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Cephalopod neurobiology: an introduction for biologists working in other model systems

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Abstract This paper concisely summarizes major aspects of cephalopod biology, behavior, and ecology providing a backdrop against which neurobiology of these animals can be interpreted. Reproduction, camouflage, motor control, memory, learning, and behavioral ecology are introduced, and thorough literature reviews of these subjects are cited for further reading. The aim of this paper is to provide a general introduction to cephalopods for use by workers currently focused on other model systems.

Keywords Behavior · Ecology · Reproduction · Motor control · Invertebrate

Introduction

Cephalopod molluscs (squid, cuttlefish, octopods, and nautilus) have very large and complex brains compared to other invertebrates (Budelmann 1995; Williamson and Chrachri 2004), and they are often cited as expressing complex behavioral traits (Hanlon and Messenger 1996; Hochner et al. 2006; Mather and Anderson 2007; Hochner 2008). Many cephalopods can learn, remember (Hochner et al. 2006; Crook and Basil 2008a; Grasso and Basil 2009), and some species have been shown to alter their behavior depending on context (Hvorecny et al. 2007;

Grasso and Basil 2009). Some cephalopods show evidence of personality (Sinn et al. 2001; Sinn and Moltschaniwskyj 2005; Pronk et al. 2010) and the ability to feel what may be interpreted as a correlate of pain (Crook and Walters 2011). Behaviors attributable to sleep and REM have been identified in cuttlefish (Frank et al. 2012). Perhaps their most publically recognized trait, cephalopods exhibit crypsis and signaling through rapid, neurally controlled changes in skin color pattern, skin texture, and body position (Hanlon et al. 1999, 2011; Messenger 2001; Hanlon 2007). Yet they have little to no color sensitivity in their own visual systems (Marshall and Messenger 1996; Mäthger et al. 2006), suggesting the colors of their skin pigments result from persistent selective predation pressure by color seeing fishes and marine mammals once those other lineages arose (Packard 1972; Grasso and Basil 2009).

Cephalopods are evolving as a model system for understanding color change (Hanlon 2007), learning, memory, and motor control (Hochner et al. 2006; Hochner 2012), and research increasingly spans from neurological through to ecological aspects. This paper provides a brief introduction to cephalopod neurobiology and related topics for use by scientists interested in cephalopods, but perhaps not yet working in that system. It concisely summarizes major aspects of cephalopod neurobiology, camouflage, learning, reproduction, motor control, and behavioral ecology, and cites comprehensive reviews for further reading in these fields, but is not meant to be an exhaustive review. It must be stressed that a majority of neurological studies of cephalopods are based on the shallow-water species *Octopus vulgaris* and *Sepia officinalis* and that while these are model animals, they do not fully exemplify the diversity of cephalopod behavioral ecology, selective pressures, and biological constraints and possibilities. While shallow-water coleoid cephalopods are the most

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commonly cited examples in this paper due to a skew in research covering those taxa, a rich literature is emerging addressing the neurobiology and behavior of *Nautilus* (Grasso and Basil 2009; Crook et al. 2009; Crook and Basil 2008a).

