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REVIEW

Short-distance navigation in cephalopods: a review and synthesis

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Abstract This paper provides a short overview of the scientific knowledge concerning short-distance navigation in cephalopods. Studies in laboratory controlled conditions and observations in the field provide converging evidence that cephalopods use visual cues to navigate and demonstrate spatial memory. A recent study also provides the first evidence for the neural substrates underlying spatial abilities in cuttlefish. The functions of spatial cognition in cephalopods are discussed from an evolutionary standpoint.

Keywords Invertebrates · Comparative cognition · Spatial learning · Hippocampus

Introduction

Cephalopod mollusks are a large and very successful taxonomic group. There are about 700 species living today throughout the seas of the world. All living cephalopods belong either to Nautiloidea, the representatives of ancient cephalopods with an external shell, or to Coleoidea, the modern cephalopods with an internal (or absent) shell. The major orders of Coleoidea are the cuttlefishes, the squids and the octopods. Cephalopod body structure and way of life have changed dramatically over the course of their evolution. Packard (1972) suggested that their evolution was driven by selection pressures imposed by competition with fishes.

Cephalopods possess all sophisticated organs required to potentially solve the spatial problems they can be confronted with in their natural environment: efficient locomotor effectors (powerful muscles of the mantle, funnel and fins) associated with elaborate sense organs. These sense organs rival the equivalent vertebrate systems in their sophistication. First among cephalopod sense organs are their well-developed eyes, which structurally resemble those of vertebrates (with the lens, iris and retina; reviewed in Budelmann 1994). Cephalopods are color-blind (Marshall and Messenger 1996; Mäthger et al. 2006), but can discriminate the plane of polarization of light (Moody and Parriss 1960; Shashar et al. 2000). Cephalopods also have excellent tactile and chemical sensitivity in their suckers (Graziadei 1964) and possess olfactory organs below and behind their eyes functioning as chemoreceptors (Gilly and Lucero 1992; Woodhams and Messenger 1974). In addition, they have an elaborate equilibration system, the statocysts, which can be compared to the vestibular system of vertebrates (Stephen and Young 1982; Young 1960). These sense organs provide information about gravity and angular acceleration necessary for controlling equilibration. Finally, cephalopods possess a system analogous to the lateral line of fishes, which they use to detect water movements (Budelmann and Bleckmann 1988).

In most modern cephalopods, a complex nervous system with a complex and multi-lobed central brain has evolved (reviewed in Nixon and Young 2003). The brain of

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octopuses and cuttlefishes is enclosed in a cartilaginous cranium and lies between the eyes. The gut passes through the brain and divides it into supra- and sub-oesophageal masses that lie between two large optic lobes (Fig. 3a, b). The brain-to-body ratio is large, somewhere between that of fishes and reptiles and that of birds and mammals (Packard 1972). This complex nervous system allows cephalopods to display good performance in a wide range of learning (reviewed in Sanders 1975; Mather 1995), including associative learning (e.g., Agin et al. 2006a; Darmaillacq et al. 2004), discriminative learning (e.g., Boal 1996; Cole and Adamo 2005), observational learning (Fiorito and Scotto 1992; but see Biederman and Davey 1993; Suboski et al. 1993) and imprinting (Darmaillacq et al. 2006). These learning abilities are associated with significant long-term memory abilities (e.g., several weeks' retention of a discrimination task in *Octopus vulgaris*, Sanders 1970; reviewed in Agin et al. 2006b; Sanders 1975). Extraordinary behavioral plasticity has been observed for communication, predation and defense (e.g., Poirier et al. 2004, 2005; reviewed in Hanlon and Messenger 1996).

