aquarium keepers have found – and eat diverse foods which in many cases require skilled handing. This picture applies less to cuttlefish and squid, which engage in less complex manipulation of their food.

The most prominent approach to explaining the evolution of large brains in recent years, however, is the the 'social intelligence hypothesis.' This was originally proposed by Alison Jolly (1969) and Nick Humphrey (1976), and also aimed initially at primates and other vertebrates. The idea is that if you look at animals with large brains and ask what they are using them to deal with, the answer is *each other*; they are tools for dealing with other members of one's own species. In general, more social species within mammals and birds do tend to have larger brains. In the case of vertebrates, this approach to explaining the evolution of large brains and intelligence is currently favored more than explanations based on foraging (Byrne and Bates 2007). This approach does not, however, seem a likely explanation for cephalopod intelligence. Some squid are very social (Moynihan and Rodaniche 1982), but octopuses and cuttlefish generally are not. It is possible in principle that the non-social groups descended from a more social ancestor, but there is presently no reason to believe this is true.

There are hints that octopuses may not be quite as asocial as has often been supposed. Field studies have sometimes found octopuses co-existing at high densities (see Boal 2006 for a survey, and Huffard *et al.* 2008 for an interesting recent case). I noted earlier that an experiment from 2011 has shown that in *Octopus vulgaris*, individuals have some capacity to recognize other octopuses they have interacted with. An unusual site was also recently found at Jervis Bay, on the east coast of Australia, by a local diver named Matthew Lawrence (Godfrey-Smith and Lawrence in press). In a flat sandy area Lawrence came across a bed of scallop shells, three meters or so in diameter, centered on a single den. Quite high densities of octopuses are often seen on this shell bed, up to five at once, and others now live round the perimeter in objects that Lawrence has brought in to the site. The octopuses seem aware of each others' presence. There are occasional fights and sometimes one will chase another out of the area. In other cases they briefly 'box' with their arms. This site does seem to be unusual even for the species (*Octopus tetricus)*, though; they are much more often seen alone or occasionally in pairs.

Further south on the Australian coast is a site of intense cephalopod sociality. Cuttlefish, like octopuses, are generally regarded as rather solitary animals. In most species they are usually seen just in ones or twos, and cuttlefish have never been seen congregating in large numbers – except at one place. Point Lowly is near the industrial town of Whyalla, in the Spencer Gulf, South Australia. Annually over the last decade or so, between April and June, Giant Cuttlefish (*Sepia apama*) have arrived and filled the shallows in thousands (Hall and Hanlon 2002). Giant Cuttlefish are the largest cuttlefish species, growing up to about a meter long. When they come they congregate along a small stretch of shore, just 10 km long or so, and engage in a three-month melee of displays, contests, fights, and sex. Many cephalopods are remarkable for their ability to change color, and produce sequences of complex patterns on their skins. Giant Cuttlefish are perhaps the most spectacular color-changers, in part because of the sheer size of the video screen that covers them. In the waters off Point Lowly they form a pulsing mosaic of reds, silver-whites, and yellow-greens.

Locals had known about them for years, and they were occasionally fished for bait. Around 1995, intensive fishing began targeting their annual aggregation. A commercial diver, Tony Bramley, followed the growth of the cuttlefish catch with alarm. Thousands were being hauled out of the sea, frozen, and shipped off to Asia for just cents per kilogram. Karina Hall, a student in marine biology, had been sent to investigate the growing fishery. She, too, realized that the fishery was anything but sustainable, and saw the scientific importance of the strangest cephalopod gathering in the world. In 1998 Bramley and Hall succeeded in organizing a temporary ban on fishing the cuttlefish during their annual aggregation, a ban that has been renewed and expanded since then. The cuttlefish numbers rebounded, and soon their annual arrival was marked by the synchronized appearance of waves of marine biologists.

