

# Octopus nervous system

Binyamin Hochner

## 1. Introduction

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The octopus together with its relatives the cuttlefish and squids form the class of modern cephalopods (coleoids). These are molluscan invertebrates that separated from their ancient ancestors, the old cephalopods, probably about 200 million years ago. The old cephalopods are virtually extinct—their last and only living representative is the shell-bearing *Nautilus*.

Comparing the body structure and way of life of the modern cephalopods with those of the nautilus and other molluscs reveals how dramatically these animals have changed over the course of evolution. From shell-protected, slowly moving scavengers they have evolved into agile, mobile predators that share the same environments and way of life with fish and successfully compete with them. Indeed, [Andrew Packard \(1972\)](#) has suggested that these evolutionary changes were driven by the selection forces imposed by bony fish (teleosts) and reptiles that invaded the sea just when modern cephalopods began to develop.

This dramatic change in behavior became possible following the development of sophisticated motor, sensory, and cognitive capabilities, such as excellent vision, highly efficient flexible arms, and the ability to learn rapidly. To gain these capabilities, both the peripheral and central nervous systems of the modern cephalopods acquired new features. The evolutionary process leading to the selection of these features involved, first, the emergence of unique systems that exist only in the modern cephalopods and, second, the selection of systems analogous in structure and function to those of vertebrates. The latter process is defined as a convergent evolutionary process ([Packard, 1972](#)). Here we use these two categories—unique systems and convergent evolution—to review the peripheral and central nervous systems of cephalopods.

## 2. Unique neuromuscular systems

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### 2.1. Chromatophore system

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Modern cephalopods are the only group of animals possessing an active "image generating neuromuscular system" ([Packard, 1972](#)). This system is composed of a large number of chromatophores distributed over the entire skin of the body. There are five types of chromatophores, each containing one of five possible pigments (black, brown, orange, red, or yellow) within a membranous sac. This pigment sac is surrounded by 15 to 25 radial muscle cells that are controlled by nerve fibers projecting directly from specific areas in the central brain (the chromatophore lobes).

When the muscles contract, the sac expands and the color becomes visible. The muscle fibers are innervated by glutamatergic motor neurons, and this synaptic connection was the first where neuromodulator action (acetylcholine and serotonin) was demonstrated ([Messenger, 2001](#)). This unique neuronally controlled image generation system allows for an unprecedented fast and localized change in body colors and thus equips the animal with a system for rapid camouflage, confusing predators, signaling, and communication. Surprisingly cephalopods themselves are probably color blind ([Hanlon and Messenger, 1996](#)). Due to mechanisms as yet not well understood, aged or denervated cephalopod skin manifests colorful "wandering clouds" that are generated by propagating waves of chromatophore muscle contraction ([Figure 1](#), video clip).

### 2.2. Flexible appendages

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The eight arms of the octopus, evolved from the molluscan foot, are a most impressive example of motion generation and control in a structure with no external or internal skeleton. (Cuttlefish and the squid have two additional rapid-extension tentacles specialized for capturing prey.) The cephalopod arm, like the vertebrate tongue and the elephant trunk, is composed mainly of incompressible muscle cells and therefore the volume of the arm remains constant. Because the muscles are organized in groups with different orientations—transverse, longitudinal, and oblique—they function as an antagonistic muscle system in which active shortening of one group causes elongation of the other. This type of functioning, in which the constant volume constraint causes the muscles to act against each other, defines these structures as muscular hydrostats ([Kier and Smith, 1985](#)).

A recent physiological characterization of the muscle cells and their mode of innervation suggests that special neuromuscular mechanisms have evolved in the octopus arm. Each small muscle cell (~0.01 x 1 mm) is innervated by three types of excitatory cholinergic motor neurons. The cells are electrically compact and thus there is no need for multiterminal innervation as is common in other invertebrates. Instead, single synaptic junctions control the membrane potential of the entire muscle fiber. Fast Ca<sup>++</sup> action potentials and oscillations

control the activation of the contractile mechanisms ([Matzner et al., 2000](#)).