Cephalopod neurobiology

Cephalopods have large nervous systems (up to 500 million nerve cells in *Octopus*) with nearly as many neurons as a dog (Hochner 2008), although as many as two-thirds of these neurons are dedicated to the nerve cords and ganglia in the peripheral nervous system (PNS) rather than the central nervous system (CNS) (*O. vulgaris*—Young 1963, 1971). The CNS is comprised of distinct brain lobes that resemble invertebrate ganglia (Hochner 2008) plus a pair of large optic lobes, which can be seven times larger than the rest of the brain in some lineages (Budelman 1995; Williamson and Chrachri 2004). Across cephalopods, there is considerable variation in the relative size and degree of centralization of brain lobes (Budelman 1995, Grasso and Basil 2009); octopus brains have the most lobes (40) and are the most centralized with the largest vertical lobes, while nautilus brains have the fewest lobes (13) and are the least centralized (Budelman 1995, Grasso and Basil 2009). In all cephalopods, the brain encircles the esophagus (Budelman 1995), limiting the size of food they can swallow and leading to long prey processing times with possible vulnerabilities to predation while eating. The oegopsid squid *Todarodes pacificus* (and possibly many other cephalopods with very small paralarvae and shortened embryonic periods) hatches with a premature brain (Shigeno et al. 2001). Reaching lengths of several centimeters and diameters of up to 800 micrometers, the squid giant fiber is used broadly as a generic model for studies of neural function (reviewed in Grant et al. 2006). The stellate ganglion near the mantle opening is sensitive to light (Nishioka et al. 1966) and appears to help regulate circadian rhythms (Houck 1982). Unlike other molluscs, cephalopods have a blood–brain barrier (Budelman 1995).

Where known, a significant portion of the central nervous system in cephalopods is dedicated to visual, tactile, and chemosensory perception (Grasso and Basil 2009) with a high degree of cross-connectivity (Budelman 1995). Electrostimulation of several different regions of the brain can elicit behaviors that are similar to each other (Zullo et al. 2009), and likewise, sensory input may feed into multiple lobes (Budelman 1995). All brain lobes have motor neurons (Zullo and Hochner 2011). The optic lobes interpret visual information for use in defense, camouflage, motor control, and learning (Williamson and Chrachri 2004).

Cephalopod camouflage

Cephalopod camouflage begins with the visual detection of the edges, contrast, and size of nearby objects and processing by the brain and optic lobe to interpret information about surroundings (reviewed in detail in Messenger 2001; Zylinski and Osorio 2011; Hanlon et al. 2011). Cuttlefish are capable of contour completion (interpreting a partial outline as a whole), which is important for identifying objects or animals for which the full view is partially obstructed, and subsequently employing the appropriate escape, hunting, or camouflage behavior (Zylinski et al. 2012). The muscles of the chromatophores and skin are then controlled in part by the lateral basal lobe and the suboesophageal lobes to change the color and texture of skin (Budelman 1995). Cephalopod skin is comprised of multiple layers (reviewed in Packard and Hochberg 1977). Backed by a muscle layer, a layer of iridophores, leucophores, and reflector cells produces structural colors including blues, greens, pinks, and whites. Two layers of chromatophores (elastic sacs of color pigments including browns, reds, and orange) are situated in a layer above the reflective layer and below the epidermis (Packard and Hochberg 1977). To produce the appearance of pigment colors, nerves contract radial muscles on the chromatophore periphery to expand the pigment sacs. Relaxation of these muscles releases the elastic chromatophores to contract again, leaving the underlying pale reflective layer visible (Packard and Hochberg 1977). Finally, cephalopods appear to use only visual input for stimulating the activation of muscles that erect papillae to produce skin textures that match those in the background environment (Allen et al. 2010).

Where known, cephalopods create a species-specific repertoire of body patterns, each determined by an anatomically fixed range of colors and presence, absence, and location of skin components (such as white spots, ocelli, and dark bars; Packard and Sanders 1971; Hanlon and Hixon 1980; Hanlon 1988). Cephalopod color change has the capacity to be rapid and frequent, facilitating numerous changes in form and color that may not only enable the ability of cephalopods to blend in with their background, but also inhibit the ability of predators to form a search image (Hanlon et al. 1999). Color change rates in the wild are highly variable. For example, *Octopus cyanea* foraging on a visually complex coral reef change phenotype nearly three times per minute (Hanlon et al. 1999). By contrast, signaling male octopus *Abdopus aculeatus* foraging and resting in a seagrass bed and on flat sandy bench change body pattern between *black and white stripes* and *camouflage* on average every 28 ± 40 min SD ($n = 61$; unpublished data). Being highly sought-after prey items, cephalopods experience important trade-offs between the

benefits of conspicuousness versus camouflage during signaling, defense, and movement. In the wild, males of the cuttlefish *Sepia apama* increase the conspicuousness of reproductive signals by moving from a heterogeneous resting background to a more uniform/lower contrast area for signaling (Zylinski et al. 2011). In *A. aculeatus*, the number of different body patterns expressed varies during locomotion, with more complexity and variation evident during slow movements than fast escape like jetting, though it is unknown whether this pattern results from biomechanical or neurological constraints (Huffard 2006).