The resulting studies revealed an unusual sex life (Norman *et al.* 1999, Hall and Hanlon 2002). At Whyalla, large males act as 'consorts,' guarding a female and chasing off other males through displays and the occasional fight. The displays between males look like a kind of competitive yoga; the males hover side-on to each other and elongate their arms and bodies, turning pale grey and white, flashing patterns across their skin. Small males, often a year younger, try to sneak matings in the resulting melee. Sometimes this is done through simple stealth, but some small males use a tactic of impersonating females, pulling their arms into the more compact shape of females and producing facsimiles of their typical colors and patterns. They often pass by and mate with the female while the consort male is intensely displaying to someone else.

The scene at Whyalla certainly shows the complexity that arises from social interaction. Once again, though, the site is unusual among cuttlefish – perhaps unique. Given its unusual status, it is alarming that over the last two years, 2011 and 2012, the numbers of animals have plummeted, for unknown reasons. Research is underway on the decline at the moment, and it seems possible that the aggregation is ending.

In any case, it does not appear likely at this stage that the evolution of large brains in cephalopods owes much to the social intelligence hypothesis. It seems more likely that these brains evolved because of the peculiarities of their lifestyle as individuals, perhaps because of the demands of finding food – and avoiding becoming food – faced by a soft-bodied and mobile animal living in shallow waters populated by fish and other vertebrates.

Experience, integration, and consciousness

What does all this information about brains and lifestyles tell us about what cephalopods themselves experience, about what it *feels* like to be an octopus? This question can seem completely intractable (Nagel 1974), but let's try to chip away at the problem. I will start with a connection between cephalopods and some interesting recent work on consciousness in humans.

Suppose we start with our own case, and look at some obvious features of the experiences that we have conscious access to. One such feature is a kind of integration. Although many processes are going on in parallel within our brains, what we are aware of at any time is a single integrated scene. In conscious experience, many different kinds of sensory information are combined, and the present is experienced as related to a recent past. Gerald Edelman coined the term 'primary consciousness' for the awareness of an integrated scene in this sense (G. Edelman 1989). This can be distinguished from 'higher-order consciousness,' the kind which involves reflection on our own thoughts, a looking inward (Rosenthal 1997).

The familiarity of the fact that conscious experience is integrated in this way disguises the fact that this integration is a significant achievement for our brains. From the 1980s, Bernard Baars and others have used this phenomenon as a clue to the neurobiology of consciousness (Baars 1988). They suggest that a particular kind of structure in our brains creates a 'global workspace,' in which a small portion of what a person's brain is dealing with is handled in a special way. It is handled in a way that is comparatively slow, sequential, and sensitive to diverse sources of information. The contents of this workspace are typically available to consciousness.

This kind of integration of processing might be something that various non-human animals have, to different degrees. The workspace theory of consciousness has been applied to cephalopods by Jennifer Mather (2008), and related hypotheses have been explored by David Edelman and others (Edelman *et al*. 2005). I will extend these ideas a little here.

If one kind of consciousness involves integration of different streams of information into a single experienced scene, what might be the evolutionary role of this sort of processing? An approach to answering this is to look at when this kind of processing is especially prominent in human life. According to Stanislaus Dehaene and Lionel Naccache (2001), it is important in a couple of specific behavioral contexts: those where people perform novel combinations of operations, where they must maintain information for explicit use over a period of time, and when they act in a deliberate manner. The first of these – the way the need to perform novel combinations of operations presses events into consciousness for us – is especially relevant, as this gives us possible connections to animal life.

The architecture of the cephalopod nervous systems is very different from ours. If some brain structure is doing this job in them, it will be different from what does the job in us. In fact, the cephalopod nervous system is so decentralized that it might seem to be a mistake to even look for this kind of unified processing. They may have a radically different style of psychological organization from us.

