REVIEW

The cephalopod specialties: complex nervous system, learning, and cognition[1]

Jennifer A. Mather and Michael J. Kuba

Abstract: While clearly of molluscan ancestry, the coleoid cephalopods are emergent within the phylum for complexity of brain and behaviour. The brain does not just have centralization of the molluscan ganglia but also contains lobes with "higher order" functions such as storage of learned information, and centres have been compared with the vertebrate cerebellum and frontal lobe. The flexible muscular hydrostat movement system theoretically has unlimited degrees of freedom, and octopuses are models for "soft movement" robots. The decentralized nervous system, particularly in the arms of octopuses, results in decision making at many levels. Free of the molluscan shell and with evolutionary pressure from the bony fishes, coleoids have evolved a specialty in cognition and they may have a simple form of consciousness. Cephalopods also have a skin display system of unmatched complexity and excellence of camouflage, also used for communication with predators and conspecifics. A cephalopod is first and foremost a learning animal, using the display system for deception, having spatial memory, personalities, and motor play. They represent an alternative model to the vertebrates for the evolution of complex brains and high intelligence, which has as yet been only partly explored.

Key words: cephalopods, brain–behaviour linkage, movement control, skin display system, learning, and intelligence.

Résumé : Si leur ascendance est clairement reliée aux mollusques, les céphalopodes coléoïdes sont émergents au sein du phylum en ce qui concerne la complexité de leur cerveau et de leur comportement. En plus de la centralisation des ganglions propres aux mollusques, le cerveau contient également des lobes de fonctions « de haut niveau » telles que le stockage d'information apprise, et des centres qui ont été comparés au cervelet et au lobe frontal des vertébrés. En théorie, le système de mouvement par hydrostat musculaire souple présente un nombre illimité de degrés de liberté, et les pieuvres constituent des modèles de robots à « mouvements souples ». Le système nerveux décentralisé, notamment dans les bras des pieuvres, se traduit par la prise de décisions à de nombreux niveaux. Libérés de la coquille des mollusques et soumis à la pression évolutionnaire des poissons osseux, les coléoïdes se sont spécialisés sur le plan cognitif et pourraient présenter une forme simple de conscience. Les céphalopodes ont également un système de signalisation par la peau inégalé pour ce qui est de sa complexité et de l'excellence du camouflage qu'il permet, qu'ils utilisent aussi pour communiquer avec leurs congénères et leurs prédateurs. Les céphalopodes sont d'abord et avant tout des animaux qui apprennent, qui utilisent ce système de signalisation pour tromper, et qui font preuve de mémoire spatiale, de personnalités variées et de jeu moteur. Ils constituent un modèle de développement de cerveaux complexes et d'intelligence supérieure distinct du modèle vertébré et dont l'étude demeure incomplète. [Traduit par la Rédaction]

Mots-clés : céphalopodes, liens cerveau–comportement, contrôle des mouvements, système de signalisation par la peau, apprentissage et intelligence.

Introduction

Cephalopods have fascinated humans for a long time. Both early classic writers of natural histories, Aristotle and Plinius, mention them in their accounts. The last 100 years saw a continuous but low-level interest in the behaviour, anatomy, and physiology of these advanced invertebrates. About 700 species of coleoid cephalopods inhabit almost every marine environment, from the deep sea to the intertidal level, from the tropics to the polar regions. Their functional morphologies reflect this variety of habitats that they can be found in. Coleoid cephalopods are molluscs, yet their morphology, physiology, ecology, and even behaviour were shaped by a coevolutionary arms race with modern teleost fish. As a result, they often developed abilities and properties convergent to vertebrates (Packard 1972; O'Dor and Webber 1986). One of the most striking features that derived from

this is that most cephalopods have prominent eyes which are important in their daily lives. Cephalopods "live fast and die young"; they grow extraordinarily quickly (by molluscan standards), they mature after a year or less, and rarely live for more than 2 years. Despite their short lives, octopuses are "brainy" animals and their behaviour is complex and diverse. The brain/body ratio of the common octopus (*Octopus vulgaris* Cuvier, 1797) is comparable to that of "lower" vertebrates and they have among the largest of any invertebrate brains. As well as controlling its behavioural plasticity and high cognitive capacity, the brain has a large size to control the animals' flexible body and skin. The brain anatomy and neuronal pathways have been extensively studied (for reviews see Young 1971; Wells 1978; Budelmann et al. 1997; Nixon and Young 2003). Cephalopods offer an important window to look at convergent evolution and general trends in brain evolution and behavioural development seen in other groups like

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[1]This review is one of a series dealing with trends in the biology of the phylum Mollusca.

vertebrates, from cephalization to the increased specialization of certain brain parts to the concentration into functional brain lobes. This is also seen through what happened to the principal molluscan ganglia throughout the evolution of cephalopods. According to Young's (1971) theory, ganglia were not enlarged but the basic nerve cords that surround the gut in a primitive amphineuran bauplan were enlarged and finally fused to create the present day brain structure seen in coleoids, which comprises up to 30–40 lobes interconnected by commissures and tracts (Nixon and Young 2003; Zullo and Hochner 2011).

Several cephalopods are ideal animals for studying the capabilities of the advanced invertebrate because of their complex vertebrate-like behaviours (Hochner et al. 2003, 2006; Hochner 2008, 2010, 2012; Shomrat at al. 2011). For a long time octopuses have been used to test several different non-associative and associative learning tasks. Sensitization, or the increased likelihood of an animal responding to a stimulus, has been demonstrated clearly in *O. vulgaris*. Reward or punishment that takes place before the presentation of a test shape will respectively decrease or increase the likelihood of an attack on the stimuli. This has been shown for visual and tactile discriminations (Wells and Wells 1958; Wells 1967), as well as for olfactory stimuli (Chase and Wells 1986). The importance of sensitization usually dwindles during discrimination training, as longer term changes become entrenched.

Habituation, one of the simplest forms of learning, is the relatively persistent waning of a response as a result of repeated stimulation without reinforcement. In an experiment with a blind octopus (Wells and Wells 1956), a plastic cylinder placed on the arm of the animal was passed under the web to the mouth, examined, and rejected. If the same object was repeatedly presented, after a few trials the octopus stops passing it to the mouth. After more trials the octopus spent only a few seconds examining it. Habituation of a visual response has also been demonstrated in Atlantic brief squids (*Lolliguncula brevis* (Blainville, 1823)) (Long et al. 1989), shown by the decline of escape jets and ring patterns on the mantle with repeated presentation of a fish predator model. The squids also showed dishabituation to the predator model after a threat stimulus. Recently, habituation has been shown in visual tasks in intact octopuses (Mather and Anderson 1999; Kuba et al. 2006a, 2006b).

Octopuses have been, and still are, extensively used in associative learning experiments (Wells 1978). The main goal of these studies was to try to describe a visual signal pathway in a seemingly not too complex animal. Octopuses also use body posture, swaying, advance and retreat, arm movements, skin colour and texture, respiration rate, and eyebar and iris diameter to exhibit subtle signs of their reactions during learning (Budelmann et al. 1997). Recently, cephalopods have also been proposed as a model to test the concept of embodied intelligence (Pfeifer et al. 2007; Li et al. 2011; Hochner 2012). Their unique soft bodies are used as biological inspiration for several attempts to construct soft-bodied robots. How to control such a flexible body raises new challenges for the engineers and calls on the biologists to make new experiments and draw conclusion, including insights from the field of robotic engineering (Li et al. 2011; Hochner 2012).

Given this range of reactions and complexity of brain control, cephalopods thus represent a unique opportunity to study a different evolutionary path to intelligence and cognition (Mather 2011b) and their brain control. This review will focus on topic areas that are well understood or specialized in cephalopods, such as movement control, skin displays, predation and foraging, navigation and consciousness, and their brain control.

Movement and its control

All behaviour involves movement, so a review of cephalopod behaviour necessarily starts with movement descriptions. Coleoid cephalopods have an unusual kind of skeletal system, a muscular hydrostat (Kier and Thompson 2003; Yekutieli et al. 2009). This kind of system has no fixed endo- or exo-skeleton, as in vertebrates and arthropods. Instead the muscles themselves co-contract and act as skeletal support, as well as vehicles for movement, assisted by connective tissue. This is possible because the fluid within the muscular hydrostat cannot change volume; for instance, an octopus arm represents a cylinder that, when elongated, also has a reduced cross-section (Yekutieli et al. 2009). Bundles of muscle fibres are arranged in three mutually perpendicular directions; in the octopus arm they are transverse, longitudinal, and oblique, with an additional thin circular muscle layer, and movement and posture are assisted by a network of connective tissue (Smith and Kier 1989; Kier and Stella 2007). Muscular hydrostatic control underlies movement of many structures, such as the arms and tentacles of squid (Kier and Schachat 2008), the adhesive octopus suckers (Kier and Smith 2002), and the buccal musculature of the octopus beak (Uyeno and Kier 2007). Because the control of octopus arms has been investigated most thoroughly and at many different levels, much of the research reported here will be about that system.

Some of the characteristics of any motor system must be its stiffness, ability to bend, and the leverage it can exert (octopuses are famous for the force that the arms can exert: Dilly et al. 1964), as well as the accuracy of localization of movement (Yekutieli et al. 2009). Kier and Stella (2007) point out that the octopus arm movements must be some combination of elongation, shortening, bending, stiffening, and torsion. An example of this variety is the arm postures of the Caribbean reef squid (*Sepioteuthis sepioidea* (Blainville, 1823)) (Mather et al. 2010), especially used in young squid for camouflage (Fig. 1). Arms and paired tentacles can bend at one or many positions along their lengths, can shorten or extend, splay away from the midline, and can also twist, rotating around their own axis. A posture called "Bad Hair" does all of these at the same time, and the octopus "Flamboyant" (Packard and Sanders 1971) positions the arms similarly. In theory, a muscular hydrostat system has an almost unlimited number of degrees of freedom (ability to move in any direction at any place). But Gutfreund et al. (1996, 1998) showed that an initial driving force and a propagating wave of muscle activation may position the bending movement of arm extension. This stereotypy is also true for arms isolated from the brain, so local motor programs in the arm may drive extension. Similarly, a transfer of prey to the mouth by arm bending may result from a collision of activation from proximal and distal, meeting halfway, to where they prey is held (Sumbre et al. 2001).

What is it like to have a cephalopod (particularly octopus) movement system? The key to the difference between octopuses and other animals might lie in the sensimotor systems of its flexible body and arms. The arm contains a widespread sensory system that allows the animal to collect mechanical and chemical information from the immediate environment and to appropriately react to the stimuli. The suckers contain a very effective mechanical and sensory system, as each sucker consists of an external structure or acetabular cup that is richly innervated by sensory cells, a control ganglion, and a stalk.