For cephalopods, as for other moving animals, knowing the spatial structure of the environment should be of prime importance for avoiding predators, searching for food, finding their way back home or remembering the location of conspecifics. This hypothesis for the existence of spatial abilities in cephalopods has led to a growing interest in studying spatial cognition in these mollusks; however, there is currently no existing review on cephalopods' spatial navigation. This paper aims to provide an overview of current scientific knowledge concerning short-distance navigation in cephalopods. In the first section, we present evidence of cephalopods' spatial abilities under controlled laboratory conditions. In the second section, we present an overview of mechanisms that cephalopods have evolved to deal with spatial tasks. Only studies of octopuses and cuttlefishes are presented because there are little data available addressing squids. In the last section, we will review field evidence addressing the functions of spatial cognition in cephalopods from an evolutionary standpoint.

Laboratory evidence for spatial abilities in cephalopods

Detour experiments

Detour behavior is the ability of an animal to reach a stimulus (a goal) when there is an obstacle between the subject and the stimulus (Zucca et al. 2005). Detour behavior is a cognitively challenging task; it suggests that the animal must maintain a spatial representation of the location of the goal after abandoning a clear view of it. After repeated trials, an animal does not need any kind of spatial representation to complete a detour, however, because the animal can learn "how" to reach the goal: this is called detour learning. For example, the animal can learn associations between particular environmental stimuli and motor responses (e.g., "I turn right, the prey is no longer visible, but if I then turn left, I will see it again").

Detour behavior is likely to be needed by cephalopods to negotiate obstacles when hunting in their natural surroundings. Laboratory studies by Schiller (1949) and Wells (1964) tested the abilities of *O. vulgaris* to solve a detour task and explored the strategies the octopuses used. In both experiments, octopuses were trained to detour around opaque partitions to reach a crab visible behind a transparent wall, but not directly accessible to them (Fig. 1). In Wells' experiment (1964), only eight octopuses out of 29 succeeded in solving the detour problem in the first trial. The failure of the majority of the octopuses could be interpreted as demonstrating an inability to show detour behavior, and hence an absence of spatial representation in octopuses. However, Regolin et al. (1994) showed that in

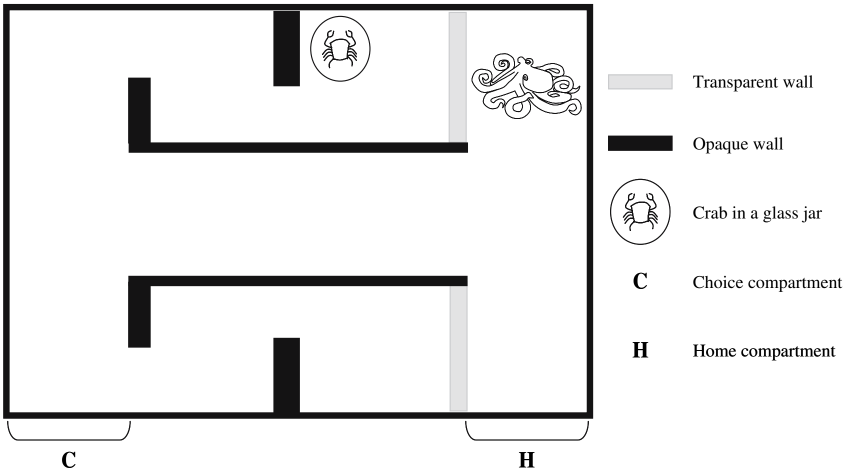

Fig. 1 Schematic representation of the detour maze used in Wells' experiments (modified from Wells 1964)

chicks, performances in detour problems can be affected by perceptual and motivational factors. In the experiments of Schiller (1949) and Wells (1964), the transparent wall that separated the octopuses from the crabs could have been such an unnatural stimulus that the animals failed to perceive it as an obstacle. With repeated trials, the octopuses showed some improvement in performance, spending less time attacking through the glass before entering the central alley, and all animals learned to complete the task. But what did the octopuses learn? Schiller (1949) suggested that octopuses needed to maintain constant tactile contact with the wall separating them from the goal. Wells later showed (1964) that if the tactile contact was lost, the octopuses needed to maintain a continuous visual fixation on the wall. Thus, detour behavior in octopuses was visually guided; bodily position was not used to compute position of the goal relative to their body. These detour experiments did not provide clear evidence for spatial representation in octopuses; however, they did show that octopuses can develop an efficient strategy to solve a spatial task.