Understanding the motor control of movement in these flexible arms is a challenge not only for biology, but also for engineering and robotics because these structures can move in any direction with practically infinite number of degrees of freedom. Comprehensive studies of the octopus arm have attempted to resolve how nature solved this problem. Insights have been gained by studying a particular movement—the arm extension. This movement is performed in a very stereotypical way, and a similar movement is employed in many behaviors that move the arm from one location to the other. The extension is initiated by creating a bend in the arm, which then propagates forward along the arm toward the tip ([Figure 2](#), video clip).

The arm extension movement was kinematically analyzed (position and velocity) in behavioral studies. The location of the bend in time and space was reconstructed from two video images taken at different angles. What emerges is that both the path and the velocity profiles of bend propagation (normalized for speed and time) have invariant features in all the movements. It thus appears that great simplification in motor control has been achieved by utilizing the same motor program for all arm extensions. This control mechanism reduces the immense number of degrees of freedom into only three; two for the direction and one that dictates the extension velocity.

Recordings of muscle activity (EMG) during reaching movements show that the neural command for the extension has a strong feed-forward component, as the initial level of muscle activation governs the peak velocity attained later in the movement. It was then found that the extension movements can be evoked in arms whose connection with the brain has been severed ([Sumbre et al., 2001](#)). These extensions, which have identical kinematic features to those of behaving animals, could be evoked either by tactile stimulation to the skin of the arm or by a short train of electrical stimuli to the axonal tract of the arm nerve cord. These results suggest a novel mechanism for the control of voluntary arm movements whereby higher motor centers in the brain send only global commands to the peripheral neural networks in the arm. These then produce the neural activation pattern prescribing the entire spatiotemporal details of the movement.

This finding is consistent with the fact that (a) the nervous system of the arms contains two thirds of the octopus's nerve cells, (b) these are connected to the brain via a relatively small number of axons ([Young, 1971](#)), and (c) the extensive and autonomous functions of the arm nervous system.

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## 2.3. The giant axon system

Giant nerve fibers are a unique solution evolved mainly in invertebrates for achieving extremely fast conductance of action potentials. The giant axons of cephalopods are important for the rapid activation of the mantle muscles during jet-propelled escape (see entry [Giant nerve fibers](#)). Their large size has permitted breakthrough experiments in elucidating the biophysical bases of action potential generation (see entries [Hodgkin-Huxley analysis](#), [Squid axon](#)) and the mechanisms of chemical synaptic transmission (see entry [Chemical transmission, the squid giant synapse](#)). (Note that the octopus is exceptional among the modern cephalopods in not having giant axons.)

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## 3. Systems that evolved convergently with vertebrates

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### 3.1. Eyes

As their predatory way of life indicates, cephalopods rely extensively on visual information ([Wells, 1978](#); [Hanlon and Messenger, 1996](#)). The structural similarity between octopus and vertebrate eyes is the most frequently cited example of convergent evolution ([Packard, 1972](#)). The octopus eye has a single large circular lens controlled by ciliary muscles; iris and eyelids control the intensity of the incoming light; and extrinsic muscles control the direction of the eye chamber. The major structural difference is that in the octopus the photo-transducing outer segments of the receptors face toward the incoming light, whereas in vertebrates the arrangement is inverted. In addition, the octopus retina contains mainly sensory cells; the neurons equivalent to those comprising the inner layers of the vertebrate retina are located in the outer cortex of the optic lobe.