The acetabular cup of the sucker (Fig. 2) consists of an infundibulum, which bears a series of radial ridges and grooves, that is covered by a chitinous cuticle or sucker lining (Girod 1884; Naef 1923; Nixon and Dilly 1977; Packard 1988). A rim of dermis and epithelium encircles the infundibulum and is separated from it by a circumferential groove. The rim is surrounded by a zone of epithelium which includes cells with inclusions that have the staining characteristics of acid polysaccharides typical of molluscan mucus (Kier and Smith 1990). At the centre of the infundibulum is an orifice that opens into an approximately spherical cavity called the acetabulum (Girod 1884). A covering cuticle is made up of a chitin-protein complex secreted by the underlying epithelium

Fig. 1. Postures of the arms of the Caribbean reef squid (*Sepioteuthis sepioidea*) (from Mather et al. 2010, reproduced with permission of Mar. Freshw. Behav. Physiol., Vol. 43, Issue 1, pp. 49, © 2010 Taylor & Francis).
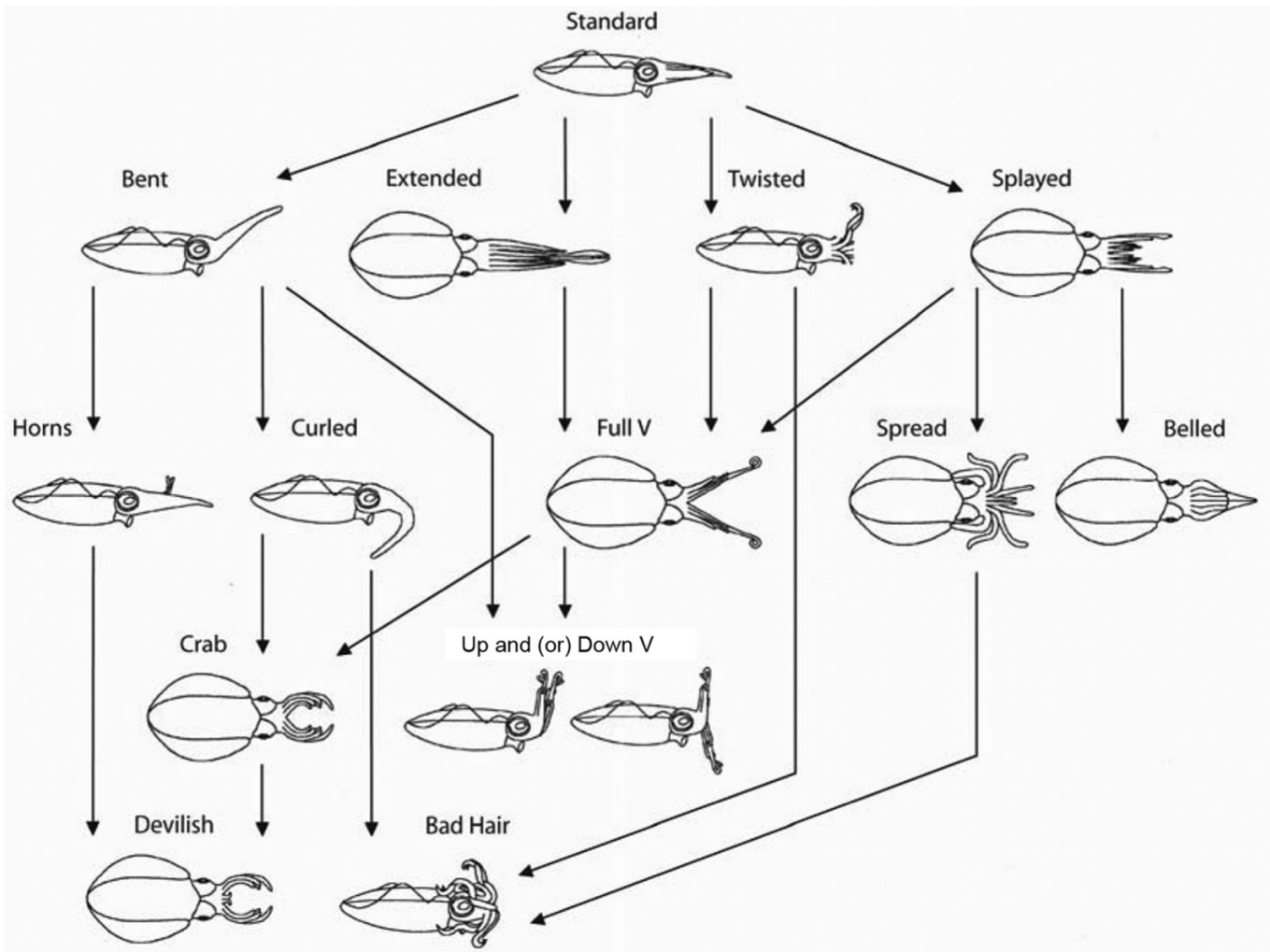
cells. The suckers are attached to the arm by a short muscular stalk (Mather 1998). The sucker ganglion, which controls the sucker, is composed of motor neurons that innervate the peduncle muscle of the suckers, as well as bipolar and multipolar interneurons of unclear function. On the opposite side of the arm from the suckers, the arm ganglia contain a higher density of nerve cells, probably because the axial nerve cord controls the activity of the suckers (Graziadei 1971). The rim of each sucker carries a huge number of primary sensory cells devoted to both chemical and mechanical senses. A single sucker of 3 mm diameter carries several tens of thousands of sensory cells (Graziadei 1971; Wells 1978) and the whole skin of the octopus is estimated to carry up to 2.4×10^8 sensory cells. Deep receptor-like stellate neurons are found at many sites within the arms and suckers (Graziadei 1965). These are branched neurons that may be proprioreceptors, monitoring muscle deformation (Wells 1978). Recent studies have physiologically demonstrated that mechanosensory information is transmitted from the intrinsic muscles in the axial nerve cord (Gutfreund et al. 2006).

Suckers are a very effective adhesion structure. The attachment force of a sucker depends on the difference between the ambient pressure and the pressure of the water enclosed by the sucker. Cavitations on most marine surfaces occur at pressures between 0 and 2100 kPa (Smith 1996), so at sea level (ambient pressure 5100 kPa), cavitation normally limits a sucker to a maximum pressure differential of 100–200 kPa. For four different species of

cephalopod tested on surfaces where cavitations would not be limiting, the pressure differential ranged from 100 to 270 kPa (Smith 1991, 1996). Smith (1996) showed that decapod suckers could produce pressure differentials several times greater than those created by octopus suckers and measured pressure differentials in decapod suckers that were as high as 830 kPa. The cost of this increased strength is likely a loss in dexterity relative to octopus suckers (Kier and Smith 2002). Dilly et al. (1964) found that a 2.5 kg octopus could exert a maximum pulling force of 18 kg; the maximum force the animal could use to push objects is about 50% of this value. Parker (1921) measured the breaking forces on either 1 or sets of 3 suckers in the California two-spot octopus (*Octopus bimaculatus* Verrill, 1883). He showed that a single sucker of 2 mm diameter had a breaking force of 0.02 kg, whereas the breaking force for three suckers was 0.07 kg. Larger suckers (6 mm) had breaking forces of 0.14 or 0.43 kg. And this is only one or a few suckers—the suborder Incirrata has hundreds of suckers.

Although a reduction in degrees of freedom is helpful in predicting arm movement, the motor system is much more complex than this description. At the next level, each arm subsystem consists of the arm itself and hundreds of suckers along its length, as well as extended stalks in some species (Nixon and Dilly 1977). The squid and cuttlefish also have a pair of extensible tentacles that can elongate by over 80% at peak extension, have peak velocities of over 2 m/s, and attach to a prey with suckers at the terminal club (Kier and van Leeuwen 1997). There is a series of ganglia along

Fig. 2. The acetabular cup of a sucker from the mimic octopus (*Thaumoctopus mimicus*) (micrograph by and reproduced with permission of David Edelman and Helen Makarenkova). Figure appears in colour on the Journal's Web site.

A: Acetablum
I: Infundibulum
1 mm
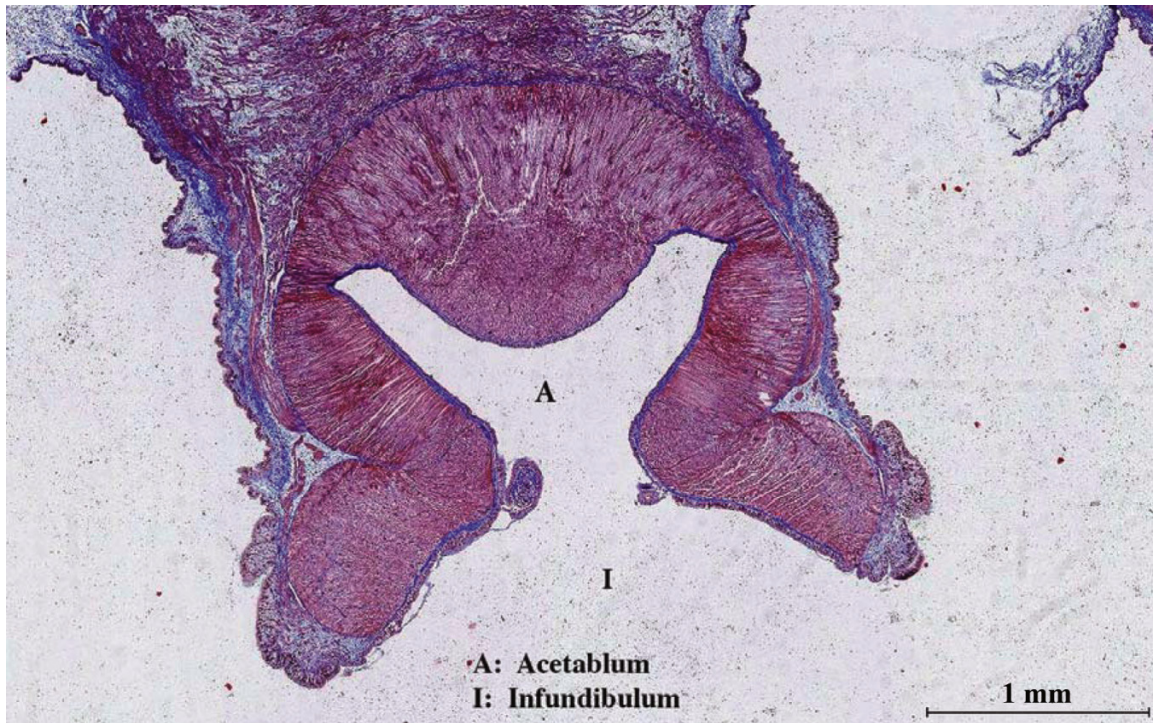
the length of the arm, and three-fifths of the octopus nervous system is not in the brain but out in the arms. Control of sucker, stalk, and arm all at once is very complex (Grasso and Basil 2009), and it has been debated how much control is peripheral and how much is central (Fig. 3). But octopus arms can perform many tasks, from bending back and grooming the body surface (Mather 1998), to snaking through an opening to explore the substrate for hidden prey (Yarnall 1969). And there are eight arms, with an interbrachial commissure at the arm bases linking them. Well-organized actions of all the arms include spreading them in a kind of parachute with the web extended over some feature of the sea bottom, then feeling underneath with arm tips to contact prey that have been captured, in the web-over (Mather 1998). Octopuses walk across the sea bottom, alternating contact mainly with the third and fourth pair of arms (Z. Faulkes, unpublished manuscript),[2] but there is no regular alternation as in the arthropods, and which pairs "walk" depends partly on the octopus' direction of movement and not its anatomical allocation. When it is advisable to mimic a ball of floating algae, an octopus can simply "tiptoe" on two posterior arms and bunch the others up beneath it (Huffard 2006).