Maze experiments

According to O'Keefe and Nadel (1978), exploratory behavior permits an animal to build a spatial representation of a new environment. Boal and colleagues asked whether cephalopods would explore an unfamiliar environment to gain a knowledge of the surroundings. First, Boal et al. (2000) examined spontaneous locomotor activity in *O. bimaculoides* when placed in a new environment. A gradual decrease in activity was observed over 3 days. Then, the authors tested the octopuses to determine if the reduced movement was associated with learning. They placed octopuses for a period of 23 h in a new environment with two burrows, only one open. After a resting period of 24 h, the octopuses were returned to the testing tank. The results showed that 16 out of 24 octopuses touched the previously open burrow first. This result was interpreted as demonstrating exploratory learning in octopuses. In a more recent investigation, preliminary tests undertaken by Karson et al. (2003) strongly suggested that the cuttlefish *Sepia officinalis* also moved around a new environment to learn about its features. These data bring the first evidence of a natural propensity in cephalopods to explore their environment; such behaviour is usually considered as a natural manifestation of spatial learning (Gallistel 1993; O'Keefe and Nadel 1978).

Maze experiments have been undertaken by several authors to reveal cephalopods' abilities to solve spatial tasks. The first maze experiment was conducted by Walker et al. (1970). The authors trained *O. maya* in a dry T-maze apparatus. The octopuses had to learn to enter a goal compartment to regain access to seawater. They were trained for 27 days with three trials a day to enter the goal compartment opposite to their initial side-turning preference. At the end of training, all octopuses were performing without errors. This experiment provided convincing evidence of maze learning ability in octopuses. Later, Boal et al. (2000) designed another spatial task comparable to a natural spatial problem. The authors trained *O. bimaculoides*, in about 20 trials, to relocate an open escape burrow among six possible locations around the periphery of a round arena. Octopuses quickly learned the location of the open burrow (i.e., improved performances after only three trials), and were able to remember the location for a week. In a more recent study, Karson et al. (2003) addressed whether cuttlefish, *S. officinalis*, also display good maze learning abilities in a visual–spatial discrimination task. The authors trained cuttlefish to exit a round arena with two exit holes surrounded by visual cues, only one exit hole being opened. Cuttlefish learned the task in a mean of 36 trials. Most recently, both octopuses and cuttlefish demonstrated the ability to solve two separate maze problems when trials with the two mazes were intermixed (Hvorecny et al. 2007). Taken together, these studies show that spatial learning is well within the abilities of at least some species of octopuses and cuttlefishes. Even if these maze experiments have not studied which sensory senses and spatial mechanisms cephalopods use to orient, they began to reveal the kinds of spatial tasks octopuses and cuttlefish are able to solve.

Mechanisms of spatial abilities in cephalopods

Use of chemical cues

Detection of chemical cues can be either through distant or contact chemoreception. Several studies have showed that octopuses and cuttlefish are capable of distance chemoreception (Lee 1992; Boal and Golden 1999). Detection of the spatial gradient of chemical cues in water could be a way for cephalopods to orient; unfortunately, there is no data yet available in the literature addressing this possibility. Among mollusks, a common way of returning to a place is to secrete a chemical trail on a solid substrate while leaving and then retrace that trail when returning. This strategy is called trail following and depends on contact chemoreception. Mather (1991a) and Forsythe and Hanlon (1997) recorded hunting paths of *O. vulgaris* and *O. cyanea*, respectively, in their natural environment (Fig. 2a, b). For long distance trips, octopuses traveled by jetting through the water when leaving (Mather 1991a) or returning home; consequently, they were not in contact with the substrate. Furthermore, the