Learning, recognition, and memory

Learning and memory appear to occur in all cephalopod lineages (see Grasso and Basil 2009 for a review of learning in cephalopods; Shomrat et al. 2008; Zullo and Hochner 2011). Associative learning paradigms have been used in laboratory experiments of cephalopod learning (Crook and Basil 2008b; Bellanger et al. 2003 and references therein). In *O. vulgaris*, consolidated long-term memory is controlled by the vertical lobe in the CNS, while short-term memory is stored in more distributed neural networks, a vertebrate-like pattern of separate memory storage sites (Shomrat et al. 2008). Omitted stimulus potentials have been documented and show correlates of anticipating an event outcome (Bullock and Budelmann 1991). Learning can be critical to the survival of paralarvae during changes in prey composition (paralarval *Doryteuthis opalescens*, Chen et al. 1996). Observational learning has been shown for *O. vulgaris* in the laboratory (Fiorito and Scotto 1992; interpreted as *Rapid imitation* by Biederman and Davey 1993) and appears to be controlled by the vertical lobe in this species (Fiorito and Chichery 1995). By contrast, although cuttlefish learning to avoid being pinched during prey-capture did so faster when observing conspecifics, these findings appeared to result from test subjects being primed for hunting by olfactory cues from prey, and not observational learning (Boal et al. 2000). Octopuses and cuttlefishes can demonstrate conditional learning in the laboratory (Hvorecny et al. 2007) and possibly in the wild. Male *A. aculeatus* in the wild exhibit mating tactics consistent with their size-based chances of winning agonistic contests (Huffard et al. 2010), suggesting learning of rank is followed by conditional use of mate guarding. Mate guarding is not exhibited by males that are small and unlikely to win contests in the local population—these males may reduce the risk of aggression by conditionally not using this tactic when likely to be unsuccessful. By contrast, males appear to mate guard and maximize mating opportunities only if they are large enough to win contests with other nearby males.

Long-term memory in cephalopods may last 5 days to 2 weeks (Fiorito and Scotto 1992; Alves et al. 2008), which is longer than repeated intra-specific interactions for most known species (Hanlon and Messenger 1996). However, this time frame may be ecologically relevant for remembering the identity of rare predators, or in cases of extended mate guarding, where a male follows and mates with a female and guards her from other males (Huffard et al. 2008).

Cephalopod social recognition is highly variable (reviewed by Boal 2006). A case of interspecific mating in the deep sea and cases of hybridization demonstrate a lack of species recognition in two deep-sea octopuses (Lutz and Voight 1994) and *Idiosepius* spp. (Nabhitabhata and Suwanamala 2008). Sex identification is mediated by visual body color displays in *A. aculeatus* (Huffard et al. 2008) but appears not to occur in blue-ringed octopuses (Cheng and Caldwell 2000), oval squids (Boal and Gonzalez 1998), and the octopus squid (Hoving et al. 2011), as evidenced by high incidence or likelihood of male–male matings. *Octopus vulgaris* can recognize familiar conspecifics possibly using sight (Tricarico et al. 2011). Despite the repeated interactions and pairing of males and females during mate guarding (Hanlon and Messenger 1996; Huffard et al. 2008; Leite et al. 2009), thus far there is no conclusive evidence of individual recognition among cephalopods in the wild (Boal 2006).