Despite the fact that they are invertebrates, cephalopods rarely show "fixed" or modal action patterns (see Barlow 1968). This would be a relative invariant sequence of actions that did not use sensory feedback during its expression, and continues to the end even without resulting input. The predatory sequence of the cuttlefish genus *Sepia* L., 1758 is possibly a modal action pattern, proceeding from orienting and arm raising to navigation to a set distance from the prey and, finally, shooting out of the flexible tentacles to capture it (Messenger 1968). Its fixity and variability have not been investigated. However, the sand digging of sepiid and sepiolid cuttlefish may be a good example of modal action patterns. These animals blow the sand out from under them with alternating forward and backward bending of the flexible funnel

(Mather 1986), and then the sepiolids sweep a particular pair of arms across the sand surface anterolaterally to cover their dorsal surface with a thin sand layer (von Boletzky and von Boletzky 1970; Anderson et al. 2002, 2004). Mather's (1986) investigation of cuttlefish burying showed that the sequence was only relatively fixed, altered by variations in the environment such as sand depth and sequence disruption, and with coefficients of variation of 25–50, depending on the substrate. In the genus *Rossia* Owen, 1834 placed on gravel, the arm sweeps were attempted even though no gravel was picked up (Anderson et al. 2004). There were consistent differences among different sepiolid species (von Boletzky and von Boletzky 1970), reminiscent of courtship postures in ducks (see Bradbury and Vehrencamp 2011), which could possibly be used for assistance with taxonomic descriptions.

Although the arms are arranged radially, the brain of an octopus is bilaterally symmetrical, so some lateralization of movement control might be expected. Early research on learning showed that input from one eye (eyes are lateral with about a 10° overlap frontally) can be transferred fairly quickly for use with the other (Wells 1978). However, if the vertical lobe is split midline, the learning cannot be transferred. For short-term visual information processing, information is passed across the optic commissures to control movement and tracking, such as in detour experiments. In fact, octopuses also show lateralization of eye use preference when viewing monocularly, though no population choice for left or right (Byrne et al. 2002), and eye use and arm use preferences may correlate (Byrne et al. 2006a). In a reaching task, octopuses strongly prefer to use the frontal arms (Byrne et al. 2006b), but each one has a "favourite" of these four. In recruitment of a second arm to accomplish a reaching task, a principle of "neighbourliness" holds, perhaps because of nervous impulses spread around the interbrachial commissure. Our lack of information about how the brain and visual system guide the arms is shown by the fact that only recently (Gutnick et al. 2011)

[2]Z. Faulkes. 1988. Octopus walking. University of Lethbridge, Lethbridge, Alta. Unpublished manuscript.

Fig. 3. Control circuits in the octopus arm (modified from and reproduced with permission of Grasso 2013). Figure appears in colour on the Journal's Web site.
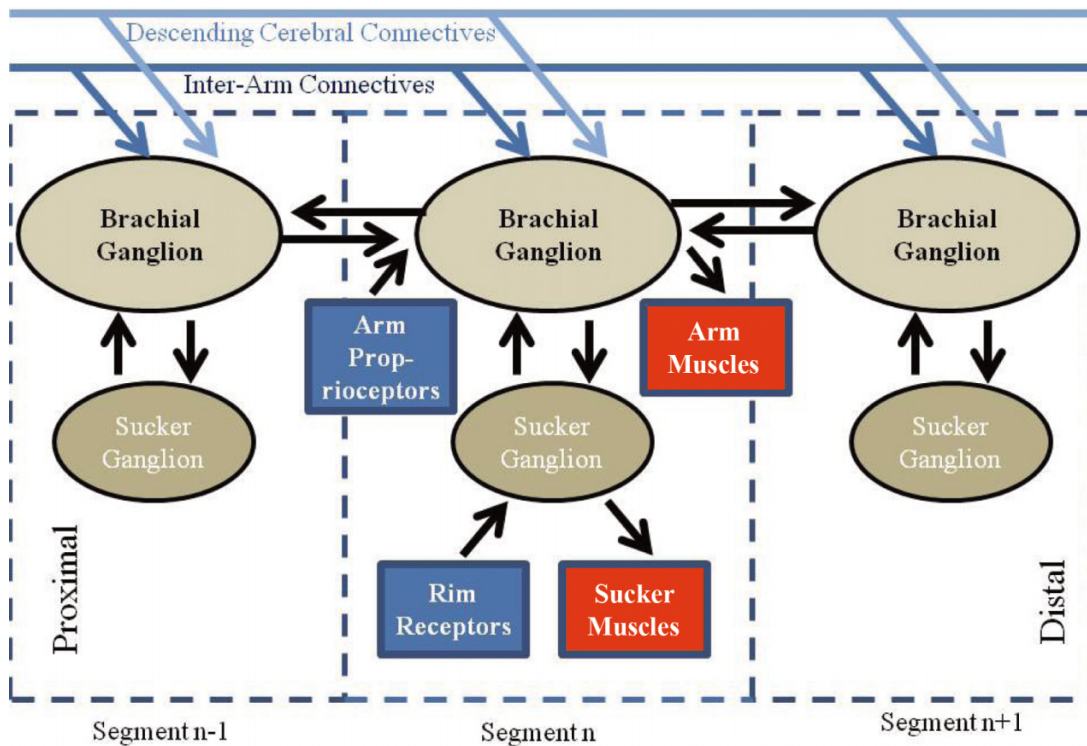
has it been proven that the octopus can complete an operant task with an arm using visual guidance.

The brain control of movements in cephalopods follows a hierarchical structure. The lower, intermediate, and higher motor centres were identified based on movements evoked by stimulation of the *Sepia* brain (Abbott et al. 1995). Lower motor centres lie in the suboesophageal lobes and send their commands directly to the motor effectors. Such centres include the fin lobe or the large motor neurons directed to the ganglia of the arms. They are controlled by the higher motor centres and also receive input from arm receptors, thus ensuring a local but limited control of the arm. Intermediate motor centres indirectly innervate the muscle effectors, the descending path passing through at least one synapse in a peripheral ganglion. These centres lie in the suboesophageal lobes and consist of large cells with axons to the arm ganglia. They also receive input from higher motor centres and arm receptors. The pedal ganglia and pallioviseceral lobe belong to this level of motor control.

The higher motor centres can evoke combined and complex, coordinated movements of several groups of muscles. They are located in the supraoesophageal brain mass and include the anterior and posterior basal lobes. The activating input to these centres comes directly from receptor analyzers and receptor organs and forms the peduncle lobe, which is called the "regulator". Higher motor centres are assumed to work hierarchically through the intermediate and lower motor centres to produce a wide variety of movements and behaviours from different body parts, like fin, arm, or mantle (Messenger 1983; Nixon and Young 2003). These paired lobes, situated on the optic tracts between the optic lobes and the central brain, might function as sites to provide visuo-motor integration and coordination. Messenger (1967a, 1967b, 1983) and Messenger and Tansey (1979) claimed that the peduncle lobes act as regulators and integrators of sensory information and motor output, analogous to the cerebellum in "lower" vertebrates (Messenger 1967a, 1967b; Nixon and Young 2003).

The suboesophageal ganglia of the brain receive information from the visual and learning areas and presumably organize complex motor output to the arms. Yet when Zullo et al. (2009) stimulated different areas of the higher motor regions, they found no evidence of somatotopic motor representation. Movements were not represented in specific spatial regions of motor areas, as they are in vertebrates. Perhaps this is true because the brain would then have to control a much larger array of cells in the eight arms. Grasso (2013) speculates that a network of local brachial modules, each centred on one of the chain of ganglia down the arms, might form patterns of activation that could be stored and remembered as a spatial arrangement. This distributed control network, he suggests, might be brain-like in the sense that it generates semi-autonomous behaviour, perhaps biased or gated by the cerebral ganglia. He reminds us that our vertebrate-centred biases may stop us from examining what must be a different control system for very complex movements.

The skin display system

Although we tend to think of motor control in terms of actions, cephalopods have another unique motor system—the most sophisticated visual skin display system in the animal kingdom. It was likely developed as a camouflage against bony fishes, which radiated explosively at about the same time as the evolution of coleoid cephalopods (Packard 1972). Although many of the details remain unclear, it is certain that visual input from the optic lobes to the lobes of the suboesophageal ganglia is the major sources for pattern formation. Animals blinded either by removing the eyes or by severing the optic tract are unable to produce regular patterns (Young 1971; Nixon and Young 2003) and patterns are muted in captivity. The colour system within the skin itself is very complex (for an excellent thorough review see Messenger 2001). There is a surface layer of yellow, red, and brown chromatophores, each of which is an elastic sac that can be pulled outward by muscles to