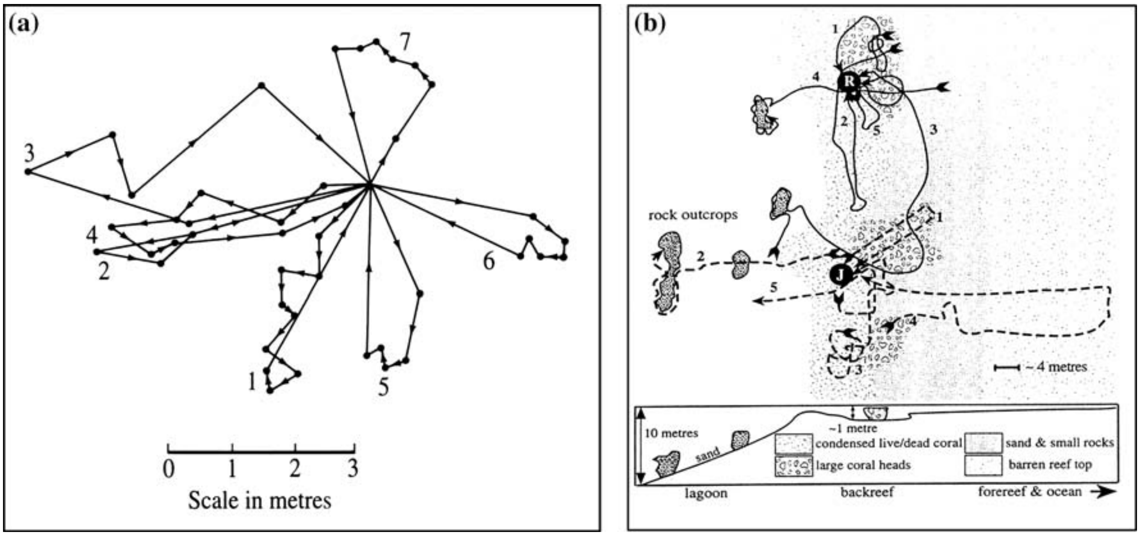

Fig. 2 Schematic representation of foraging trips. **a** Successive hunts numbered from 1 to 7 of a juvenile *Octopus vulgaris* (from Mather 1991). **b** Successive hunts of two specimen (J and R) of *Octopus cyanea* (from Forsythe and Hanlon 1997)

octopuses did not retrace their outgoing paths when they returned. In *O. vulgaris*, the trail overlap was only 32% (Mather 1991a). Finally, in both studies, the octopuses sometimes made tortuous hunting paths, and then swam directly back to their den afterward. Based on these data, the authors rejected the hypothesis of trail following in octopuses and suggested that octopuses have accurate knowledge of the seascape. No study yet supports trail following in octopuses; however, this absence of evidence does not exclude the possibility that octopuses could use this strategy in particular environmental conditions (low visibility, for example).

Use of visual cues

Single landmark

The complexity of cephalopods' visual system and their high performances in visual discrimination tasks (cuttlefish: Cole and Adamo 2005; octopuses: Boal 1996; Wells 1978) suggest that cephalopods could use visual landmarks to orient. Landmarks can be used in a variety of ways to provide information about the location of the goal. For example, an animal can learn to go to a particular landmark (a beacon) marking the location of a goal, regardless of the motor behavior involved. This behavior can be called landmark guidance, beaconing (Gallistel 1993) or stimulus-approach behavior (Schmajuk and Thieme 1992). An animal can also use the configuration of several landmarks to localize the goal; this behavior can be called piloting (Gallistel 1993).

