**Cephalopod chromatophores: neurobiology and natural history.**

**Abstract**

The chromatophores of cephalopods differ fundamentally from those of other animals: they are neuromuscular organs rather than cells and are not controlled hormonally. They constitute a unique motor system that operates upon the environment without applying any force to it.

* Each chromatophore organ comprises an elastic sacculus containing pigment, to which is attached a set of obliquely striated radial muscles, each with its nerves and glia. When excited the muscles contract, expanding the chromatophore; when they relax, energy stored in the elastic sacculus retracts it.
* The physiology and pharmacology of the chromatophore nerves and muscles of loliginid squids are discussed in detail.
* Attention is drawn to the multiple innervation of dorsal mantle chromatophores, of crucial importance in pattern generation.
* The size and density of the chromatophores varies according to habit and lifestyle.
* Differently coloured chromatophores are distributed precisely with respect to each other, and to reflecting structures beneath them.
* Some of the rules for establishing this exact arrangement have been elucidated by ontogenetic studies.
* The chromatophores are not innervated uniformly: specific nerve fibres innervate groups of chromatophores within the fixed, morphological array, producing 'physiological units' expressed as visible 'chromatomotor fields'.
* The chromatophores are controlled by a set of lobes in the brain organized hierarchically. At the highest level, the optic lobes, acting largely on visual information, select specific motor programmes (i.e. body patterns); at the lowest level, motoneurons in the chromatophore lobes execute the programmes, their activity or inactivity producing the patterning seen in the skin.
* In Octopus vulgaris there are over half a million neurons in the chromatophore lobes, and receptors for all the classical neurotransmitters are present, different transmitters being used to activate (or inhibit) the different colour classes of chromatophore motoneurons.
* A detailed understanding of the way in which the brain controls body patterning still eludes us: the entire system apparently operates without feedback, visual or proprioceptive.
* The gross appearance of a cephalopod is termed its body pattern. This comprises a number of components, made up of several units, which in turn contains many elements: the chromatophores themselves and also reflecting cells and skin muscles.
* Neural control of the chromatophores enables a cephalopod to change its appearance almost instantaneously, a key feature in some escape behaviours and during agonistic signalling. Equally important, it also enables them to generate the discrete patterns so essential for camouflage or for signalling.
* The primary function of the chromatophores is camouflage. They are used to match the brightness of the background and to produce components that help the animal achieve general resemblance to the substrate or break up the body's outline.
* Because the chromatophores are neurally controlled an individual can, at any moment, select and exhibit one particular body pattern out of many. Such rapid neural polymorphism ('polyphenism') may hinder search-image formation by predators. Another function of the chromatophores is communication. Intraspecific signalling is well documented in several inshore species, and interspecific signalling, using ancient, highly conserved patterns, is also widespread. Neurally controlled chromatophores lend themselves supremely well to communication, allowing rapid, finely graded and bilateral signalling.

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