Motor control

Cephalopods have redundant appendages supported by a hydrostatic skeleton with high degrees of freedom (Kier and Smith 1985; Kier and Stella 2007). Squids, cuttlefishes, and nautilus are further supported by a flexible pen, a calcium carbonate “cuttlebone,” and an external shell, respectively (Hanlon and Messenger 1996). High-level motor control in cephalopods takes place in the basal and peduncle lobes of the CNS (Budelmann 1995; Hochner et al. 2006). This includes interpreting gravitational sensory input from the statocysts, much like the vertebrate vestibular system (Williamson and Chrachri 2004). In octopuses, stimulation of multiple regions in these lobes leads to complex movements using multiple arms or more (Zullo et al. 2009). Lower motor functions, including single-armed movements, appear to be controlled by the PNS (Budelmann 1995; Sumbre et al. 2001). Extension of severed octopus arms by mechanical and electrostimulation demonstrates that nerve cords and ganglia of the arms alone can control this movement (Sumbre et al. 2001). This arm movement is a fundamental aspect of reaching toward an object, defense (e.g. ‘whip’ used against fish and conspecifics—*A. aculeatus* Huffard 2007), and compliant bipedal locomotion (Huffard et al. 2005). The rich

repertoire of body movements and locomotor options (Huffard 2006), with a large degree of flexibility, appears to be mediated by a hierarchical organization of muscle control that also reduces the amount of CNS processing necessary to control the redundant appendages (Gutfreund et al. 1998).

It is hypothesized that a gating mechanism of the cephalopod brain inhibits the PNS, but can be released by sensory input and higher commands (Zullo and Hochner 2011). Similarly, two centers in the vertical lobe of *O. vulgaris* act in opposition to inhibit and promote attack on prey (Young 1964). Individual variation in these control mechanisms may be involved in the tendency of some individual cephalopods to vary consistently in their avoidance or reactive behaviors—otherwise interpreted as personality (Sinn and Moltschaniwskyj 2005).

Cephalopod maturation and reproduction

Cephalopods are gonochoristic (Rocha et al. 2001), with no known cases of hermaphroditism outside isolated cases of pseudohermaphroditism (*Ancistrocheirus lesueurii*—Hoving et al. 2006). Where known, the gonad begins to differentiate into either an ovary or testis around the time of hatching, although this process does not appear to be under hormonal control (*Sepia*—Richard and Lemaire 1975 in Mangold 1987). The optic gland in the brain releases hormones that control aspects of gamete development and sexual maturation (*O. vulgaris*—Wells and Wells 1972; Mangold 1987; Di Cosmo and Di Cristo 1998). Sex steroids including gonadotropin-releasing hormone can serve vertebrate-like functions and act as broad spectrum neurotransmitters and neuromodulators involved in memory and movement (*O. vulgaris*—Kanda et al. 2006). Many workers have suspected the possibility that hormones or pheromones influence mating behavior of cephalopods in the wild (Hanlon and Messenger 1996). In at least one squid, chemical cues in egg masses evoke agonistic behaviors and may be involved in triggering mass spawning (Cummins et al. 2011).

Male cephalopods produce spermatophores that vary in size by three orders of magnitude across species [1 mm in *Idiosepius biserialis* (Hylleberg and Nateewathana 1991) and over 1 m long in *Enteroctopus dofleini* (Pickford 1964)], and range in total number by two orders of magnitude, from fewer than ten to a few hundred (Voight 2009). These sperm packets are deposited internally into the oviducts in octopods (Hanlon and Messenger 1996) and externally around the mouth or mantle in squids (Mangold 1987) and cuttlefishes (Wada et al. 2005). Sperm move from the spermatophore to seminal receptacle sites in squids (Mangold 1987) or the oviducal gland in octopods (Bauer 1998) for long-term storage in mixed batches from

multiple males, where they are fertilized during the process of egg-laying and spawning (Hanlon and Messenger 1996) up to 5 months after mating or longer (*Bathypolypus arcticus*—O'Dor and Macalaster 1983). Both males and females appear to be promiscuous (Hanlon and Messenger 1996; Huffard et al. 2008), and egg batches where known have multiple paternity (Buresch et al. 2001; Voight and Feldheim 2009). In at least one type of octopus, males can assess the mating history of females and alter their preferences accordingly (Cigliano 1995). In the dumpling squid, *Euprymna tasmanica* polyandry is associated with larger eggs, although the underlying mechanisms controlling this and other benefits of promiscuity remain unknown (Squires et al. 2012).

