Biology and Life History of Cephalopods

an interim meeting of the international cephalopod community

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Other Minds: Similarities and Differences

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I will discuss how recent work on octopus behavior bears on the question of whether, to a significant extent, animals with very different brain designs share cognitive similarities.

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for Prof. ***Peter Godfrey-Smith***
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Visual attack on the moving prey by cuttlefish

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Visual attack for prey capture in cuttlefish involves three well characterized sequential stages: attention, positioning, and seizure. This visually guided behavior requires accurate sensorimotor integration of information on the target's direction and tentacular strike control. While the behavior of cuttlefish visual attack on a stationary prey has been described qualitatively, the kinematics of visual attack on a moving target has not been analyzed quantitatively.

A servomotor system controlling the movement of a shrimp prey and a high resolution imaging system recording the behavior of the cuttlefish predator, together with the DeepLabCut, a pose estimation method based on transfer learning with deep neural networks, were used to examine the tactics used by cuttlefish during a visual attack on moving prey.

The results showed that cuttlefish visually tracked a moving prey target using mainly body movement, and that they maintained a similar speed to that of the moving prey right before making their tentacular strike. When cuttlefish shot out their tentacles for prey capture, they were able to either predict the target location based on the prey's speed and compensate for the inherent sensorimotor delay or adjust the trajectory of their tentacular strike according to the prey's direction of movement in order to account for any changes in prey position.

These observations suggest that cuttlefish use the various visual tactics available to them flexibly in order to capture moving prey, and that they are able to extract direction and speed information from moving prey in order to allow an accurate visual attack.

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Mapping and understanding the function of RNA in the Octopus brain

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Coleoid cephalopods possess the most complex nervous system among invertebrates. Recent studies have identified high levels of RNA-editing in the cephalod nervous system. Thus, there may be a link between RNA biology of the coleoid cephalopods and the cognitive success of this group. However, previous studies have focused on polyadenylated transcripts and thus the knowledge about other RNA species and their relation to the nervous system is still missing.
Here, we report the assembly of a draft transcriptome (adenylated and non-adenylated) of the *Octopus vulgaris*. To accomplish this, we have performed full-length RNA transcript sequencing ("Flam-seq", Legnini et al, Nature Methods 2019) of 18 different tissues from adult animals. In addition, we have performed small RNA sequencing of the same tissues.

Computational analyses of these data suggest that we have created a useful catalogue of RNA species in this animal. We believe that this catalogue will aid to generate insights into unique RNA-mediated mechanisms of cephalopods.

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Mapping location, projections, spatial arrangement and response properties of peripheral nociceptors

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Identifying and characterizing different neuronal cell subtypes has always been challenging in cephalopods, due to the complexity of the nervous system and lack of validated methods for identifying functional divisions within discrete brain regions. We have previously used behavioral assays, pharmacology and electrophysiology to identify nociceptive sensory afferents in peripheral ganglia and CNS in squid and octopus, but anatomical arrangement and functional properties of individually-identified cells has proven elusive.

In this project we are using calcium imaging of peripheral ganglia in semi-intact preparations of the squid, *Euprymna scolopes*, to map response properties, spatial arrangement and local circuit involvement of primary afferent nociceptors. We show that primary nociceptors and 2nd-order neurons are located in the stellate ganglion, and that there is somatotopy of sensory neurons both in the medial-lateral and rostral-dorsal planes.

Ongoing work is aimed at revealing whether somatotopy of primary afferents is preserved into higher order brain structures, and if central nociceptive circuits articulate with the higher cognitive centers of the brain.

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The evolution of intelligence in cephalopods

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Theorists working on the evolution of brains and intelligence have argued that sociality has been key to the evolution of complex cognition. However, the tests of these theories have relied on data from more social animals—primates, birds, and recently cetaceans. These theories and empirical tests predict that big brains co-evolve with long lives, long juvenile periods and complex social organization.

Coleoid cephalopods, with their short lives, little to no nurturing of young, and at most simple social organization, pose a challenge to these social brain theories. A new theory, the cultural brain hypothesis, tries to generalize theories of brain evolution and has suggested another pathway of asocial learning with different predicted brain correlates, such as a contracted juvenile period and lack of relationship with group size. Coleoid cephalopods are an ideal test of these predictions. We are beginning a research project to compile a large database of publications on Coleoid starting with brains, bodies, behavior, life history, sociality, reproductive patterns, and ecology, assisted by the existing data of Borrelli (2007). Using this dataset, we hope to learn more about the evolutionary roots of cephalopod intelligence. Such a dataset will be useful in itself, but will also show gaps in our knowledge and point out patterns in the evolution of intelligence that we might not have expected. The assistance of the community of cephalopod researchers will be most helpful in targeting areas and emphases, and identifying caveats and challenges that we may miss in this project.