A series of laboratory experiments investigating cephalopods' ability to use visual landmarks to orient were carried out by Mather (1991a) using octopuses. First, this author trained octopuses (*O. rubescens*) to go to a piece of plastic tubing (the beacon) to find a food reward located within a featureless circular tank. Mather showed that the octopuses learned to approach the plastic tubing even when it was moved around the tank. These results showed octopuses' ability to rely on a single landmark to label the location of a goal. Interestingly, Mather also showed that when a box and a dish were added in the tank, the octopus moved first to the larger landmark (the box), and next, oriented to the plastic tubing associated with food. We can interpret such results as learning a stimulus-approach association when a single landmark is available (beaconing), and possibly learning stimulus-approach behaviors linked together in chains to compose a route when several landmarks are available. Results were not definitive, however, for either orienting using landmarks in chains or for orienting using the geometrical relationships between landmarks. Simplified strategies such as use of landmarks in chains are widespread in other invertebrates, such as arthropods. Ants learn and recognize landmarks distributed along a route, and they correct their course relative to these landmarks (Collett et al. 1992). It would be interesting to study if the same strategy has evolved in cephalopods.

In a second experiment, Mather (1991a) tested whether octopuses rely on visual landmarks to find the entrance of their den in their natural environment (stimulus-approach behavior or beaconing). The author used the transformational approach, a common experimental technique pioneered by Tinbergen (reviewed in Cheng and Spetch

1998). Changing different aspects of the environment is a common tool used to understand which cues an animal relies on. Mather (1991a) placed artificial landmarks around the entrance of the den of several *O. vulgaris*. After 2 days, the author displaced the landmarks one meter away. The returning octopuses went directly to their homes, appearing to rely on more conspicuous and stable natural landmarks. We can hypothesize, then, that a visual landmark that is stable and more accurate or reliable across time is more likely to be used by octopuses.

Alternatively, the octopuses could have been using a strategy called path integration. Path integration allows animals to deduce their position relative to their starting point (direction and distance) from their own movements and then use this information to return home directly after a tortuous path. This strategy occurs very widely in the animal kingdom, from arthropods to humans (ants: Wehner 2003; crabs: Layne et al. 2003; mammals: Etienne et al. 1996), and could have also evolved in octopuses.

Multiple landmarks

The cross-maze spatial task has been extensively used to explore spatial learning strategies in a wide range of models (rats: Restle 1957; fish: Odling-Smee and Braithwaite 2003). This procedure allows the authors to ask several questions: do the animals use the array of visual cues (place strategy) to solve the maze? Or do they use a body-centered algorithmic behavior (list of instructions such as “turn left…”; response strategy)? Karson (2003) demonstrated that cuttlefish could be trained to exit a round, open maze using proximal visual cues (which could be a form of place strategy), right/left orientation (response strategy), or a combination of both types of cues. Alves et al. (2007) designed a spatial learning procedure using a cross-maze to test, which strategy cuttlefish used spontaneously. They devised cross-mazes with either proximal visual cues (just above the surface of the water) or distal visual cues (around the testing room). In these mazes, the cuttlefish *S. officinalis* learned to enter a dark and sandy compartment at the end of a goal arm in a mean of 25 trials. After acquisition of this task, the authors created a conflict between the algorithmic behavior (response strategy) and the visual cues identifying the goal (place strategy). When cuttlefish were trained with distal visual cues, most of them relied on response strategy, and when trained with proximal visual cues, the two strategies were used equally often. These results confirmed the existence of both response and place strategies in cuttlefish, similar to results described in vertebrates (e.g., Gibson and Shettleworth 2005). Moreover, the availability and salience of visual cues seemed to determine whether the cuttlefish used the response or place strategy to solve the maze. This study revealed cuttlefishes’ spontaneous behavioral flexibility in solving a spatial task.

An animal using the configuration of several landmarks to localize its goal (piloting) relies on geometric properties such as distances, angles or directions. Although no study has yet attempted to directly test the piloting hypothesis in cephalopods, Mather (1991b) provided some interesting preliminary observations. When octopuses hunt, they can consume their prey at the capture site or they can bring it back to their den to consume it. Mather (1991b) showed that the greater the distance between the capture site and the home den, the more likely the octopus was to eat the prey where it had been caught. The author interpreted this result in two ways: the octopus could have made an estimation of its distance to home using the energy it had expended as it moved out to forage, or the octopus could have spatial knowledge of the surroundings of its den.