Where known, female cephalopods produce a single batch of oocytes that are matured and spawned either synchronously before brooding and then death (Mangold 1987; Anderson et al. 2002), or over a series of multiple spawning events for which a portion of available oocytes mature in each round (reviewed in Rocha et al. 2001). For cephalopods that brood their eggs (primarily octopuses—Hanlon and Messenger 1996, but also two squids, *Gonatus onyx*—Seibel et al. 2005; *Bathyteuthis berryi*—Bush et al. 2012), egg care might interfere with or preclude feeding, meaning that multiple spawning would incur significant metabolic costs from repeated periods of reduced or no food intake. Brooding in open habitats would incur the additional cost of exposure to predation, especially for those species with exceptionally long embryonic periods of over several years as predicted for species in cold water (Boletzky 1994, as follows *Graneledone*—Voight and Drazen 2004).

As in many invertebrates, cephalopod body size determines fecundity (Boletsky 2003). Fecundity can reach two million eggs per spawning bout in *Dosidicus gigas* (Staaft et al. 2008), though is considerably lower in smaller species (e.g. fewer than 200 in *Idiosepius*—Nabhitabhata and Suwanamala 2008). In some shallow-water octopuses, extreme examples of multiple spawning (referred to as “iteroparity”) appear to be associated with small body size in order to increase lifetime fecundity despite a limited ovary capacity (Boletsky 2003).

Secondary sex characteristics and externally obvious (to humans) indicators of maturity do not appear to be ubiquitous in cephalopods. In octopuses, typically males though sometimes also females of many species develop a small number of especially enlarged suckers on certain arms (Robson 1929), the development of which can signal the peak of maturity (*O. cyanea*—Van Heukelem 1973). These enlarged suckers may be used for intraspecific signaling and/or sex identification during mating and/or aggression (*O. vulgaris*—Packard 1961). The absolute and relative diameter of enlarged suckers can vary by up to threefold

between males in a single population (*Abdopus* sp. “Hawaii,” Huffard, and Himes unpublished data), providing a possible means for sexual selection (Voight 1991). Otherwise, external indicators of maturity in cephalopods appear limited to highly visible gonads (most prominent in gravid individuals), which are sometimes accentuated through body color patterns during reproductive displays (*Loligo vulgaris reynaudii*, Hanlon et al. 2002; *Sepioteuthis lessoniana*—Boal and Gonzalez 1998), and may also serve a role in sexual selection.

With few possible exceptions, young cephalopods do not overlap in time and space with their parents and have no opportunity to learn from or compete with parents. After egg deposition or the brooding period, they either crawl away from the egg or enter into planktonic communities for an estimated time of a few days (*D. gigas*—Staaf et al. 2008) to 6 months (Villanueva and Norman 2008) before assuming the adult habitat. However, in theory, young might overlap with parents or siblings in those cephalopods with multiple spawning periods and/or crawl-away young, especially for those species that form spawning or brooding aggregations at the same site year after year, or those species for which males may revisit a site in two seasons (e.g. *Graneledone* sp.—Voight and Drazen 2004; *S. apama*—Hall and Hanlon 2002).