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Squid camouflage to substrate

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Coleoid cephalopods are known to rapidly camouflage to its environment to protect themselves from predators. They achieve this mainly by expanding and contracting neurally controlled pigment containing cells called chromatophores in their skin. Thus far, studies concerning cephalopod substrate camouflage were covering almost exclusively benthic species such as European cuttlefish, *Sepia officinalis* species complex and pharaoh cuttlefish, *Sepia pharaonis* species complex. These cuttlefish spend much of their early life sitting on a substrate without much movement. It makes them ideal subjects for quantifiable analysis of cephalopod camouflage.
In contrast to benthic cuttlefish, oval squids of *Sepioteuthis lessoniana* species complex are considered to represent semi-pelagic animals that spend most of their time in a water column and use countershading as primarily defense mechanism.
In this study, we demonstrate that *S. lessoniana* Sp.2 (Shiro ika, white squid) from Okinawa archipelago (Japan) in laboratory settings display two different types of substrate camouflaging behavior: 1) substrate camouflage in motion (dynamic motion camouflage), and 2) situational substrate camouflage.

In the motion camouflage, chromatophores expansion follows the substrate reflectivity. In the situational camouflage, the squids deploy body pattern including three chromatic expression (uniform, mottled and disruptive), five postural (hovering, resting, curled arms, spread arms, straight arms, upward curl) and corrective formation (alone, group, touching and piling).

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Get The F(ish) Out: octopuses punch during collaborative interspecific events

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Cooperation and collaboration are ubiquitous in nature, providing immediate direct benefits and/or future indirect benefits to participating partners. Octopuses and various species of fishes are known to form multi-partner hunting groups, where the formers pursues prey within rock and coral crevices, while the latter scour the sea floor and guard the water column. Groupers use referential gestures to signal hidden prey locations to octopus partners, thus these groups increase prey opportunities for all participants. However, in heterogeneous multi-specific groups, some species may benefit more than others, which can lead to conflicts over the distributions of investment and payoffs.

Here we report a series of observations where different *Octopus cyanea* individuals engage on active displacement of partner fish during collaborative hunting. To this end, the octopus performs a swift, explosive motion with one arm directed at a specific fish partner, which we refer to as "punching" (n=8 events). From an ecological perspective, actively punching a fish partner entails a small energetic cost, but simultaneously imposes a cost on the targeted fish partner, i.e. subtraction of an immediate opportunity to catch prey, relocation to a more external or less advantageous location in the group, or even eviction. Thus, punching serves as a control mechanism, the nature of which (e.g. sanctions, aggression, punishment) is dependent on the ecological context of the interaction, and on how the benefits are yielded from inflicting costs to fish partners.

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Experiments exploring the limits of cognition and observational learning in *Octopus vulgaris* using mechatronics and video enrichment

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Experiments with *Octopus vulgaris* have shown that this species is capable of using electromechanical sensors to control electronics and robotic devices even when not motivated by food, and that *O. vulgaris* also can correctly interpret videos of crabs as showing prey, or conspecifics as rivals. Animals are able to intensely watch these videos over long periods of time from a distance while understanding (after trying unsuccessfully) that the crabs or conspecifics in the video cannot be reached because of the glass wall of the aquarium. *O. vulgaris* also has been shown to be duped by toy crabs, and experiments with mammals (up to Gorillas and Orang Utans) as well as birds (penguins and parrots) have shown that even these highly intelligent animals are duped and/or intrigued by clearly artificial robotic lookalikes of conspecifics.
The combination of these observations allows to conduct repeatable, scientifically rigorous experiments that unambiguously prove the existence of social observational learning of *O. vulgaris*, opening up an efficient way to explore the upper limits of cognitive and learning abilities of the species by using training videos that are animations of life-like but artificial “teacher” octopuses, thereby allowing to teach real octopuses advanced cognitive skills that no real octopus has ever learned by other means before, because a real “teacher” octopus that learned these skill the slow, natural way, is not needed anymore.
It also allows to experiment with simplified animations of “teacher” octopuses that are less real life-like and more cartoonish.