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### 3.2. Statocyst

Cephalopod statocysts and the vertebrate vestibular system are another example of convergent evolution. The pair of octopus statocysts, which are embedded inside the cartilage at the lower part of the brain capsule, supply neural information required for balance and orientation ([Young, 1971](#); [Hanlon and Messenger, 1996](#)). As in vertebrates, the cephalopod statocyst comprises two systems, one for sensing gravity (macula/statolith) and the other for detection of angular acceleration (crista/cupula). The mechanisms that have evolved for these two functions are amazingly similar to those of vertebrates and are based on detection of mass movement by mechanoreceptor cells (hair cells). ([See Williamson, 1995.](#))

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### 3.3. Centralized brain

The size of the modern cephalopod nervous system (normalized to body weight) lies within the same range as vertebrate nervous systems—smaller than birds and mammals but larger than fish and reptiles ([Packard, 1972](#)). In comparison with lower molluscs, the cephalopods show an extreme change in the number and organization of nerve cells and the cephalopod brain is as complex as those of lower vertebrates. For example, the *Aplysia* nervous system contains 20,000 neurons (see entries by [Kupfermann](#) and [Byrne](#)), whereas the nervous system of the octopus comprises 500 million cells. These developments in the nervous system most likely form the basis for the dramatic change in behavior—from a more stereotyped form in *Aplysia* to the octopus's highly adaptive fishlike behavior as an active hunter.

The octopus's nervous system is organized as a hierarchy of functional levels (see classic entry by JZ [Young](#)); morphologically, it is divided into three parts. The central brain (40 to 45 million cells) surrounds the esophagus and is situated inside a cartilaginous capsule. It is composed of 64 lobes that maintain a basically invertebrates' organization with outer cell body layers and inner neuropil. Stimulation and lesion experiments have helped to assign possible functions to several of these lobes ([Wells, 1978](#)).

The other two parts of the nervous system, the optic lobe and the nervous system of the arms, are situated outside the brain capsule and may be defined as dedicated systems or autonomous systems. (In addition, there are several peripheral ganglia, e.g. the stellate ganglion where the giant axon synapse lies.) Each of these systems contains more nerve cells than the central brain; the two optic lobes contain 120 to 180 million cells and the peripheral nervous system of the arms roughly 350 million cells. These two large systems are connected by a relatively small number of fibers to the brain, suggesting that they send highly processed information to the brain and that the arms at least receive high order motor commands from it.

The input from the retina to the optic lobes consists of about 1000 decussating optic nerve fibers (chiasm), which rectify the visual image entering the optic lobe. It is believed that much of the analysis of visual signals, feature detection and also visual memory are performed in the optic lobe. Little is known about the physiological properties of the visual system.

The peripheral nervous system of the arm is distributed along the arms in a chain of approximately 300 ganglia that constitute the arm nerve cord. The nervous system of the arm also processes the immense quantity of sensory information gathered by several million tactile and chemical sensory cells in the skin and suckers of each arm. It has now been shown experimentally that the distributed nervous system of the arms controls not only local reflexes, but also entire movements (see 2.2, [Sumbre et al., 2001](#)).

Particular areas of the brain are especially interesting because they show a morphological organization strikingly similar to areas of the vertebrate brain that mediate similar functions ([Packard, 1972](#)). For example, the deeper layers in the vertebrate retina are similarly organized to the three cortical layers of the cephalopod optic lobe. The structure of the peduncle lobe, in which small granular-like cells give rise to arrays of parallel fibers, resembles the arrangement in the folia of the vertebrate cerebellum. The peduncle receives inputs from both the visual system and the statocyst and has cerebellar-type effects on motor function. The vertical lobe (VL), the highest in the central brain hierarchy, resembles the vertebrate hippocampus, both in its involvement in learning and memory and in its morphological organization (see below). If these similarities are seen as the outcome of convergent evolutionary processes, they may highlight the importance of connectivity in brain function rather than cell structure and/or cellular and/or biophysical properties.

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### 3.4. Learning and memory

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#### 3.4.1. Behavior

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The outstanding behavioral capabilities of the octopus were already known to the ancients thousands of years ago. Modern researchers have been attracted by the behavior of this fascinating animal since the beginning of the 20th century. Since then the behavior of the octopus (mainly *Octopus vulgaris*) has been extensively studied, and its learning abilities have been characterized.