Spatial memory and neural substrates

Two kinds of spatial memory have been commonly distinguished in the literature: reference spatial memory and working spatial memory. Reference spatial memory encodes spatial information that is likely to remain stable and reliable across time. In contrast, working spatial memory is retained only long enough to complete a particular task, after which the information is discarded, presumably because it is no longer needed. Both Mather’s studies (*O. vulgaris*, 1991a, b) and Forsythe and Hanlon’s study (*O. cyanea*; 1997) showed that octopuses hunted in several different directions around their home on successive hunts and even on successive days (Fig. 2a, b). Based on her observations, Mather (1991a) suggested the existence of working spatial memory in octopuses for where they had already hunted. Reference spatial memory in octopuses could refer to the spatial knowledge of the surroundings.

The vertical lobe complex is a highly associative structure of the cephalopods’ central nervous system. It is situated in the extreme dorsal part of the supra-oesophageal mass. This complex consists of several lobes closely interconnected: the vertical (VL), superior frontal and subvertical lobes (Fig. 3b). The vertical complex has been structurally compared to the hippocampus of vertebrates (Young 1991). Neural networks in both structures consist of sequences of matrices with numerous interacting channels. Parallel pathways are mutually reinforcing (Young 1991). Hochner et al. (2003) found that the VL of octopuses manifests long-term potentiation similar to that observed in the hippocampus of vertebrates. Thus, the VL is a structure of particular interest for studies of the neural substrates of spatial learning mechanisms in cephalopods.

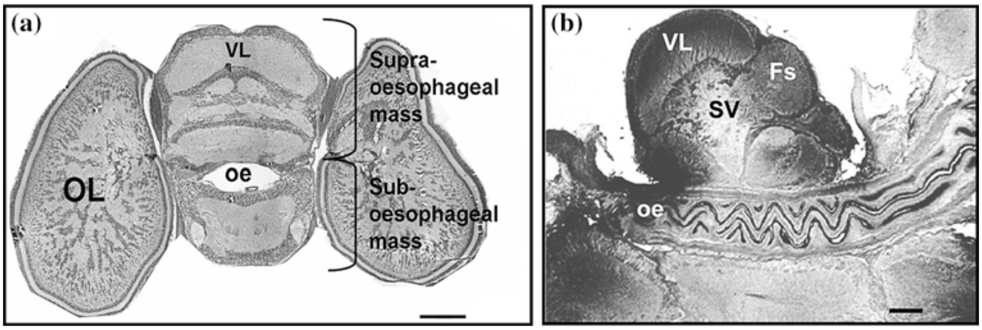

Fig. 3 Photomicrographs of the central nervous system of *Sepia officinalis*. **a** Frontal section (*scale bar* 1 mm). **b** Sagittal section (*scale bar* 500 µm). *oe* Oesophagus, *OL* optic lobe, *VL* vertical lobe, *SV* subvertical lobe, *Fs* superior frontal lobe

Graindorge et al. (2006) have made electrolytic lesions in either the ventral or the dorsal parts of the VL in cuttlefish *S. officinalis*. Sham-operated and VL lesioned cuttlefish were trained in a spatial learning procedure using a T-maze and were tested in an open field. The results showed that ventral lesions of the VL led to impairment in the acquisition of spatial tasks whereas dorsal lesions increased locomotor activity in an open field. This research established for the first time functional analogies between the VL and the hippocampus (locomotor activity level and memory). Future studies will address more precisely the function of the VL in spatial learning.

