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Current Opinion in Neurobiology

Learning and memory in *Octopus vulgaris*: a case of biological plasticity

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Here we concisely summarize major aspects of the learning capabilities of the cephalopod mollusc *Octopus vulgaris*, a solitary living marine invertebrate. We aim to provide a backdrop against which neurobiology of these animals can be further interpreted and thus soliciting further interest for one of the most advanced members of invertebrate animals.

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Current Opinion in Neurobiology 2015, **35**:74–79

This review comes from a themed issue on **Circuit plasticity and memory**

Edited by **Thomas Mrsic-Flogel** and **Alessandro Treves**

For a complete overview see the Issue and the Editorial

Available online 14th July 2015

http://dx.doi.org/10.1016/j.conb.2015.06.012

The octopus: a 'model' of the brain

About fifty years ago an English zoologist and neuroanatomist, John Zachary Young, published 'A model of the brain' [1]. The book is an account of decades of studies on predatory responses and learning abilities of several species of cephalopods, mainly the common octopus, *Octopus vulgaris*. In its aim, J.Z. Young tried to answer to the question 'how do brains work'. He adopted the approach utilized by 'communication engineers' and cybernetics: the 'brain' is acting as the computer of a homeostat [1].

In the model, a mnemon (i.e. a visual/tactile feature with associated memory value resulting from experience; [2,3••]) is activated by a given input (visual and/or chemo-tactile) to a specific set of classifying cells and switched on/off on the basis of other inputs that depend on the taste-pain circuits. The output of these units is summed up to produce an overall attack strength (i.e. predatory response), in contrast to the opposite inputs that build a retreat. These 'strengths' are combined to determine the final attack/retreat responses.

The 'model' is the result of hundreds of experiments where the predatory response of *O. vulgaris* has been dissected to deciphering its neural control ([4]; for review see also: [5,6••,7,8,9,10•,11,12,13]). It is noteworthy to mention that in several occasions the 'model' found its cybernetic application [14–16]. The mnemon model developed by Clymer [14] is based on a visual feature with associated memory value resulting from experience that is activated by a given visual input to a specific set of classifying cells and switched on/off on the basis of other inputs that depend on the taste-pain circuits. The output of these units, corresponding to the attack command, is further summed-up to produce an overall attack strength, in contrast to the opposite units (retreat command) that in a similar way build an overall retreat strength. These values, or strengths, are then combined and determine the final attack/retreat response [14]. Interestingly, the results produced by Clymer's model are comparable to those obtained from proper experiments with live animals, including the responses resulting from short- and long-term changes in behavior and interference on learning performance when spacing between trials is reduced in time [14]. In a similar way, Myers developed a modified 'cybernetic circuit' based on octopus' mnemon taking into account findings on neural networks and learning in simulated environments [15].

The octopus: a cephalopod

The common octopus is one of the most famous representatives of the class Cephalopoda (i.e. nautilus, cuttlefish, squid and octopus), a numerically small but ecologically and scientifically significant taxon of invertebrates belonging to the phylum Mollusca. The richness of behavioral capabilities of these animals fascinates human beings since the antiquity [6••,17]. Together with other cephalopod species, octopuses also represent a very important resource for human consumption [18].

The class Cephalopoda includes about 700 exclusively marine-living species considered to have rivaled fishes during evolution [19••,20•]. Cephalopods demonstrate a refined and extraordinary ability to adapt their morphology and behavioral repertoire to their living environment [6••,20,21]. Examples among many are: (i) special locomotion including fast jet propulsion, bipedal and tiptoeing [22–24]; (ii) active changes of body patterning achieving crypsis, polyphenism, mimicry and communication including hidden channels [5,25–27]; (iii) special