Fig. 4. A compendium of the major skin displays of the Caribbean reef squid (*Sepioteuthis sepioidea*) (photograph by and reproduced with permission of James Wood and Ruth Byrne).
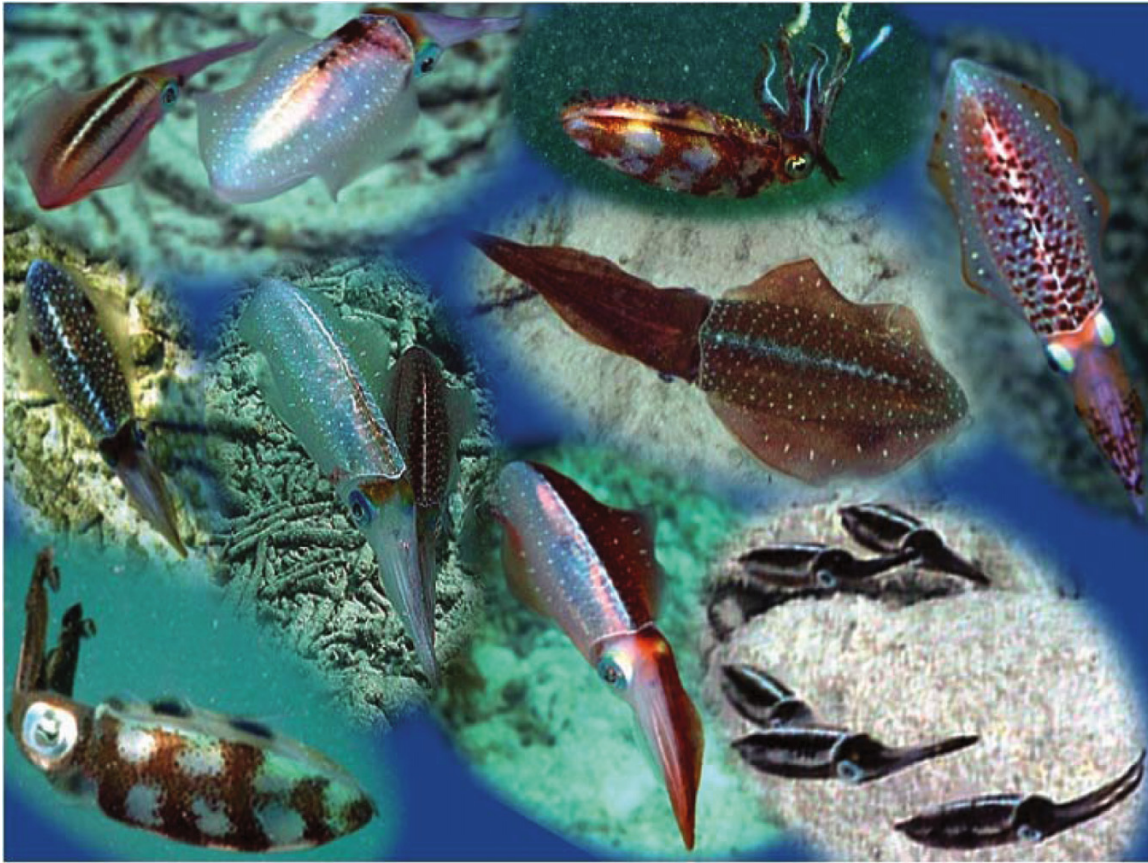
reveal its contents and all of which are under direct neural control (Fig. 4). Chromatophore density ranges from 8 to 230/mm², depending on the species, and also varies across the lifespan (Packard 1985), with pelagic paralarval stages often having few and widely spaced chromatophores. Packard (1995), who has spent a lifetime studying the arrangement and control of the chromatophoric system, noted that they were arranged in local groups and could be designated as morphological or physiological units. Morphological units, such as patches and grooves, are static, whereas physiological ones are dynamic events resulting from activation of a particular set of nerves in a specific area (Messenger 2001). These areas of projection (Froesch 1973) have been called chromatomotor fields. However, recent cluster analysis of components based on photographs revealed that the areas of common pattern projection, called "expressive fields", were not always the same as those to which the motor nerve branches projected (Leite et al. 2009). Perhaps this is because the chromatophore system is partly a self-organizing one (Packard 2001). Surprisingly, much more remains to be discovered even about the structure of this subsystem.

Below the chromatophores, and therefore revealed when the chromatophoric muscles relax and the elastic sacs contract, are reflective leucophores and iridophores (Denton and Land 1971). Iridophores are multilayer stacks of thin electron-dense platelets, made of chitin or protein (Cooper et al. 1990), usually arranged parallel to the skin, providing the blue and green components of skin colour. Although they had been assumed to be passive reflectors, Cooper et al. (1990) showed that acetylcholine hormones may change the state of the material in the platelets and result in a change in iridescence, which may be involved in signaling. The leucophores are broad-band reflectors, which may therefore make a spot on the skin. Packard and Sanders' (1971) "White spots" appear white (Cloney and Brocco 1983), but will actually reflect the predominant wavelengths in the environment and are likely important for the general colour resemblance to the background that cephalopods can use as part of camouflage (Hanlon and Messenger 1996) (Fig. 5).

Other components of body appearance are muscular. In sepioids and octopods, dermal musculature within the skin can change the apparent texture of the skin, matching the substrate from smooth to rugose. Papillation can be general on the skin surface, yet papillae are often localized; the papillae above the eyes of the North Pacific giant octopus (*Enteroctopus dofleini* (Wülker, 1910)) can be a few centimetres in height and are often called "horns". Cephalopods have no fixed skeleton and are often found in locations that stimulate them to express body postures and positions in three dimensions, such as mantle/body shape (see the octopus "ogive": Packard and Sanders 1971), body and arm position (see the cuttlefish "Flamboyant": Hanlon and Messenger 1988), and complex arm position as in the *S. sepioidea* "Crab" (Mather et al. 2010). Whole-body movement can be deliberately concealing, as when the octopus *Abdopus aculeatus* (d'Orbigny, 1834) "walks" across open areas on two of the eight arms, bunching up the others and swaying, apparently mimicking a clump of algae (Huffard 2006).

Hanlon and Messenger (1988, 1996, p. 36) describe a hierarchical model that allows us to see an ordered arrangement of components of appearance. The smallest parts are "elements", which combine to "units" of chromatophore expansion, contraction of papillae mantle and muscles. These units make up postural, locomotor, and textural "components", all of which combine to make a body pattern that in turn is a part of a "behaviour". Some pat-

Fig. 5. A bumblebee two-spot octopus (*Octopus filosus*) using background-matching camouflage (photograph by and reproduced with permission of Ruth Byrne).

terns such as the eye-spot deimatic or dymantic (Moynihan 1975), with its pale background, are expressed across the whole body, whereas other such as the octopus eyebar (Mather et al. 2009) are local; the agonistic squid zebra-striped display can vary widely in the area of skin across which it is expressed (Mather 2004). Because of the fine modulation of control by the muscles, chromatophores can expand or contract in milliseconds and across square millimetres, leading to the expertise of displays such as the Passing Cloud (Mather and Mather 2004), which moves a "shadow" across the mantle and down the arms towards potential prey.

Behind this expressive ability is neural control by the brain. Cephalopods have excellent visual acuity, though not colour vision, with neurons projecting to the large optic lobe. In cuttlefish, stimulation of the optic lobes produces display components or even body patterns (Chichery and Chanelet 1976), suggesting direct linkage to the visual input. From there, signals are sent to the lateral basal lobes, then to the chromatophore lobes whose neurons output directly to the chromatophores. Control is nevertheless at several levels and hormones are likely involved. For instance, cuttlefish have countershading, darker above and lighter below, as camouflage in two directions (Ferguson et al. 1994). When the animal is rotated 90° in the roll plane, the countershading automatically switches. The excellent bottom-matching camouflage of the common cuttlefish (*Sepia officinalis* L., 1758) (Barbosa et al. 2008) is driven by pattern recognition of the eyes, yet it is not clear how automatically the pattern is matched. But the eyespot deimatic of squid and cuttlefish is selectively produced for visual predators (Langridge 2009) and is aimed in the direction of approaching fish (Mather 2010), and see Adamo et al. (2006) for cuttlefish.

Given the complexity of the system, it is not surprising that most accounts of displays have not gone beyond repertoires. Since Packard and Sanders (1971) worked on the repertoire of *O. vulgaris*, many authors have evaluated the patterns of cephalopods from the three major orders. Notable efforts were the evaluation of many species from the Great Barrier Reef (Roper and Hochberg 1988) and the investigation of functional organization of chromatophores in the slender inshore or arrow squid (*Doryteuthis plei* (Blainville, 1823) = *Loligo plei* Blainville, 1823) (Hanlon 1982). Hanlon and Messenger (1996, Table 3.1, p. 34) gathered a list of cephalopods whose body patterns have been identified in detail before 1996. To this list should be added the octopus *Octopus insularis* Leite, Haimovici, Molina and Warnke, 2008 (Leite and Mather 2008) and the southern reef squid (*Sepioteuthis australis* Quoy and Gaimard, 1832) (Jantzen and Havenhand 2003) for their reproductive patterns. Other components of body appearance are muscular hydrostats (Allen et al. 2013). It is a major task to know all the repertoire of a single species, perhaps only possible with ethological studies over several years in the natural environment. Moynihan and Rodaniche (1982) conducted such a study of *S. sepioidea*, but they had no quantitative analyses and jumbled together patterns, postures, and textures. In contrast, in the same species, Byrne et al. (2003) developed a graphic model of the patterns in Photoshop. The best repertoire is that of *S. officinalis* by Hanlon and Messenger (1988), from which they produced their hierarchical model of elements, units, and components.

Perhaps because of this thorough background, two separate groups were able to evaluate the variation in camouflage patterns as a tool to understand the perceptual abilities of cuttlefish (Shohet et al. 2007; Barbosa et al. 2008). After all, the cuttlefish

must be able to see patterns in the substrate that it can subsequently match by a skin display pattern. The authors divided the camouflage patterns into three (uniform/stipple, mottle, and disruptive), in order of increasing contrast and unit size. They found that the choice of patterns was mainly driven by a combination of edges, contrast, unit size, intensity, and configuration of background objects. Surprisingly, even though cephalopods have only one visual photopigment and thus are colour blind, they seemed able to match colours of the background (Mäthger et al. 2009). Such subtlety of assessment suggest that the matching is by no means automatic but that cuttlefish may do some perceptual processing (2 1/2-D sketch; Marr 1982) before pattern production. Automaticity of production is not true of the eye-spot display. Langridge et al. (2007) found that the dots were expressed in the presence of a visually predatory fish but not to lesser spotted dogfish (*Scyliorhinus canicula* (L., 1758)), which hunt using chemical cues, and Langridge (2009) that they were expressed to a predator that was not a major threat but still a potential one. This selectivity was also found in *S. sepioidea* (Mather 2010), which expressed the dots directionally, often to several species of parrotfish (genus *Scarus* Forsskål, 1775). Such selectivity must have been learned over the long term and may have been cued in by tactile information about a fish's swimming pattern or by its appearance. In the case of both display groups, much remains to be learned, and a glance at the repertoire shows that most patterns of components are uninvestigated even for well-known species.

Two issues about the display system are still under debate. First, although the skin system probably evolved for camouflage, displays are commonly used, though minimally in the octopuses, for communication during reproduction. There is certainly a wide variety of them even within species (European common squid, *Loligo vulgaris* Lamarck, 1798: Hanlon et al. 1994; *S. australis*: Jantzen and Havenhand 2003). "Sneaker" male Australian giant cuttlefish (*Sepia apama* Gray, 1849) are able to mimic the appearance of a female and take a reproductive opportunity even when another "dominant" male is guarding her (Norman et al. 1999; Hall and Hanlon 2002). Moynihan (1985) suggested that the variable displays of *S. sepioidea* comprised a visual language on the skin, with major and minor components taking the place of our nouns, verbs, adjectives, and adverbs. Further systematic investigation of these patterns by Mather (2004) suggested that, as one would suspect for reproductive displays, they were relatively stereotyped and peripheral areas did not change the "meaning" of the larger central displays. There is no doubt that the display system has the ability to vary and modify the repertoire to make a language-like communication system, but Mather (2004) concluded that the squid had not done so because they had "nothing sufficiently complex to say" with it.

A more recent contention is whether octopuses, mostly Indo-East Pacific species on sand or mud habitats, have the ability to mimic the appearance of other distasteful species. A collection of short observations with little data suggested that octopuses "looked like" flounders when they swam with arms pressed together along the horizontal plane, and that they were mimicking a sea snake when they had two arms outstretched laterally and banded in black and white. Such resemblance was thought to include particular postures and actions, but there was no proof of predatory receivers to whom the display were directed or even that the models were present in the same environment as the octopuses. Apparent flounder mimicry in the Atlantic longarm octopus (*Macrotritopus defilippi* (Véranyi, 1851)) was documented by Hanlon et al. (2010), with analysis of swimming duration, speed, style, posture, and colouration. Although the behaviours of octopus and flounder were similar, this "flounder-like" swimming was also found in a laboratory-reared octopus, suggesting that the behaviour was not learned. As flounders are not distasteful, there also seems no obvious benefit to an octopus that is mimicking one. Probably octopuses have evolved camouflage ability that allows them to match many features of their environment, and other animals are sometimes such a feature. But at what level is such mimicry controlled, whether octopuses are adaptively copying only features of distasteful species, and if visual fish predators are repelled by the mimic have yet to be investigated.

