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Cephalopod learning and memory

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26 memory experiments addressing the main challenges individuals face during their daily lives: where
27 and when to go, and what to eat. Determining the type of information cephalopods learn and
28 remember and whether they use such information to overcome ecological challenges will highlight
29 *why* these invertebrates evolved large and sophisticated brains.

30 Historically, cognitive studies on cephalopods focussed on non-associative forms of learning –
31 the simplest yet fundamental form of learning that does not require stimuli association. For instance,
32 sensitisation – the repeated exposure to a stimulus resulting in progressive amplification – has been
33 studied in octopuses. Other studies have studied habituation in a range of cephalopods using a variety
34 of stimuli across different modalities. For example, habituation has been studied in the context of: a
35 visual stimulus (*i.e.*, novel object) in octopus; a sound stimulus in cuttlefish; the presence of a false
36 predator in squids; and an unfamiliar environment in nautiloids. Studies on sensitisation and
37 habituation were followed by decades of experiments using associative forms of learning – a simple
38 form of learning whereby the learner associates a specific response to an object or stimulus resulting
39 in a positive or negative outcome. Through this form of learning, octopuses have been taught to solve
40 discrimination tasks where they can discriminate various visual stimuli differing either: in size, shape,
41 brightness, or orientation (Figure 2b). Octopus also show an impressive capacity for chemotactile
42 discrimination, as they can learn to discriminate between objects differing in texture or in taste. Using
43 these paradigms, two separate learning and memory systems have been described in octopus: the
44 visual and the chemotactile learning systems. As in other animal species, distinct short- and long-term
45 memory stores were demonstrated in octopuses. Their short-term memory is more labile with
46 information and can be either forgotten or incorporated into a more stable long-term memory.

47 Visual discrimination learning tasks have also been successfully used in cuttlefish and squids
48 demonstrating that both these groups are also rapid learners. However, more intricate details of the
49 learning and memory ability of cuttlefish was revealed using a paradigm called the “prawn-in-the-
50 tube” task (Figure 2a). In this task, cuttlefish learn to inhibit catching unobtainable prey (*i.e.*, prawns)

51 enclosed in a glass tube. This paradigm has been extensively used to determine what cuttlefish actually
52 learn and memorise during this task. It appears that they can learn through multiple processes; both
53 the pain induced when the individual's tentacles hit the tube and their ability to memorise the visual
54 (light polarization) and tactile features of the glass tube can inhibit future attempts of attacking prey
55 in the tube. This task has revealed that cuttlefish exhibit temporally separated short- and long-term
56 storage, producing a biphasic (two-phases) memory curve. Optimal memory retention was observed
57 between 20 – 60 minutes following initial training, suggesting that the short-term memory trace decays
58 before the long-term memory is consolidated. Using a similar procedure, long term memory has been
59 demonstrated in sepiolid squids and shown to last at least 12 days. In nautilus, a biphasic memory
60 curve, similar to that of cuttlefishes, was demonstrated using a classical conditioning procedure: a light
61 predicting the arrival of a food reward. These studies were mostly designed to better understand the
62 physiological bases of memory. In recent years, other learning tasks have attempted to address how
63 cephalopod learning and memory is used to overcome ecological challenges.

64 **Learning where to go**

65 In order to limit their time exposed to predators, cephalopods need to travel efficiently within
66 their home range between safe resting places and foraging grounds. It is well-known that most octopus
67 species are central place foragers and that they can return directly to their den for shelter after a
68 meandering foraging trip, without retracing their outbound routes. In the giant Australian cuttlefish,
69 field studies have shown that individuals come back to specific rocky outcropping areas after foraging
70 excursions. Even nautilus that possess some means of defence (*i.e.*, a hard outer shell) might need
71 to learn safe locations within coral reefs after scavenging for food.

72 We now know that cephalopods have sophisticated sensory systems, which they use to navigate
73 their underwater worlds. Laboratory experiments have addressed exploratory learning abilities in
74 cephalopods, a natural demonstration of spatial learning. Other studies have focussed on their
75 accuracy when solving spatial tasks and the types of spatial cues they tend to collect for future use.

