



#### Review

# The neural basis of visual processing and behavior in cephalopods

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#### SUMMARY.

Colecid cephalopeds (octopuses, squids and cuttlefishes) are the only branch of the animal kingdom outside of vertebrates to have evolved both a large brain and camera-type eyes. They are highly dependent on vision, with the majority of their brain devoted to visual processing. Their excellent vision supports a range of advanced visually guided behaviors, from navigation and prey capture, to the ability to camouflage based on their surroundings. However, their brain organization is radically different from that of vertebrates, as well as other invertebrates, providing a unique opportunity to explore how a novel neural architecture for vision is organized and functions. Relatively few studies have examined the cephaloped visual system using current neuroscience approaches, to the extent that there has not even been a measurement of single-cell receptive fields in their central visual system. Therefore, there remains a tremendous amount that is unknown about the neural basis of vision in these extraordinary animals. Here, we review the existing knowledge of the organization and function of the cephaloped visual system to provide a framework for examining the neural circuits and computational mechanisms mediating their remarkable visual capabilities.

#### Introduction.

Cephalopods, particularly octopuses, squids, and cuttlefishes, present a fascinating opportunity for investigating the neural basis of vision. In some ways, their visual system is similar to ours'. Despite being part of a branch of the animal kingdom related most closely to slugs and snalls, cephalopods have evolved a large brain comparable in size to that of some vertebrates'. Evolution also paired this large brain with a pair of camera-type eyes that are remarkably similar to ours, with a pupil and lens that projects a high-resolution image onto a retina densely packed with photoreceptors'.

However, many aspects of the cephalopod visual system are profoundly different from those of other animals. The only neurons in the retina are photoreceptors, which transmit signals directly to the brain via the optic nerves, and surprisingly, the brain itself sends a large number of projections back to the photoreceptors. in the eye". The cephalopod brain bears no direct resemblance to the vertebrate brain, consisting of a series of fused ganglia". and it is dominated by vision, as the optic lobes occupy roughly two-thirds of the central brain. The exterior layers of the optic lobe have a striking morphological similarity to the retina of vertebrates, but are located within the brain rather than within the eye. Behaviorally, cephalopods share many advanced visual capabilities with vertebrates, such as the ability to use vision to navigate, detect prey, and learn to recognize objects. But they also possess unique capabilities that are beyond those of vertebrates. including the ability to sense aspects of light that are outside our perception, and the ability to rapidly change their skin patterning to camouflage instantly to their surroundings.

For a visual neuroscientist, there is tremendous appeal in the prospect of studying a powerful visual system that is radically unlike any other, and yet relatively unexplored at the neural level. Decades of research have revealed some basic aspects of the cephalopod visual system, including its basic anatomy and the behaviors it drives. Nevertheless, there remains a tremendous amount that is unknown about how this independently evolved visual system actually functions at the neural level, making this a competting open field for study. Did the cephalopod brain converge on similar visual computations to other species? Or did cephalopods evolve completely different, and perhaps unexpected, solutions to analyzing visual scenes with neural circuitry?

Here we review what is known about the neural basis of cephalopod vision, including both classic work and recent studies that have begun applying modern techniques to investigate its organization and function. We focus on three main aspects of vision — visual behaviors, neural circuit organization, and neural function. We also highlight promising areas of study that we hope will accelerate research on cephalopod vision in the future.

Throughout this review, we focus on the coleoid cephalopods (octopuses, squids, and outtlefishes), which all have camera-like syes and elaborated visual systems that mediate complex visual behaviors. However, even within the coleoids, there is a large diversity of body plans, lifestyles, and ecological niches, with a corresponding diversity of visual system organization and function. Hence, it is an oversimplification to describe 'the' cephalopod visual system, particularly since many studies of cephalopod vision have focused on a limited handful of model species. Nonetheless, our goal here is to present a high-level synthesis, drawing on findings from different species and delineating both general principles and specific results.



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