Predation

Cephalopods are predators, and they are physically well equipped to catch and consume mobile prey. The many arms are lined with adhesive suckers (see the section on Movement) in the incirrate octopods, cuttlefish, and squid, and the latter two groups also have the very extensible pair of tentacles (Kier and Schachat 2008). Many of these suckers are lined with papillae or hooks so that adhesion to a captured prey is more certain (for a description of the variety of suckers see Nixon and Dilly 1977). In addition, the web between the arms is expandable in octopuses so that arms and web can form a flexible parachute-like structure (Yarnall 1969) to trap prey. Cephalopods have both a paralytic cephalotoxin in the posterior salivary gland and a digestive one in the anterior that can begin to dissolve structures such as tendons which articulate between joints of crustaceans (Nixon 1987). The buccal mass at the base of the many arms contains a chitinous parrot-like pair of beaks, the molluscan rasping radula, and a hole-drilling salivary papilla that produces chemicals that break down calcium-based skeletons (Nixon 1980) (for the musculature controlling this structure see Uyeno and Kier 2007). The result of such structural diversity is flexibility in, for instance, octopuses gaining access to bivalves. They can pull on the valves, drill a hole to inject the toxin, or chip at the edges of the valve to again to give entry to a toxin (Anderson and Mather 2007), although pulling is probably the primary strategy (Steer and Semmens 2003).

Although it has seldom been experimentally proven, vision is the primary sense that guides the predation of squid and cuttlefish (for the cuttlefish attack see Messenger 1968) and is the first-stage guidance for octopuses (Mather 1991*a*). In the deep ocean, vision may become increasingly sensitive to match the decreased light intensity, or increasingly acute to pick up the bioluminescence that is very common in deep-sea organisms (Zylinski and Johnsen 2013). Where vision is ineffective, chemotactile senses are much more important and the cirri rather than suckers and the balloon-like spread web may be vital for sensing. Although octopuses use vision to navigate around their home range, contact with hidden prey is chemotactile, with one or several arms extended into holes or crevices to make contact with prey (Yarnall 1969; Mather 1991*a*; Leite et al. 2009). Different capture strategies may be necessary for different prey sizes (northern shortfin squid, *Illex illecebrosus* (LeSueur, 1821): Foyle and O'Dor 1987) or different species (cuttlefish: Duval et al. 1984). Yet, as befits a group heavily dependent on learning, there is a variety of cephalopod strategies to gain access to prey, as discussed by Hanlon and Messenger (1996).

Predatory tactics are often divided into ambush and cruise searching, although animals seldom use only one of these tactics; rather saltatory or stop-and-go search (O'Brien et al. 1990) is common, at least in octopuses. Cephalopods often ambush prey as they rest buried in sand (sepiolids: Messenger 1968; von Boletzky and von Boletzky 1970) or hiding in their homes (octopuses: Mather 1991*a*). It is difficult to know whether this is a genuine predatory strategy or a casual capture as a result of a chance encounter. Many cephalopods actively search for, chase, and capture prey, especially squid foraging on fish (Foyle and O'Dor 1987) and cuttlefish (Messenger 1968). But prey rarely is in easy view, so a variety of strategies helps the cephalopods to encounter them. The octopus web-over allows it to perform a speculative capture of unseen but trapped prey (Yarnall 1969; Mather 1998; Forsythe and Hanlon 1997; Leite et al. 2009). In addition, if a crustacean has evaded capture by such an action, a big blue octopus (*Octopus*

Fig. 6. Scavenging fish accompanying a foraging *Octopus insularis* (photograph by and reproduced with permission of Tatiana Leite).


cyanea Gray, 1849) can send a dark "Passing Cloud" colour pattern anterior-wards towards the prey to startle it (Mather and Mather 2004). Cephalopods can find prey by manipulating the environment, as cuttlefish and octopuses may move sand around with arms or jets of water from the funnel to capture hidden crustacean or bivalve prey (Hanlon and Messenger 1996). There are casual reports of cephalopods "luring" prey by imitating edible species with part of their body. This has been suggested for arm waving by cuttlefish (Messenger 1968) and *S. sepioidea* (Moynihan and Rodaniche 1982) and especially for buried *Rossia* sepiolids that extend, pale, and wave a tentacle tip above the sand (Anderson et al. 2004). *Sepioteuthis sepioidea* may follow a fish that is foraging on the coral rubble surface, presumably hoping to catch prey that have escaped from capture attempts; this was observed by the first author as squid followed sharptail eels (*Myrichthys breviceps* (Richardson, 1848)) (J.A. Mather, personal observation). This is an interesting turnaround, as scavenging fish follow hunting *O. vulgaris* in Bermuda and at many other locations (Mather 1992) for the same opportunity (Fig. 6). Our information about the predatory tactics used by cephalopods is most likely limited by our chance to observe them, as the wide variety of opportunistic strategies is obvious, and casual observation is often our only source of information about some tactics.

Classical foraging theory (Stephens and Krebs 1986) assumed that animals' prey choices were driven by the trade-off between energy expenditure during prey location and capture and energy gain from the food consumed. But in what Moynihan and Rodaniche (1982) called the "difficult and dangerous" marine environment, such a simplistic approach does not show the whole picture, and Mather et al. (2013) discusses octopod foraging under the threat of predation. Stephens et al. (2007) have a book that updates and addresses this complexity and takes learning, conspe-

cific influences, and the threat of predation into consideration. It is on this background that evaluation of the food choices of octopuses, often assumed to be generalist predators catching whatever prey they encountered, needs to be assessed.

It is relatively easy to evaluate the prey choices of octopuses, because they leave the skeletal remains of prey as discards outside their sheltering homes (e.g., Ambrose 1984; Mather 1991a; Vincent et al. 1998; Leite et al. 2009). Although these are biased particularly if sampling is infrequent, as prey remains are buried, swept away, or eaten by scavenging fish (Mather 1991a), a reasonable sample is possible with frequent sampling or taking evidence only from prey with octopod drill holes (Hartwick et al. 1978). Octopuses take prey of many species; an extreme example is *O. vulgaris* in a small shoreline stretch of Bonaire that discarded the remains of 75 prey species (Anderson et al. 2008). A simple listing is inadequate, however, as most populations show diet specialization on one or a few species (Ambrose 1984; Vincent et al. 1998; Leite et al. 2009; Mather 2011a; Scheel and Anderson 2012). Ambrose (1984) showed convincingly that prey choice of *O. bimaculatus* was based on a balance of laboratory preference (for crustaceans) and availability in the field (snails of the genus *Tegula* Lesson, 1832), resulting in 37% of the diet being of an only moderately preferred guilded turban snails (*Tegula aureotincta* (Forbes, 1850)). Similarly, *E. dofleini* in Alaska consumed most crustaceans but avoided the fairly common hairy crab (*Hapalogaster mertensii* Brandt, 1850) (Vincent et al. 1998). As well, although chitons formed the majority of live suitable prey in the area, they were seldom consumed (Scheel et al. 2007). Although chitons have a formidable grip on rocky surfaces with their muscular foot, *O. vulgaris* in Bermuda could drill through one of their dorsal shell valves to weaken the muscles by poison (J.A. Mather, personal observation).

Fig. 7. A flow chart of the foraging strategies of octopuses (from and reproduced with permission of Mather et al. 2013). Figure appears in colour on the Journal's Web site.
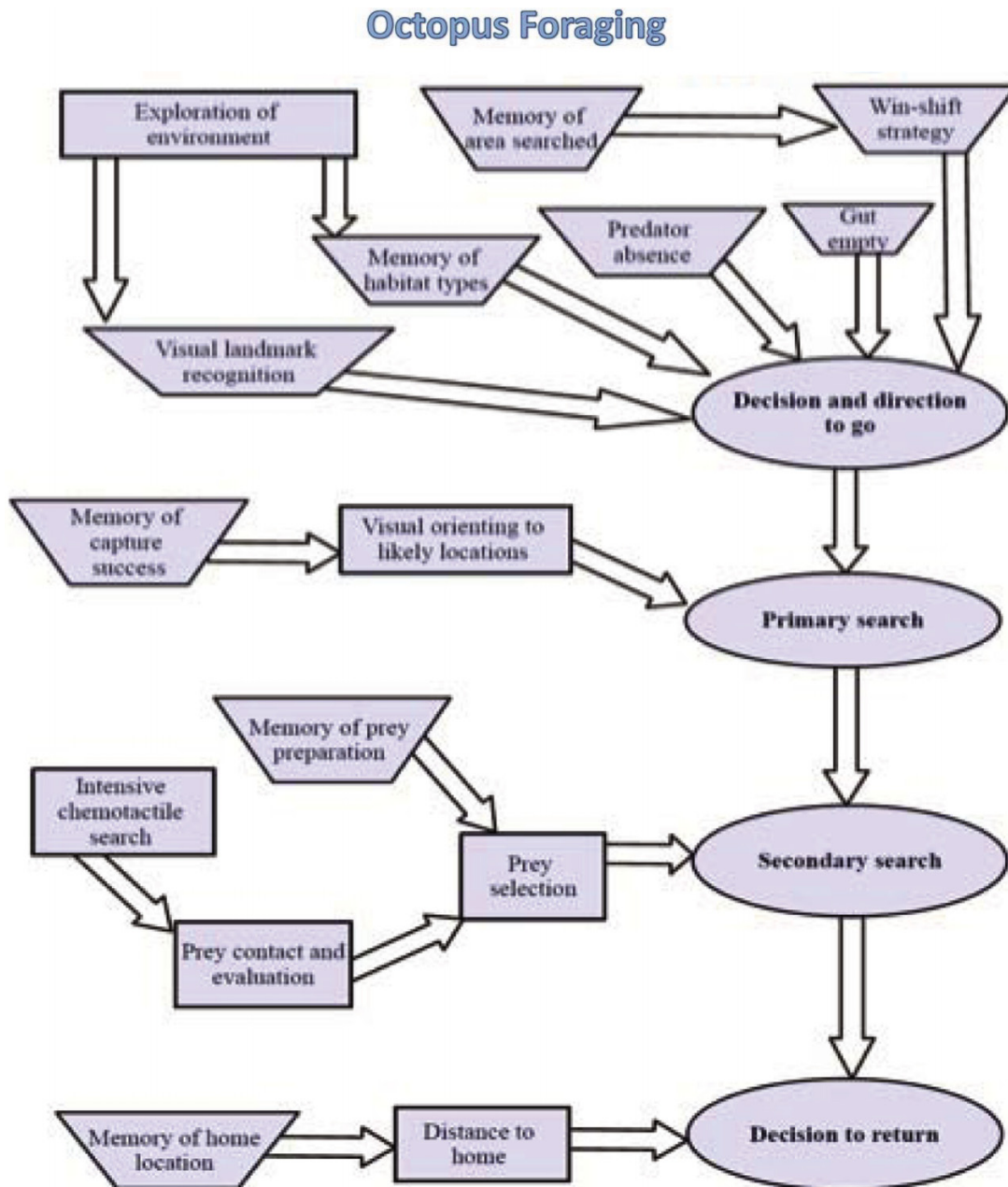

Such preference might also be based on the difficulty of handling and penetrating prey, as *E. dofleini* made different prey choices of bivalves when they were live and closed up, versus open and "on the half shell" (Anderson and Mather 2007). Octopuses might be rate maximizing foragers (Scheel et al. 2007; Scheel and Anderson 2012), as they preferred larger individuals within a prey species and larger species of prey. Alternately, given that they foraged under risk of predation (Mather et al. 2013), octopuses could be time minimizing so that exposure to predators was limited (Leite et al. 2009) (Figs. 7, 8). The combination of large numbers of prey species and numerical selectivity for a few species might also be explained if octopuses foraged selectively in particular areas (Mather 1991a) where preferred prey were located (fragile-shelled bivalves of the genus *Lima* Bruguière, 1797 in Bermuda), and yet took prey such as fish (Leite et al. 2009) that were contacted in chance encounters. Also, the well-known octopod

preference for crustaceans (see Mather 2011a) might occur because of a need for particular nutritional components (Rigby and Sakurai 2005; Onthank and Cowles 2011). The situation is clearly complex.