As solitary hunters, octopuses are exploratory, attending to any novel object in their visual field. They show sensitization, habituation, conditioning, associative learning, visual and tactile discrimination learning, as well as the ability to learn about and solve detour problems, mazes, and problem boxes (see Wells, 1978; Hanlon and Messenger, 1996). The octopus also uniquely demonstrates observational learning, in which a naive octopus observes a trained octopus attacking a previously positively rewarded target only four times before the observer itself prefers attacking the same target. The observer learns much faster than the demonstrator octopus (Fiorito and Scotto, 1992). This "observational" memory remains stable for at least 5 days after the observational phase. All these findings reflect the outstanding behavioral adaptations that evolved in the octopus and other modern cephalopods.

### 3.4.2. Neurobiology of learning and memory

Possibly exceeding the level of functional specificity of the vertebrate brain, specific areas in the octopus brain are dedicated to learning and memory. As mentioned above, the VL, for example, appears exclusively involved in learning and memory (Young, 1971; Wells, 1978; see Young's classic entry). Removal of the VL does not affect the overt behavior of the animal but impairs long-term memory for new tasks.

Drawing on extensive behavioral investigations, morphological data and lesion studies, Boycott, Young, and Wells and colleagues hypothesized organizational schemes for the visual and tactile learning and memory systems in the octopus brain (see Figure 3,4 in Young's classic entry). It was suggested that these systems consist of multiple matrices of intersecting axons, whose synapses (if equipped with the right plasticity) form associations between conjunctions of sensory signals (visual or tactile) and their outcomes.

The MSF and the VL together form the main visual learning system (see Figure 4 in Young's classic entry). The VL is composed of only two types of morphologically typical invertebrate monopolar neurons (Figure 3): 25 million small amacrine cells (the smallest in the octopus brain, 6 to 10  $\mu\text{m}$  dia) that converge onto only 65,000 large neurons ( $\sim 17 \mu\text{m}$  dia). The axons of the large cells form the only output of the VL; the neurites of the amacrine interneurons are confined within the lobe. The lobe receives only two inputs, of which numerically the largest is the 1.8 million axons from the MSF lobe (Figure 3, Young, 1971).

The MSF lobe contains only one type of neuron, which is thought to integrate visual and taste information. The MSF neurons convey this integrated signal to the VL via a distinct tract running between the VL neuropil and its outer cell body layer (Figure 3). The parallel organization of the VL allows each MSF axon to make *en passant* synapses with many amacrine neurons along the VL (Figure 3, see Young's classic entry and Young, 1971). Furthermore, the afferent bundles from the MSF lobe interweave elaborately in the VL and exchange fibers so that every part of the VL can receive fibers from all parts of the MSF lobe (Young, 1971). The wide distribution and redundant nature of the synaptic connections may increase the capacity for multiple associations.

Obviously physiological characterization of these brain circuits and their plastic properties is required to test hypotheses on their function. Such experiments have only recently become possible following the development of an *in vitro* slice preparation of the VL-MSF system, which allows intracellular recording from the small cells in the VL (Hochner et al 2003.)

As in vertebrate hippocampus preparations, the large number of cells in the VL and their laminar organization permit extracellular recording and stimulation, enabling analysis of field potentials evoked by stimulating the tract from the MSF lobe. Such stimulation evokes a large graded positive-negative biphasic potential shortly after the stimulus artifact (Figure 4). This field potential is composed of activity in the axonal tract. It is followed by a second, smaller, mainly negatively going wave, which is a synaptic field potential. As in vertebrates, this synaptic potential is glutamatergic because it is blocked by CNQX and kynurenate. Intracellular recordings also reveal synaptic inputs evoked by MSF tract stimulation. This preliminary physiological interpretation is consistent with the anatomical studies and reveals many similarities to the physiological properties of the vertebrate hippocampus.