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Cephalopod Cognitive Evolution

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Large-brained vertebrates (e.g. apes, cetaceans, corvids) share slow life histories and challenging social environments, suggesting that these two factors play a key role in the evolution of intelligence. However, coleoid cephalopods (octopus, cuttlefish and squid) question this view. These shell-less molluscs evolved large brains supporting strikingly rich behavioural repertoires (e.g. tool use, complex anti-predatory strategies and mating tactics) although they do not engage in complex social bonds and have fast life histories (e.g. lifespan < 2 years, terminal reproduction). It has been proposed that cephalopod cognitive evolution may have been shaped primarily by predatory and foraging pressures, but a challenging mating context may also have played a role. The disappearance of the shell in coleoids may have resulted in higher rate of unavoidable mortality (due to stronger predation), thereby preventing the evolution of slow life histories. However, future research will be essential to test the influence of life history and of different selective pressures in cephalopod cognitive evolution. In parallel, a systematic investigation of cephalopod cognition is also needed to quantify the cognitive complexity in these molluscs.
Ultimately, these lines of research have the potential to shed light on alternative routes for the emergence of cognitive sophistication in non-human animals.

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Embodied organization of motor control in a soft-bodied animal – *Octopus vulgaris*

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Octopuses provide an outstanding example of successful motor behaviors expressed in a flexible body. In skeletal animals, the interfacing of sensory and motor information for motor planning is based on representation in body-part coordinates. In contrast, in hyper-redundant soft-bodied animals like the octopus, this control approach is impractical as it would require infinitely large number of variables (DOFs) to represent the soft body. Octopuses overcame this difficulty through the coevolution of unique features at all levels of body and brain; from the neuromuscular system of the arms up to the organization of the central brain's higher motor centers. The overall embodiment of all these unique properties helps explain how the "alien"-looking body of the octopus simplifies locomotion control and how the special distribution of the central and peripheral nervous system simplifies control of goal-directed arm movements. It also helps explain why higher control centers in the brain are not organized somatotopically as in vertebrates and why arm coordination in locomotion involves probabilistic control rather than a deterministic CPG. Finally, the overall embodiment can explain why motor learning employs 'strategy-learning' rather than 'skill-learning'.
The octopus demonstrates that embodied organization, a concept developed in robotics, is an important evolutionary principle showing how adaptation of the body to the task helps simplify its control.

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A journey around Cephalopod Research and possible future avenues

Graziano Fiorito
talk delivered on behalf of coworkers

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Cuttlefish, squid and octopus provided fascinating cases for studying biological, neural and behavioral plasticity.
I will surf around some of the most recent interesting findings including: genomes (namely: *Octopus bimaculoides*, *Callistoctopus minor*, *Octopus vulgaris*, *Euprymna scolopes*, *Octopus sinensis*, *Architeuthis dux*)[1], an huge effort about five years; the role of extraocular photoreceptors in light-activated chromatophore expansion; RNA-editing capabilities; *Dosidicus gigas* use of bioluminescence to illuminate "semantically complex" communication patterns and in foraging. Cephalopod genomes are also mentioned taking into account on-going research around orphan and cephalopod specific genes. Further examples are provided based on: ***i.*** the exploration of the organization of 'brains' in cephalopods and their complexity; ***ii.*** neural cell numbers and their variations among individuals; ***iii.*** the neural plasticity and underlying molecular fingerprint; ***iv.*** marked inter-individual variability in behavioral performances arising through the reciprocal influence of environmental and behavioural factors.
Following J.Z. Young (1985), exploration of the properties of aggregates of neurons should be explored, with octopus' "various neuropils" providing "the material ... needed, just as the giant fibers of the squid ...testing of new methods for the study of membranes". Exploring the biological plasticity in cephalopods may help to study modular organization of the brain and its evolution, orchestration of neuromodulators (single cells sequencing recent approaches may be one example), cross-modality, and central vs periphery (what this 'means' for cephalopod/mollusc nervous systems).
It is suggested to act as an interdisciplinary forum for scientific interaction that would further our knowledge and understanding by facilitating cross-talk and collaboration among groups of scientists from very different fields who otherwise might not have opportunities for exchanging ideas so directly. My ultimate goal is to stimulate discussion around future efforts and possibly facilitating further some unexplored research avenues.

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1 listed in order of year of publication