Cephalopod behavioral ecology

Cephalopods occupy all marine systems, including hydrothermal vents (Voight 2005), seamounts (Norman et al. 2005), and intertidal shorelines (Norman 2000). Some species are able to occupy euryhaline habitats (*Loliguncula brevis*—Vecchione 1991; *Callistoctopus aspilosomatis* and *A. aculeatus* for brief periods—CLH unpublished data). Social associations and complex social behavior do not appear to occur outside of reproduction (Hanlon and Messenger 1996). Mate competition may occur in all species that mate in group situations (Hanlon and Messenger 1996; Huffard et al. 2010). In the wild, the longest confirmed associations between two individual cephalopods appear to be about 1 week (*A. aculeatus*—Huffard et al. 2008), which coincides approximately with the duration of long-term memory in octopuses (*O. vulgaris*—Fiorito and Chichery 1995; Alves et al. 2008). Based on stomach content analyses and laboratory observation, cannibalism appears to be common in this lineage (Ibáñez and Keyl 2010) and is hypothesized to influence male mating tactics (Sauer et al. 1992), male mating position (Hanlon and Forsythe 2008; Huffard and Godfrey-Smith 2010), and evolutionary history (Grasso and Basil 2009).

Difficulties in mark recapture and tagging studies hamper studies of cephalopod home ranges and navigation in the wild (Semmens et al. 2007), although telemetry

(Aitken et al. 2005) and pop-up satellite tags (Stewart et al. 2012) have been used successfully. Deep-sea squids can be limited and perhaps guided by oceanographically defined boundaries (*D. gigas*—Bazzino et al. 2010). The Giant Pacific octopus (*E. dofleini*), which is commonly displayed in public aquarium settings, ranges over 50,000 m² in 20 days (Scheel and Bisson 2012). Navigation and spatial memory appear to incorporate visual (Mather 1991) and possibly chemical cues, and may be controlled by the vertical lobe (reviewed by Alves et al. 2008). In the laboratory, male cuttlefishes cover a greater area and use visual cues more often than females (Jozet-Alves et al. 2008), a result that is consistent with greater foraging distances for male *A. aculeatus* over that of females in the wild (Huffard and Davis, unpublished data). Some cephalopods that form spawning aggregations may live long enough to visit the aggregation site in more than one season (*S. apama*, Hall and Hanlon 2002; *Loligo bleekeri*, Itawa et al. 2005), so in theory, it is possible that they may use social cues to identify and return to the site (as in some iteroparous reef fishes, Warner 1988), or possibly distance chemoreception (Woodhams and Messenger 1974; Hanlon and Messenger 1996) and/or homing behavior (as in some semelparous fishes; Dodson 1998).

As in other animals (Heithaus et al. 2008), cephalopods have the potential to impart behaviorally mediated ecosystem-level impacts on the natural communities in which they live. Neurological influences on behavior, feeding ecology, anti-predator escape, attack during foraging or competition, and locomotion have the potential to influence body size, competition, fecundity, and population sizes. Shallow-water cephalopods must feed often and eat large amounts of food (small fish, crustaceans, and bivalves, depending on the species) to support their high growth rates [up to 10 % body weight per day (Itami et al. 1963; Hanlon and Messenger 1996)]. At the same time, they are eaten by most carnivorous marine animals large enough to consume them, and generally expose themselves to high risks of predation when they leave sheltered areas or draw attention through movement, as is often necessary during feeding (Hanlon and Messenger 1996). Food intake and water temperature appear to be the major determinants of growth and body size (Forsythe 2004), especially if these influences occur during the rapid increase in mass during the early life stages (Semmens et al. 2004; Brady 2008). In turn, environmental influences on growth can lead to population-level responses in body size and fecundity (*D. opalescens*—Brady 2008). Ultimate body size also typically determines the outcome of resource competition (Corner and Moore 1980; Cigliano 1993; Huffard et al. 2010), and possibly home ranges (Scheel and Bisson 2012) in cephalopods. Interestingly, where known larger body size (when comparing individuals of the same species) is

associated with shyness in feeding (*E. tasmanica*—Sinn and Moltschaniwskyj 2005). It will be exciting to see further research address how discrete differences or changes in the neural and hormonal control of feeding, growth, and behavior may influence survival, fecundity, population sizes, home ranges, and predation rates in cephalopods.

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