Tetanic stimulation of the MSF tract mostly leads to a large and enduring increase in the synaptic field potential (Figure 4), suggesting an activity-dependent long-term enhancement of the synaptic connections. These results indicate the existence of robust plastic properties at the main synaptic input to the vertical lobe, which are similar to long-term potentiation (LTP) in the vertebrate brain. Current experiments suggest that this LTP has several Hebbian characteristics and at least some connections show LTP, which depends on the postsynaptic response.

These results suggest that a convergent evolutionary process has led to the selection of similar networks and synaptic plasticity in evolutionarily very remote species (but with similar behaviors and modes of life). These evolutionary considerations substantiate the importance of these cellular and morphological properties for neural systems mediating complex forms of learning and memory.

## 4. See also

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[Octopus brain \[Classic paper\]](#)

[Motor control, invertebrate](#)

[Multisensory convergence and integration](#)

[Visual system development, invertebrates](#)

[Evolution of vertebrate brains](#)

[Learning and memory](#)

## 5. References

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Fiorito G, Scotto P (1992): Observational learning in *Octopus vulgaris*. *Science* 256:545-547 [[MEDLINE](#)]

Hanlon RT, Messenger JB (1996): *Cephalopod Behaviour*, Cambridge: Cambridge University Press

Hochner B, Brown ER, Langella M, Shomrat T, Fiorito G (2003): A learning and memory area in the octopus brain manifests a vertebrate-like long-term potentiation. *J. Neurophysiol.* 90:3547-3554

Kier WM, Smith KK (1985): Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zoological J Linnean Soc* 83:307-324

Matzner H, Gutfreund Y, Hochner B (2000): Neuromuscular system of the flexible arm of the octopus: physiological characterization. *J Neurophysiol* 83:1315-1328 [[MEDLINE](#)]

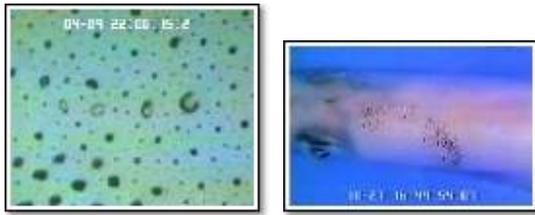
Messenger JB (2001): Cephalopod chromatophores: neurobiology and natural history. *Biol Rev* 76:473-528 [[MEDLINE](#)]

Packard A (1972): Cephalopods and fish: the limits of convergence. *Biol Rev* 47:241-307

Sumbre G, Gutfreund Y, Fiorito G, Flash T, Hochner B (2001): Control of octopus arm extension by a peripheral motor program. *Science* 293:1845-1848 [[MEDLINE](#)]

Wells MJ (1978): *Octopus*. London: Chapman and Hall [[MEDLINE](#)]

Williamson R (1995): The statocysts of cephalopods. In: *Cephalopod Neurobiology*, Abbott NJ, Williamson R, Maddock L, eds. Oxford: Oxford University Press, pp. 503-520 [[MEDLINE](#)]