Some experimental work suggests there is a good deal of autonomy in the arms of an octopus; the arms' nervous systems often seem "curiously divorced" from the central brain (Hanlon and Messenger 1996, p. 15). As some see it, the plan of the octopus body and nervous system was an opportunity for the evolution of a distinctive kind of smartness. There has been a convergence here between thinking in biology and in robotics. Some years ago Rodney Brooks, a roboticist at Massachusetts Institute of Technology, argued for the advantages of highly decentralized robot designs, lacking any CEO-like controller (Brooks 1991). Brooks tried to put several smaller control devices throughout a robot's body, set up so that they did not talk to each other much, but worked together harmoniously in the context of the whole robot. Brooks made this argument on engineering grounds – he thought the result would be better robots. In Italy, a group headed by Cecilia Laschi has made a connection between this approach to robotics and the biology of the octopus; they are using the octopus as the basis for design of a soft-bodied robot (Laschi et al. 2008). Their hypothesis is that making a robot on the octopus design will lead to a kind of practical intelligence, avoiding the informational traffic-jams that a more centralized design tends to bring (see also Pfeiffer et al. 2007).

However, a recent experiment by Tamar Gutnick and her colleagues in Binyamin Hochner's lab in Israel has shown that octopuses can exert a significant degree of central control over their arms when they need to. An octopus can learn to use vision to guide a single arm along a complex maze-like path to get food (Gutnick *et al.* 2011). This is not merely a matter of allowing the arm to follow a chemical gradient, as the arm has to leave the water at one point to reach the target location. Visual information must be used to guide the arm to its destination. The study also noted, though, that when octopuses are doing well with this task, the arm finding the food does what looks like its own local exploration at various stages, crawling and feeling around. There may be a mixture of loci of control here, with central control of the arm's general location, but fine-tuning of the search by the arm itself.

The context of this task fits the account given by Dehaene and Nacchache of when conscious processing is used in humans – in novel situations where tailored and non-habitual action is needed. The experiment links Dehaene and Nacchache's suggestions about attention and conscious processing to Kathleen Gibson's proposal about the demands of extractive foraging, which often requires novel actions and problem-solving.

In some philosophical discussions, the existence of *consciousness* in an animal is taken to be the same thing as it *feeling like* something to be that animal. The word 'consciousness' is used in many different senses and there is not much point insisting that it be used one way rather than another. But I think that the question of whether an animal is conscious is different from the question of whether it feels like something to be that animal, and some important points can be obscured by pushing the two questions together.

The phenomenon that we get a handle on through the ideas about consciousness outlined above have a special connection to the integration of information. 'Primary consciousness' in this sense looks like a real thing that is worth investigating. But suppose it is suggested that if an animal does not have primary consciousness in this sense, it does not feel like anything to be that animal. That, I think, would be a mistake. Consider another human phenomenon that obviously feels like something: pain. A lot of pains, at least initially, are *intrusions* into other, more integrated, experience. Is there any reason to think that an animal without an inner workspace, without integrated primary consciousness in the

Edelman-Baars-Dehaene sense, cannot feel pain? I don't see any evidence at present for such a view (Braithwaite and Boulcott 2007). Pain is an aspect of experience that seems to require a different kind of explanation.

If this is right, then explaining the subjective side of our mental lives involves explaining at least three phenomena. One is comprised of experiences like pain which are undeniably *felt*, but seem to have no essential connection to the integration and flexibility that are the focus of workspace theories. A second phenomenon is the kind of conscious experience that involves integration and attention. The third is reflective or higher-order consciousness, where we turn our gaze on our own thoughts, a capacity that may be tied to the internalized use of language and other distinctively human capacities (Rosenthal 1997, Carruthers 2008). I have marked these out as three distinct phenomena, though they probably blend into each other in complicated ways.

I conclude with more questions than answers. To what extent has the path of cephalopod evolution given these animals psychological similarities with their distant vertebrate relatives, and to what extent has it created something truly alien? Do octopuses deal with novel tasks and situations in a way that involves something like attention and consciousness, as it does in animals like us? Or are they too different from us for these concepts to even be applicable? The features that make cephalopods so fascinating are the same features that make these questions so hard to answer.

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