Behavioral ecology of spatial abilities in cephalopods

Space utilization in cephalopods

Field studies have been undertaken to better understand space utilization in octopuses. Many octopuses spend most of their time in protective shelters (reviewed in Boyle 1983, 1987). Depending on the species, they use several types of dens, also called “homes”, including holes in the hard substratum (*O. cyanea*; Forsythe and Hanlon 1997), sheltered niches under rocks (*O. dofleini*; Hartwick et al. 1978), within mollusk shells (*O. joubini*; Mather 1982), and in rocks or litter of human origin (*O. vulgaris*; Katsanevakis and Verriopoulos 2004). Octopuses can also extensively modify a site by digging out sand and moving rocks (*O. bimaculatus*; Ambrose 1982; *O. vulgaris*, Mather 1994). An octopus can occupy the same den over a period of days (*O. cyanea*; Forsythe and Hanlon 1997; *O. vulgaris*; Mather and O’Dor 1991), weeks (*O. cyanea*; Yarnall 1969; *O. dofleini*; Hartwick et al. 1984; Mather et al. 1985; *O. vulgaris*; Mather 1988) or even months (*O. bimaculatus*; Ambrose 1982), after which it shifts to a new den. Occupancy duration is linked to den size and possibly the presence of preferred prey (Mather 1994).

Laboratory studies showing exploratory behavior in octopuses (see above) suggest that we could expect octopuses to either explore a new area and then choose the best place for its new den, or quickly choose a new den and afterwards explore their surroundings. Mather (1994) observed *O. vulgaris* as they foraged and stopped to choose a new den; they explored little before choosing the dens and their homes were subsequently extensively modified. The author suggested that octopuses are always evaluating and exploring new areas to gain knowledge of their environment.

Octopuses are considered to be central place foragers (Mather 1991a, b). Mather and O’Dor (1991) studied the hunting trips of juvenile *O. vulgaris* off the coast of Bermuda and showed that the octopuses (49–115 g) hunted in a circular area (15 m in diameter) centered approximately on their den. In a related study, juvenile octopuses routinely hunted away from their dens on complicated trips that averaged 55 min in duration and 9.3 m in distance (Mather 1991a). Forsythe and Hanlon (1997) recorded hunting paths of *O. cyanea* (300–700 g). Trips for these octopuses averaged 118 min in duration and up to 120 m in distance. Some spatial abilities must have evolved in octopuses to allow them to find their way back home after each of these hunting trips and, potentially, allow them to remember the distribution of food patches and already depleted areas.

Cuttlefishes are thought to rely primarily on crypsis for defense (Boletzky 1983; Hanlon and Messenger 1988). They can dig into the sand for concealment (Mather 1986) and they can also change the color and texture of their skin to match the background. Aitken et al. (2005) have suggested that the giant Australian cuttlefish, *S. apama*, may also use dens. The authors used a Radio Acoustic Positioning and Telemetry system (RAPT) to monitor cuttlefish movements. During the first few days of monitoring, cuttlefish were continuously detected with the tracking system (continuous data were obtained); thereafter, there was a strong reduction in quantity of data obtained. The authors suggested that the cuttlefish may have been hiding in dens (rock crevice, no signal), and sometimes going out to hunt (signals). From these observations alone, we cannot determine if each cuttlefish was using a single shelter from 1 day to another or multiple different shelters, and if sheltering is a widespread behavior in cuttlefishes. Aitken et al. (2005) also showed high site fidelity in individual *S. apama*, with cuttlefish confining their hunting to a restricted area. We can hypothesize, therefore, that cuttlefishes, like octopuses, may have spatial knowledge of their surroundings at least to optimize their hunting time.

In many animals, spatial abilities also appear to be crucial for social behaviors. In cephalopods, both octopuses and cuttlefishes are generally considered to be solitary, except during reproduction (Boal and Golden 1999; Yarnall 1969). Octopuses typically avoid each other. In *O. vulgaris*, Altman (1967) observed dens close together but there were no signs of interactions between neighbors. In *O. cyanea*, after visual contact, one octopus slowly extended an arm to make physical contact, after which the other octopus typically swam off (Yarnall 1969; Forsythe and Hanlon 1997). In *Abdopus aculeatus*, Huffard (2007) observed individual males occupying dens adjacent to those of particular females. The males mate-guarded and copulated repeatedly with the adjacent female for multiple days. There is yet no clear evidence of an octopus consistently defending its home range against conspecifics, however; thus, most authors consider that octopuses are non-territorial.