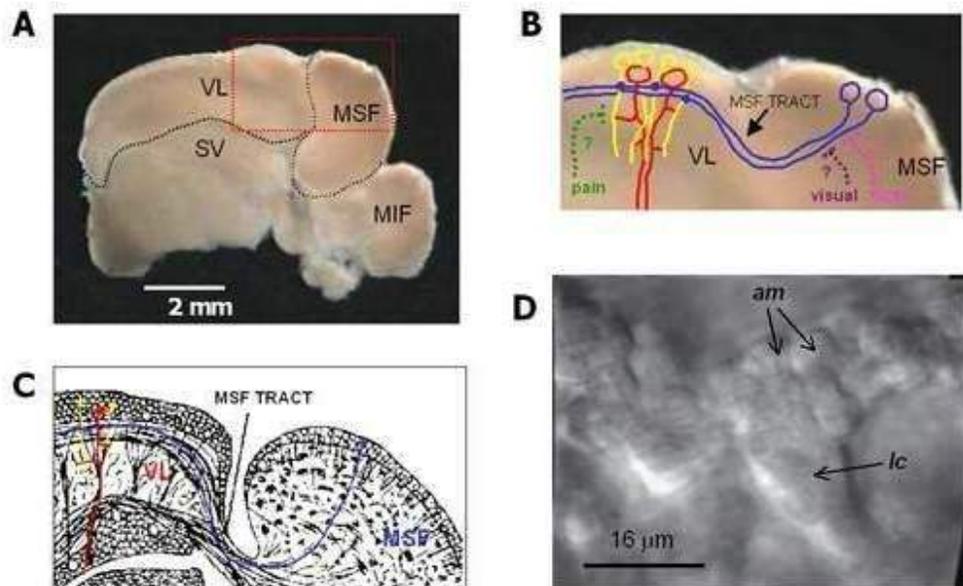
Squid chromatophores 'Wandering clouds' in denervated squid skin in action

**Figure 1.** Video clips showing coordinated activity of the chromatophores. (Kindly contributed by Prof. A. Packard, the Zoological Station, Naples, Italy.) (See more examples at [www.gfai.de/www\\_open/perspg/g\\_heinz/biomodel/squids/squids.htm](http://www.gfai.de/www_open/perspg/g_heinz/biomodel/squids/squids.htm).)