One of the directions that the study of foraging of octopuses is moving towards is evaluating the individual. This is logical because evolutionary pressures act on the individual, but invertebrates have generally been studied as invariant units of the population or the species. The study of animal personalities (Gosling 2001) has burgeoned over the last decade (see Carere and Maestripieri 2013), and this book includes a section on individual differences in invertebrates (Mather and Logue 2013). A recent set of papers in *Current Zoology* (Mather and Carere 2012) highlights some of our knowledge of personalities in invertebrates. Individual differences in behaviour are also evaluated from an ecological perspective as behavioural syndromes, looking at the trade-offs

Fig. 8. A diagram of strategies used when octopuses forage under the risk of predation (from and reproduced with permission of Mather et al. 2013). Figure appears in colour on the Journal's Web site.

Octopus Foraging Under Predation
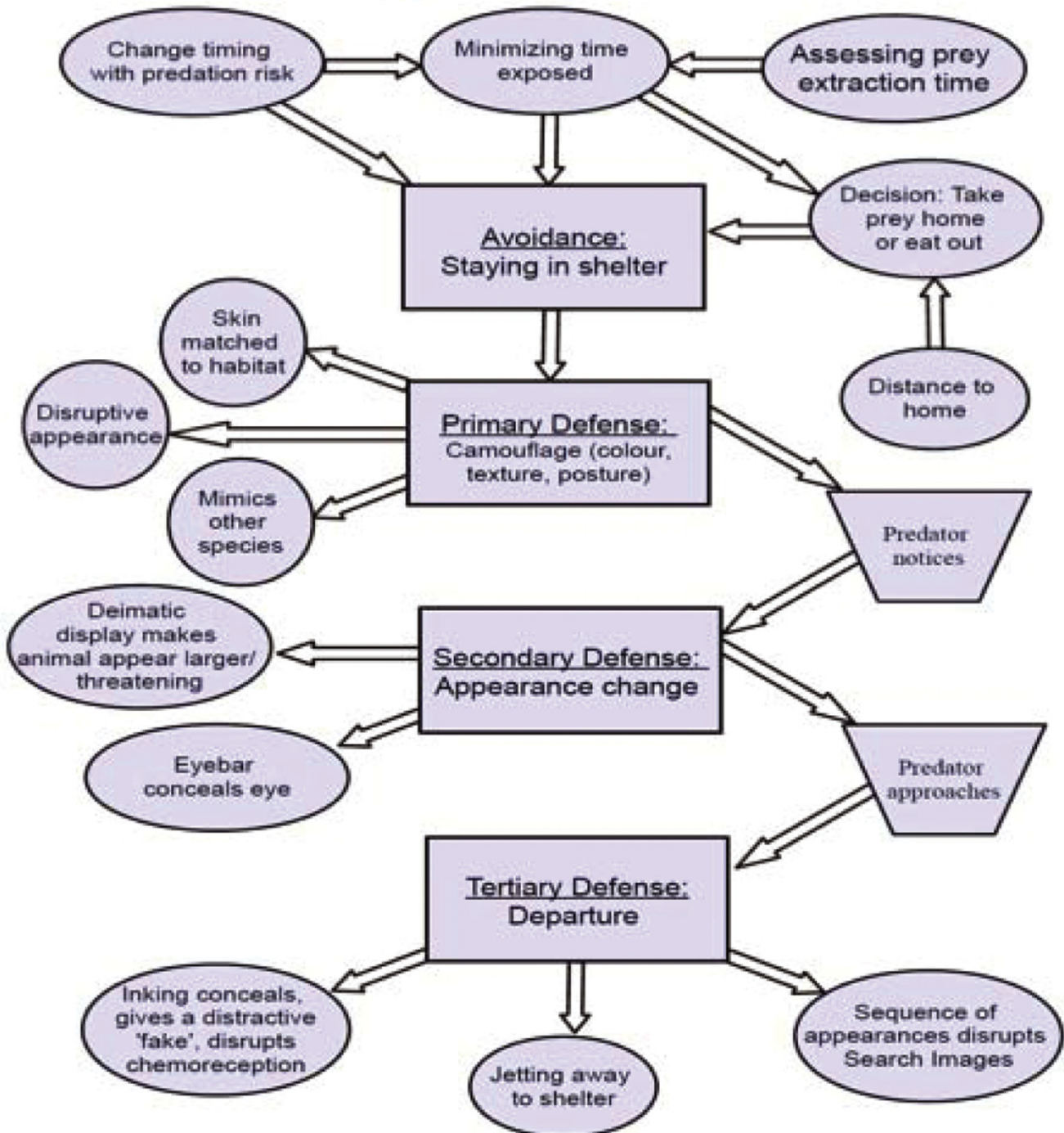
between gains in one situation or at a part of the lifespan versus losses at another (Sih et al. 2004). Mather and Anderson (1993) were the first to evaluate personality differences in octopuses, and Sinn et al. (2001) found individual differences in the developmental trajectory of young octopuses. D. Sinn took the study of individual differences to a small and short-lived southern bobtail squid (*Euprymna tasmanica* (Pfeffer, 1884)) and was able to look at heritability, population difference in, and ecological effects of

difference along the shy–bold continuum (for the latest of the series of four papers see Sinn et al. 2010).

The investigation of individual differences in prey choice of octopuses began with a study of the population of *O. vulgaris* in Bonaire (Anderson et al. 2008), which used Cardona's niche breadth index to show that the population was generalist but the individuals were often specialist. Investigation of individual differences across octopus species (Mather et al. 2012) and across

population of one species, *E. dofleini* (Scheel and Anderson 2012), showed that this variation is pervasive. Individual selectivity for particular prey species can be general, as for crabs by *O. cyanea* in Hawaii (Mather 2011a), or widely varied, as *E. dofleini* in Puget Sound specialize on different crab or clam species (Scheel and Anderson 2012). Such specialization by individuals might be because of microhabitat selection (though the Bonaire and Bermuda *O. vulgaris* were from very localized populations), given that octopuses are heavily dependent on learning. Still, Carere and Locurto (2011) suggest that animal personalities might influence learning, and this intervening step might be the result of exploration, leading to exploitation of a particular supply of a prey species. Such an assumption needs to be tested.

A separate topic, developmental acquisition of information about and decisions around prey choice, is difficult to study because most cephalopods have a paralarval stage of weeks to months, when they live in the open ocean, a different habitat than the benthic or nektonic one of octopuses and cuttlefish. They are very small and only morphological similar to adults (Villanueva et al. 1995), and are difficult to study in this habitat. One exception to the presence of this early paralarval stage is the cuttlefish *Sepia*, which hatches from the egg as a miniature adult (von Boletzky 1983; Guerra 2006) and hunts using the same visual cues as adults. The study of development of reaction to prey in *S. officinalis* has been an important area for our understanding of the development of learning strategies (Darmaillacq et al. 2013).

Earlier research (Wells 1962) demonstrated that naïve newly hatched cuttlefish had a strong preference for linear figures extending vertically, which resemble the crustacean genus *Mysis* Latreille, 1802 that they often choose as prey. It appeared difficult for them to learn not to attack such a visual figure (enclosed in a glass test tube). Particularly in the first month of life, cuttlefish had short-term but not long-term memory (Messenger 1971; also see Dickel et al. 1997). This innate preference of naïve animals was confirmed more widely by Darmaillacq et al. (2004), who found a strong preference for shrimp over crabs and fish. Such development of learning capacity parallels the development of the vertical lobe (Messenger 1973), which stores information about visual choices in octopuses (Wells 1978), and this was suggested long ago by Wirz (1954). The process is similar to that of mammals, which have a set of early reflexes that give way to later learned responses as the cortex develops (Cole et al. 2005), and see also prey choice of newly hatched turtles (Burghardt 1967).

However, these hatchlings were naïve and probably brought into the laboratory as eggs and given little experience with a normal environment. Newly hatched and even pre-hatchling cuttlefish learn about prey, and this learning shapes their later preferences (Darmaillacq et al. 2013). First, cuttlefish offered only crabs shortly after hatching preferred the same species at 7 days (Darmaillacq et al. 2004), and the length and intensity of exposure during this sensitive period predicted the efficiency of this familiarization. Again this parallels the process of imprinting—early, persistent quick, and generalizable learning that is fixated on future sexual partners in vertebrates. Such preferences can be fine-tuned; naïve hatchlings prefer black crabs over white ones, but change this preference if they are exposed only to white crabs (Guibé et al. 2012). It is not only preferences that are learned, as juvenile and adult cuttlefish catch crabs by a "jumping" strategy rather than tentacle ejection; newly-hatched cuttlefish use tentacle ejection often and only gradually switch to the more effective arm-grasping strategy (L. Dickel, unpublished doctoral thesis).[3]

Surprisingly, this early learning is possible even before hatching, as the crab–prey preference learning can be induced in the week before the cuttlefish hatch (Darmaillacq et al. 2008). Even though ink that is included in the egg capsule, probably as protection, must decrease visual acuity, pre-hatching "embryos" for which the capsule has swelled and is less opaque can still discriminate general shapes. As well, it is becoming apparent that cuttlefish have brain lateralization, as demonstrated in a side-turning preference in a T-maze (Alves et al. 2007) that appears to depend on visual lateralization, as in octopuses (Byrne et al. 2002). Hatchlings have already established this lateralization, as they learn to prefer crabs that are viewed with the right eye (Darmaillacq et al. 2013). As exposure also speeds development of antipredator behaviour (Poirier et al. 2004, 2005), it appears that rather than being driven by fixed reflexes, hatchling cuttlefish are a fine-tuned learning machine with innate preferences which can be altered by exposure to different microhabitats.