Cuttlefishes are considered to be solitary for the major part of their life cycle. They seem to tolerate conspecifics without being attracted by them. In *S. apama*, the giant Australian cuttlefish, a large spawning aggregation occurs every winter over a restricted area of rocky reef in South Australia (Hall and Hanlon 2002). Some aspects of their complex mating system have been compared with those of leks. It is not known how cuttlefish find their way to spawning aggregations, and it remains to be determined whether group stability in any cephalopod species depends on social recognition between individuals or on spatial learning (reviewed in Boal 2006).

Spatial abilities and cephalopods' life styles

Cephalopods are considered to have a "live fast and die young" life-style (O'Dor and Webber 1986); they grow quickly, and few of them live more than 2 years (reviewed in Boyle 1983, 1987). They are also exposed to strong competition and predation pressures. It appears reasonable to assume that spatial learning abilities must have evolved to allow them to spend a minimum amount of time exposed to predators while foraging. The evolution of cephalopods is closely linked to the reduction and internalization of the shell (Ward and Bandel 1987). In the benthic, cryptic cuttlefishes, the shell is mainly implicated in buoyancy regulation (Birchall and Thomas 1983). In the fast-moving squids, a cartilaginous pen is all that remains of the shell, and it serves as a support for musculature. In the secretive octopuses, the shell has almost disappeared, allowing them to hide in small crevices or holes in the substrate. These evolutionary trajectories demonstrate clear connections between morphology and behavior, with each group adapting with one of the defensive strategies typically described for cephalopods: camouflage, escape or shelter occupancy. Consequently, it is likely that each group of cephalopods has faced specific spatial problems and has evolved specific spatial strategies.

Cephalopods are found in a wide range of aquatic habitats; for example, some live in visually rich coral reefs while others live in the surface waters, or in the deep ocean where little or no light penetrates. Even within a species, populations may not share identical environmental conditions. It is reasonable to hypothesize, therefore, that cephalopods have evolved a large array of adaptive spatial strategies. Future studies that facilitate between- and within-species comparisons will provide a better understanding of the genetic and ecological components of variation in spatial abilities. Comparisons with other invertebrate and vertebrate models, such as arthropods or rodents, would also be important for understanding the evolution of navigational strategies in the animal kingdom.

Conclusion

Tinbergen (1963) outlined four major questions that can be asked in ethology. They are often categorized as proximate explanations for behavior (causation and development) or ultimate explanations for behavior (functions and evolution).

At the proximate level, laboratory studies in controlled conditions as well as observations in the field have yielded clear evidence for spatial abilities and have provided some evidence for the spatial mechanisms that cephalopods use to orient. Multiple studies support the importance of visual cues to navigation and the use of both response learning and place learning strategies. Preliminary evidence suggests that the vertical lobe complex could be performing functions analogous to the hippocampus of vertebrates. Cephalopods' sophisticated nervous and sensorimotor systems may support a wide range of strategies. No study has yet addressed developmental questions associated with cephalopod spatial abilities. However, cephalopods appear to be good biological models for such studies because of the wide range of habitats they exploit and their high behavioral flexibility during ontogenesis (Dickel et al. 2000; Hanlon and Messenger 1988; Poirier et al. 2004, 2005). It remains for future studies to provide a more complete understanding of orientation mechanisms in cephalopods.

At the ultimate level, field studies of shallow water octopuses support the hypothesis that the spatial abilities of cephalopods are important in both defense and foraging. While numerous studies have provided some data for spatial orientation in octopuses, field data for cuttlefishes and squids are largely lacking. Improved information about the functions of spatial abilities in all three groups will facilitate the understanding of spatial cognition from comparative, ecological and evolutionary perspectives.

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