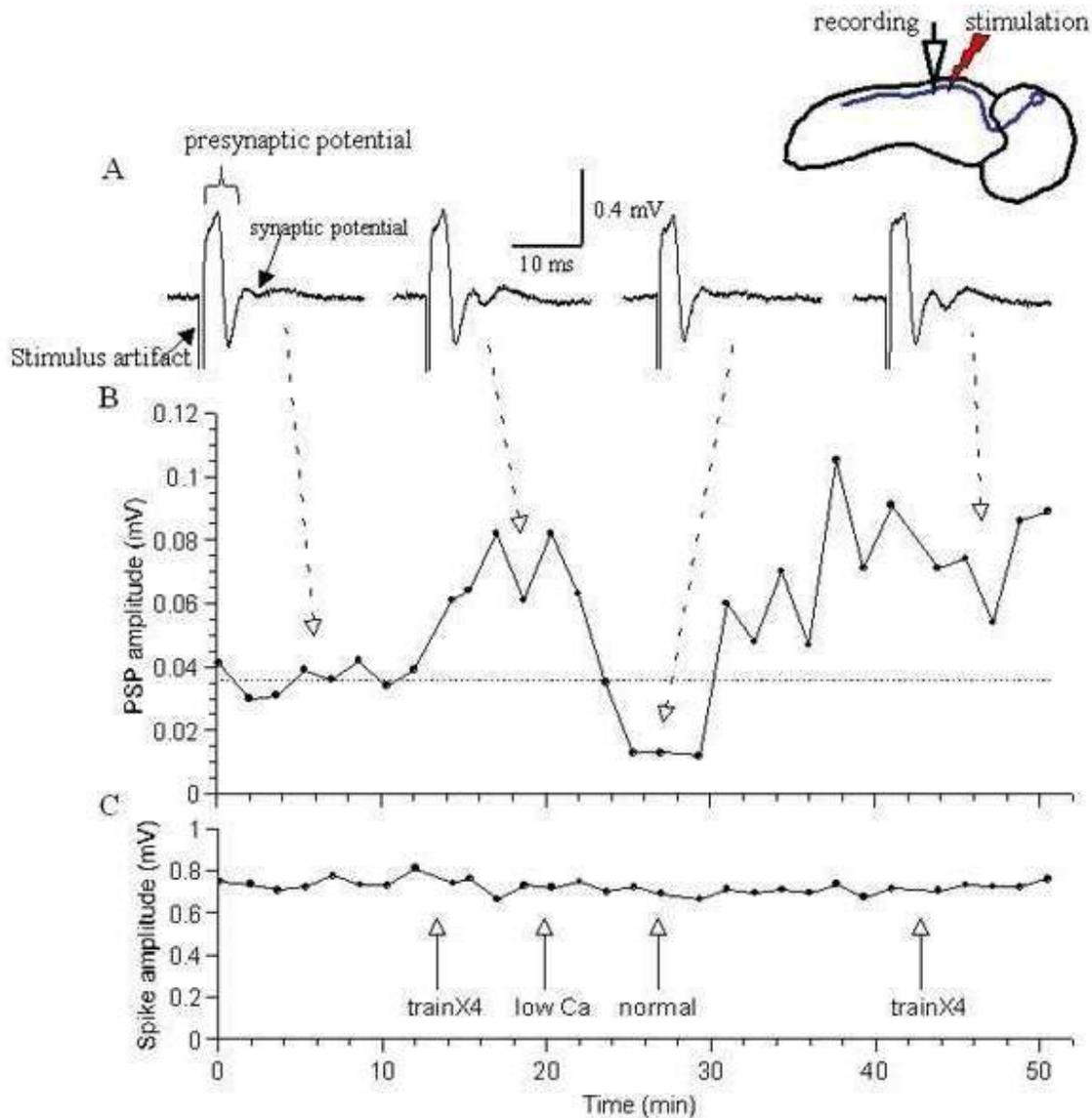
Slow motion Actual speed

**Figure 2.** Video clips showing a trained octopus reaching toward a target. For more information and examples see <http://lobster.ls.huji.ac.il/~tamnun/>



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**Figure 3.** Basic morphology of the slice preparation of the octopus vertical lobe (VL)- medial superior frontal lobe (MSF) system. **A**, A sagittal slice from the medial part of the supraesophageal brain mass showing the VL and MSF located dorsally to the medial inferior frontal (MIF) and subvertical (SV) lobes. **B**, Enlargement of the area within the red rectangle in A with a superimposed schema showing the MSF neurons (blue) innervating the amacrine cells (yellow) in the VL via the MSF tract. These then synapse onto the large efferent cells (red). Possible taste, visual, and pain inputs are also marked (the schema is based on [Figure 2 in Young's classic entry](#) and [Young, 1971](#)). **C**, As in B, the neurons and tract are superimposed on a scheme of the corresponding area in the octopus brain (based on [Figure 2 of Young's classic entry](#)). **D**, High magnification image of an in vitro slice taken with infrared differential interface contrast (DIC) optics showing the amacrine (*am*) and the large efferent cells (*lc*).



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**Figure 4.** Long-term potentiation (LTP)-like phenomena in the vertical lobe slice preparation. Extracellular recording and stimulation as depicted in the inset. **A**, Averages of 10 responses taken during time segments shown by the broken arrows. The *stimulus artifact*, *presynaptic potential* activity of the axonal tract, and the extracellular *synaptic field potential* are indicated in the left record. **B**, The PSP amplitude, measured as the amplitude of the negative synaptic wave from averages as in A. **C**, The peak-to-peak amplitude of the presynaptic potential. The experimental time scheme is shown in C. The response was tested every 10 seconds. Following ~13.5 minutes of control, 4 short tetani were delivered (20 pulses, 50 Hz, 10s intertetanic interval). Following the increase in PSP amplitude, Ca<sup>++</sup> concentration was lowered (1 mM) and the PSP almost disappeared. Perfusion of normal artificial seawater restored the PSP to the potentated level. Additional tetanization (at ~43 min) did not lead to a further significant change in PSP amplitude. No consistent changes in the presynaptic spike were detected during the entire experiment (C).