Cognition

In July of 2012, a group of scientists from a wide range of areas concerned with consciousness signed the Cambridge Declaration on Consciousness, which declared that nonhuman animals, including mammals, birds, and even octopuses, had the neural substrate to generate consciousness. Words like consciousness, as well as cognition, mind, and intelligence, are not usually used to refer to invertebrates. But in the case of cephalopods, they should be. Studies of learning are often, by necessity, limited in the environmental variables they test and prone to simplistic conclusions, but research on cephalopod behaviour has begun to look past the straightforward laboratory tests and study cephalopods in more complex situations. Thus, the octopus solving the problem of how to get at the clam inside the shell (Anderson and Mather 2007), the cuttlefish male disguising himself as a female so he can sneak a copulation with a guarded female (Norman et al. 1999; Hall and Hanlon 2002), and the octopus carrying around a coconut shell to act as a shelter when it pauses in its hunting and needs a place to hide (Finn et al. 2009) are all examples of complex behaviour, problem solving, and planning. These are in contrast to the automaticity and stereotyped behaviour that we expect from invertebrates.

Neisser (1967), talking about humans, described cognition as "all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered and used" and Shettleworth (2010) produced a similar definition for animals as "the mechanisms by which animal acquire, process, store and act on information from the environment". She also mentions that we should not be concerned with first-order processes (operating on direct perceptual input, as cuttlefish camouflage might do) when we investigate cognition. Instead, we need to evaluate second-order processes, operating on first-order processes, as when octopuses (Mather 1991b) and many other animals, successfully take a detour home after displacement from their outbound foraging path. The term "mind" suggests a self-organizing system that inputs information and then organizes it to be used in the appropriate time at the appropriate location and in the appropriate circumstance. This is a light world away from the fixed behaviours, automatically released and continuing without feedback, that we describe for reflexes, and the cephalopods are not only learning specialists but show little of this behavioural fixity (Mather 1998).

Why would cephalopods have evolved this flexibility and thoughtfulness? Packard (1972) pointed out that the coleoids had evolved in the Jurassic period, at the same time that bony fishes were undergoing an explosive radiation. These fishes, which still dominate the world's oceans and have complex behaviour themselves (Brown et al. 2011), act as cephalopod animals' prey, predators, and even scavengers (Mather 1992). Richardson (2010) suggests that animals developed cognitive ability when other an-

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[3]L. Dickel. 1997. Comportement predeteur et mémoire chez la seiche (*Sepia officinalis*), approches développementale et neuro-éthologique. Université de Caen, Caen, France. Unpublished doctoral thesis.

imals became significant. He sees the animal as needing the ability to integrate complex fleeting information into an internal image of the object, then use this to predict the behaviour of the object and produce useful responses to it. Cephalopods abandoned the protective shell, sped up the molluscan metabolic efficiency, adopted fast locomotion, and condensed a centralized brain to control these calculations. Godfrey-Smith (2002) suggests that a demanding environment will produce pressure for cognitive development and Mather et al. (2013) points out that cephalopods evolved in the most complex and demanding nearshore oceanic environment. It is challenging both in terms of finding prey and in terms of avoiding predation, and see Moynihan and Rodaniche's (1982) comment about "a difficult and dangerous environment".

Despite this, and probably because of both the behaviourist view of animals as automata and our lack of understanding of the complexity of animals' behaviour (Shettleworth 2010), the scope and complexity of animals' behaviour was not understood. But now we know about tool-using crows, deceiving monkeys, dogs' understanding of humans' gestures, and bees' dance language (Shettleworth 2010). Much of our information in these areas has come from naturalistic observation of animals in their normal environment. Scientists are also activated by Griffin's (1976) contention that animals have awareness. He contended that they have conscious intentions, beliefs, and self-awareness, and they think about alternatives and make plans. Although the mental lives of animals (and often humans) is difficult to perceive and often nearly impossible to prove, the assumption has stimulated much research. With their formidable learning ability, octopuses have been poised to join the group of "thinking" animals.

Although early research on the brain–behaviour relationships of octopuses revealed their simple ability to perceive and learn and also the brain areas that seemed to control storage of information (Wells 1978), one set of investigations revealed the octopuses' complex ability. Octopuses have an eye that is very similar to that of mammals, with good visual acuity, and a sophisticated visual processing system in the optic lobes. Sutherland (1960) hoped to use the task of visual form recognition to understand how a "simple" animal was processing characteristics of the visual world (people have been underestimating the octopus for a long time). He first found that octopuses were better at discriminating vertically oriented figures from horizontally oriented ones than obliques, a competence which is also true for mammals. But he went on to train them to discriminate a circle from a square, a W-shaped figure from a V-shaped one, a large figure from a smaller one, and even a reduplicated pattern of internal dark and light bars (Sutherland et al. 1963). They were not discriminating patterns by any simple rule, instead Muntz (1970) concluded that the octopuses were encoding the important discrimination, or learning what to learn. Given two relevant cues, they learned the discrimination more quickly than with one (Messenger and Sanders 1972) and transfer tests showed that some octopuses used one and some the other. Octopuses given a discrimination that was too fine to be immediately perceived could nevertheless be trained to discriminate it (Sutherland et al. 1965). But so can bees (Zhang and Srinivasan 1994). What became clear is that if a concept is defined as an internal category of information which is activated by an external instance, the octopuses were forming concepts about rewarded and unrewarded shapes and using them to solve discrimination problems.

One problem with testing octopuses' cognitive abilities by the paradigm of presenting them with paired visual stimuli and rewarding a choice of one and generating a shock with the other (Wells 1978) is the ecological validity of the task. As discussed in the section on foraging, prey species do not "fall out of the sky", rather cephalopods have a number of strategies to locate prey that is usually in hiding (see the discussion by Hanlon and Messenger 1996), and octopuses in particular do not rely on visual cues to recognize prey (Yarnall 1969; Mather 1991a). It is a tribute to the octopod visual capacity that they are able to perform these tasks, but chemotactile exploration (see the discussion of arms) is a more likely immediate prey-finding tactic. Given this separation, for what tasks could the visual system have evolved? One possibility is the ecologically valid one of navigation.

For any mobile animal, goal-directed movement in space is vital, and this has been studied in species from several phyla. Shettleworth (2010) has an extensive discussion of mechanism of spatial cognition, though she does not mention the cephalopods. And a summary discussion of a group in the Strungmann Forum (Wiener et al. 2011) suggests that mobile animals have a "Navigation Toolbox". Such a toolbox could consist of simple and relatively automatic sensory and motor processes. But built upon this level could be higher order spatial primitives, aspects of the environment such as optic flow, landmarks, and velocity that can be processed to gain information about one's location changes. A third level is spatial constructs, made up of representations constructed from the primitives and giving, for instance, position in space or a representation of an area sometimes called a cognitive map—and see Shettleworth's (2010) discussion of this term. Cephalopods are startlingly mobile, sometimes over long distances (see Alves-Jozet et al. 2013), and the research on their movement in space suggest different species are using different levels of this "toolbox".

Simple responses may establish adaptive actions, particularly in the early life stages. Dispersion of paralarvae is partially accomplished at hatching by positive phototaxis, leading newly hatched young up towards the water surface, and by negative phototaxis (as well as relative size), causing paralarvae to sink to the bottom of the sea for settlement (Villanueva and Norman 2008). In the planktonic phase, the presence of prey may increase the turning rate of paralarvae, causing them to stay near prey in a patchy environment (Villanueva et al. 1996). Information about long-distance migration is often acquired from fisheries data (Semmens et al. 2007) and suggests some similar mechanisms. Many species, especially open-ocean squid, migrate daily vertically (Villanueva 2009) in the daytime-down, nighttime-up pattern, probably triggered by light levels and sometimes attracted by the location of prey, although there are actually several movement patterns (Hanlon and Messenger 1996). Nearshore octopuses may move offshore as adults, perhaps to mate or returning to the near shore for this activity. Other cephalopods make once in a lifetime migrations, sometimes to a location for mating and spawning (Hall and Hanlon 2002). *Illex illecebrosus* has a complex life cycle, with hatching in the eastern Caribbean, movement northwards with the assistance of the Gulf Stream, a juvenile stage off the Grand Banks and movement towards the mid-ocean at adulthood, and transport of egg masses towards the Caribbean again by the Labrador current (O'Dor and Dawe 1998).

Not surprisingly, the shorter distance movements of shallow-water octopods are better examined and understood (Alves et al. 2008). Many octopus species (Mather 1991b) and even some sepioids traced by radio telemetry (Aitken et al. 2005) return to a sheltering home (Mather 1994) after foraging within a limited home range (and see the section on Foraging). The mechanism by which they return to the home may use several of the levels of the navigational toolbox. Many gastropod mollusks, for instance, use trail following to return to a scar on the rock to which their shell margins are fitted, a device for conservation of moisture and discouragement of predators. In their foraging, they lay down a mucus trail that can be sensed on the return journey (Cook et al. 1969) and that may be directional, an additional cue for return (Cook and Cook 1975). Mather (1991b) for *O. vulgaris* and, to a lesser extent, Forsythe and Hanlon (1997) for *O. cyanea* found that octopuses foraging in the shallows near shore did not use such a simple sensory strategy for accomplishing their return.

The *O. vulgaris* trail overlap was only 32%, and the majority of the returns were made by direct jet propulsion, sometimes from a distance of over 6 m. Such returns suggest guidance by visual cues such as landmarks and memory of cues gathered during the outward trip or on other hunts (Mather 1991b), a second-level use of information about physical aspects of the environment. In the laboratory, octopuses could learn to orient to a beacon (a single landmark), for a food reward, and could re-orient when the landmark was moved. With several cues, they appeared to orient to the larger one first and the small one second. This suggests that the octopus was building up a representation of different aspects of the spatial layout, which might be considered a simple cognitive map and is representative of Wiener et al.'s (2011) third level (and note the small *n* in this study; it should be repeated). The suggestion of a constructed representation is supported by two more observations from Mather's (1991b) fieldwork. First, she documented 11 displacements of hunting octopuses, and they either jetted directly to their home or followed obvious or previously used landmarks to their home.

But a second set of observation that suggests they not only had a representation of the space around them but also of their use of it (working memory) came when she documented the areas in which octopuses hunted over several days (Mather 1991a). Given that they had headed out in one direction on day 1, they hunted on another in day 2, and so on presumably because prey would not be replaced after capture and win-switch foraging would be an adaptive pattern. Thus, they knew not only where home was but where they were in relation to it and where they had been in days past (this intensive continuous tracking would not have been possible without the assistance of volunteers from Earthwatch). This certainly suggests some kind of mapping of the spatial array in which they moved, though note Shettleworth's (2010) discussion of what such a map might mean. Interesting enough, the brain areas underlying navigation still seem to be poorly understood.

Graindorge et al. (2006) investigated the effects of vertical lobe lesions on the performance of cuttlefish in a navigation task. Lesions in different parts of the vertical lobe resulted in different behavioural alterations. If the lesions were applied to the dorsal part of the vertical lobe system, the only significant difference from control animals was an elevated general activity in an open-field test. The reason for this might be that the vertical lobe is thought to be involved in inhibitory learning (Sanders 1975) and therefore a lesion might result in the loss of a central off switch otherwise regulating locomotor activity. Interestingly, these behavioural alterations were caused by very small (only 3%–5%) removal of the tissue of the vertical lobe. Also, the authors showed that the vertical lobe system has a direct involvement in motor control. A second group of animals that had lesions applied to the ventral part of the vertical lobe showed a significantly reduced long-term retention of a learned navigation task. The problem with this finding—as the authors point out—is that the lesions might also have damaged the tracts that run between the frontal lobe and the vertical lobe system.

Field observations are just that, not controlled and idiosyncratic. What of laboratory studies of orientation? Initially, Wells (1964) found that octopuses could not detour around an opaque partition to catch a crab viewed through a glass window, and assumed they did not have a spatial representation. However, the window could have been an unnatural stimulus situation (and see use of mirrors), and he later showed that octopuses which maintained a fixed orientation to the wall could follow it. We know now that this limitation is logical, as octopuses have functionally monocular vision (Byrne et al. 2002). In a methodological study that was not followed up, Walker et al. (1970) showed octopuses could be trained to make choices on a T-maze, though they did not use a proper control to exclude landmark navigation because they did not isolate the experimental arena from the outside. Boal et al. (2000) used the same task, escape into a burrow when the water

level was lowered, to prove that *O. bimaculoides* could make similar choices. She and her colleagues extended this competence to *S. officinalis* (Karson et al. 2003) and subsequently showed this species could solve two different maze problems when the trials were intermixed. Different orientation strategies were revealed, as immature cuttlefish and mature females preferred a motor sequence learning strategy (Alves et al. 2007), while mature males were guided by visual cues. Males also moved more in an open-field area, and these observations mimic those of some mammals that show a sex difference in both spatial memory and exploration, correlated with habitat use (Jones et al. 2003).

In the era of operant and classical conditioning, research was tightly focused on what animals could learn when a particular situation was narrowly presented to them. But to build maps of their environment, animals must explore (Gallistel 1993). Although exploration is difficult to document in the laboratory (Renner 1990), octopuses used manipulative exploration and even play behaviour (Mather and Anderson 1999; Kuba et al. 2006a, 2006b, 2006c). For a different kind of exploration, that of space, Boal et al. (2000) recorded octopuses' activity in a novel environment and watched it decrease over 3 days (this is casually observed by many octopus keepers). Animals subsequently used information gained by this exploration to find burrows when the water level was lower, so they did indeed learn about their environment during exploration. Thus, it is obvious that cephalopods have the capacity to construct a map of their environment and use it for subsequent action, although the observations are piecemeal and more testing is needed to establish the processes by which this learning is carried out.

In this account, little has been said so far about the social lives of cephalopods and that is because there is not much to recount (Boal 2006). There is no generational overlap, as squid and sepioids die after mating and female octopuses die after tending their eggs. Most cephalopods are actively cannibalistic (Ibáñez and Keyl 2010). As the sexes are permanently separate, mechanisms for gathering for reproduction, finding and identifying a mate, and ensuring fertilization are vital, but for the most part seem to be fairly simplistic and, in addition, are poorly known. More complex reproductive tactics are found in some cuttlefish (Norman et al. 1999; Hall and Hanlon 2002), squid (Jantzen and Havenhand 2003), and in the octopus *A. aculeatus* (Huffard et al. 2008), but for now these appear to be the exceptions.

This lack of sociality is important to cephalopod cognition. The social intelligence hypothesis, originally fabricated for primates (Jolly 1966) but more recently extended to other group-living mammals and birds (Emery et al. 2007), suggested that it was the understanding and prediction of conspecifics' behaviour for which complex intelligence developed. In practice, this has led to an extensive set of studies of animal deception as a way to prove that they have a "theory of mind" and that they "know what a conspecific is thinking". Such deception seems possible in food caching by birds (Clayton et al. 2007) and food hiding in chimpanzees (Hare et al. 2000). There is considerable debate, both theoretically over whether social complexity requires cognitive complexity (Barrett et al. 2007) and practically as to how to measure it (Lurz 2011). But with minimal sociality, cephalopods' cognition must have evolved as a result of different, nonsocial pressures. To be fair, a foraging theory of evolution of brain size has been advanced for monkeys (see Shettleworth 2010), but its reach is limited and it does not take into consideration the complex predator-rich environment that cephalopods face (Mather et al. 2013).

If foraging in the face of predatory threat is the pressure that might lead cephalopod intelligence to evolve, what might be the important stimuli and how might cephalopods "read" them? The setting in which we study their behaviour is rarely sufficiently complex. A field study of *S. sepioidea* by Mather (2010) gave some clues as to how cephalopods might evaluate predator behaviour

and prepare responses. Squid, in the near shore and vulnerable to attack from all directions, were understandably "jumpy", with eight moves of more than a metre from their resting position per hour (a mode of 2 m). They responded to approaches of over 30 fish species, although the most common ones were the herbivorous parrotfish and predatory bar jack (*Caranx ruber* (Bloch, 1793)) and yellowtail snapper (*Ocyurus chrysurus* (Bloch, 1791)). But responses to these species were quite different. Squid moved away more to faster-approaching snapper and parrotfish, and allowed parrotfish to come much closer, under a metre away for an approximately 300 cm long squid. Different cues elicited different responses within and across species, only the parrotfish and the bar jack eliciting the zebra or deimatic dots skin displays (Mather 2010). Could the squid be "mind reading" the intention of the fish? It is more likely that they were picking up small movement or postural cues, but the necessity to do such complex evaluations suggest a heavy pressure to succeed in these calculations.

The presence of such cognitive complexity and close monitoring of and learning about one's environment suggests but does not prove that an animal has conscious awareness. Bekoff and Sherman (2004) believe that we can evaluate animals' understanding of selves on a continuum, ranging from self-referencing to self-awareness and self-consciousness. Self-referencing is matching a target individual to oneself, a necessity for finding an appropriate mate and not necessarily conscious. Certainly cephalopods match themselves to others during the courtship process, exchanging courtship and agonistic skin signals. Such displays are far from automatic; *S. sepioidea* display them unilaterally on the side towards the intended target (Mather 2004). Rather than an automatic assignment of oneself to species and sex, they can use the displays to manipulate others, and this may be evidence for self-consciousness.

Self-awareness is the discrimination of oneself from others and one's possessions from theirs. As cephalopods are mobile and nonterritorial, they do not need to have a sense of possessions. But the octopuses' hunting patterns (Mather 1991*b*) clearly suggest a sense of self. Returning to a central home after foraging excursions means that they must have had a sense of "self in environment" (and see the section on Navigation). The lack of trail following and the return home after displacement suggests that they were building up a "map" of their environment, but the fact that they avoided foraging in recently hunted environments also suggest their ability to place and remember themselves within this environment. As the "decision" as to whether to consume a prey in local hiding or return home to eat it was heavily influenced only by how far it was to the home, they could also evaluate the relative distance of home and self (Mather 1991*b*).

What of self-consciousness, the sense of one's own body as self? Gallup et al.'s (2002) mirror test has been used as the "acid test" for animals' self-awareness. When an animal looks into a mirror, does it direct exploratory behaviour seen in the image to itself, or does it even recognize the image in the mirror as "me" by other means? Octopuses failed even the easier aspect of the mirror test; although they oriented towards their image in the mirror, there was no difference in their behaviour in this condition, compared with a view of conspecifics (J.A. Mather and R.C. Anderson, submitted manuscript).[4] But a mirror is a very unnatural stimulus, and octopuses had equal difficulty carrying out a detour task when the prey was visible through a window (Wells 1964). We have no reason to suspect that just because cephalopod and mammal eyes are similar structures, that the processing of visual information will be similar also. It is intriguing to note that octopuses can recognize different human individuals (Anderson et al. 2010), but it is not clear whether they can recognize individual conspecifics. Tricarico et al. (2011) used a familiarity paradigm

to suggest that octopuses reacted differently to known individuals, but problems with the statistical analyses limited their conclusions.

Rather than asking about levels of awareness, it might be useful to think of how a conscious animal would evaluate its environment. Nonhuman animals' awareness will not have the complexity that is expected for humans, with our language, meta-cognition, and the ability to make self-reports. Visual information might not be processed in the same way by cephalopods and mammals, and there is much we need to learn about chemoreception. Information about the self might be processed in a dual system, as suggested by Grasso (2013). But the possession of primary consciousness, an evaluative capacity that wields an attentions "spotlight" (see Baars 1997), may be widespread in many animal species. In cephalopods, there is seldom a direct response to incoming stimuli. Instead, they are assessed, sorted, and placed in memory for later retrieval and decisions about how to act on them. Thus, octopuses explore (Mather and Anderson 1999; Boal et al. 2000) and Sutherland's (1960) octopuses learned a concept of the important visual cue discriminating the two figures. Anderson and Mather's (2007) octopuses built up a repertoire of the appropriate response to extract clams from their protective shells and oriented the activity on the shell accordingly. Karson et al.'s (2003) cuttlefish could remember two sets of spatial cues and respond appropriately even when the trials were intermixed. The Bermuda octopuses (Mather 1991*b*) could remember where they had hunted in the previous few days and avoid these areas, and Finn et al.'s (2009) octopuses could carry around a coconut shell for later use as shelter. Both squid (Mather 2010) and cuttlefish (Langridge et al. 2007) could aim the startle dot displays appropriately to an approaching fish.

All these pieces of information argue that the cephalopods are constructing internal schemas of important aspects of the environment and storing them until they are needed later. But observation suggests that they are also using Baars' (1997) attention spotlight to extract the important information from their environment. When a stimulus such as a crab (Boycott 1954; J.A. Mather, personal observation) or a specific person (Anderson et al. 2010) is placed in an octopus' visual field, it often does not take direct action. Instead, it does a vertical movement called a "head bob". Because adult octopuses mostly use monocular vision, they do not have the accurate assessment of distance to a stimulus that binocular animals such as humans (Foley and Matlin 2010) possess. But a movement such as the head bob (many mammals make horizontal movements in a similar situation) allows a monocular animal to pick up motion parallax cues that give accurate positional information. In other words, faced with a situation to which it might respond, the octopus instead opts for "more information, please", attends to the stimulus at hand, and stores the relevant visual information for later actions.

And this is extended with motor play (Mather and Anderson 1999), when octopuses are shifting from what Hutt (1966) describes as extracting information about what an item is to investigating what it does. Using these processes, the highly exploratory and heavily learning-dependent cephalopods indeed offer us a different evolutionary route to the development of intelligence and cognition, one which we have just begun to understand.[3]

Acknowledgements

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[4]J.A. Mather and R.C. Anderson. Do octopuses recognize themselves in mirrors? Submitted manuscript.

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