76 Cuttlefish, for example, can rely on internal (motor sequence) and/or external cues (proximal and distal
77 visual cues) to locate a shelter within a maze. Furthermore, they learn to use the *e*-vector orientation
78 of polarized light (global cues) in parallel with landmarks (local cues) to orient. Importantly, cuttlefish
79 can use either type of cue (global or local) when one becomes unavailable. Memorising redundant
80 spatial information might provide cuttlefish with a selective advantage to flexibly adapt to
81 environmental changes: *e.g.* water turbidity or bottom topography might prevent cuttlefish from
82 perceiving landmarks from long distances. Nautilus can also learn to use proximal and distal visual
83 cues, and flexibly switch between these cues when salient ones become unavailable, despite living
84 most of their life in near darkness. But nautilus, like octopus, preferentially rely on distal visual cues
85 when proximal visual cues are displaced.

86 Cuttlefish prefer to spend their time on the bottom but they also swim into the water column
87 and move around vertical barriers. As with most marine animals that move through an inherently 3D
88 environment, cuttlefish acquire and store vertical and horizontal spatial information separately. When
89 facing conflicting information, cuttlefish preferentially rely on the vertical dimension. This separate
90 encoding might be useful to flexibly use spatial information, such as during detour tasks (a task
91 requiring the subject to travel around a barrier to obtain a reward). Despite the need to navigate a 3D
92 environment, nearly all cephalopod research on locomotion and navigation has been examined in less
93 dimensions. To date, only one study undertaken in nautilus has directly tested 3D spatial learning.
94 Using artificial coral reefs, nautilus showed an increased exploration when topographical features of
95 a familiar 3D arena were modified. This result suggests that nautilus have the ability to learn
96 topographical features in 3D dimensions.

97 **Learning about time**

98 Availability of food and presence of conspecifics and predators vary over space and time. Using
99 temporal information is thus useful to control or adjust the expression of certain behaviours, such as
100 foraging behaviour. To investigate this area of research scientists have started assessing whether

101 cephalopods possess more complex cognitive abilities. Abilities that surpass simple associative learning
102 and involve flexible, innovative and spontaneous remembering, decision-making, or planning.

103 At a circadian level, food availability may depend on both temporal and spatial information. It
104 has been shown that cuttlefish can learn to search for food in different locations at different times of
105 the day, each location being associated with a specific period. Furthermore, they can adjust their
106 foraging behaviour according to the future availability of their preferred prey (*i.e.*, shrimp),
107 demonstrating that they can learn when an event is likely to happen. Specifically, cuttlefish reduce
108 their consumption of crabs (*i.e.*, less preferred prey) during the day when shrimp will predictably be
109 available at night, but not when shrimp is unavailable at night. This flexible behaviour depends on both
110 previously learnt rules (*i.e.*, temporal patterns of food availability) and expectations concerning the
111 proximate future (*e.g.*, tonight, my preferred prey will be available). During a delayed gratification task,
112 cuttlefish appear to consider time duration when evaluating whether a preferred prey is worth waiting
113 for or not. Individuals were all able to wait for their preferred but delayed prey (50–130 s), thereby
114 showing self-control. However, as delay durations increased, individual cuttlefish began to succumb to
115 temptation and were more likely to consume the less preferred but immediately available prey.

116 Keeping track of time using interval timing is of prime importance for different species to flexibly
117 adjust their foraging behaviour. This is particularly important when species need to keep track of food
118 or prey that can decay or replenish at different rates. Cuttlefish are able to integrate the ‘what-where-
119 when’ components of unique foraging events, an ability called episodic-like memory. Specifically, they
120 remember what they have eaten, where, and how long ago, in order to optimize their foraging
121 behaviour by keeping track of replenishing rates of different food items. Cuttlefish can also adjust their
122 foraging behaviour by retrieving the perceptual features that were tied to the source of a previous
123 foraging event, namely whether they had smelt or seen the prey item. Research on octopuses suggests
124 that they do not keep track of time like cuttlefish. Instead, they might use other memory processes to
125 encode time such as learning the order of different events. Indeed, field studies have shown that

126 octopuses avoid recently visited grounds on subsequent foraging trips, suggesting that they memorise
127 where and when they previously foraged to avoid depleted areas.

128 **Learning about food**

129 Learning and memorising relevant locations within a home range is paramount to determine
130 where and when to go hunting. But it is also important to learn which type of prey to hunt. It is thought
131 that cephalopods possess 'innate' processes of prey recognition so that they know what to hunt as
132 soon as they hatch. However, other types of learning have been shown to counteract innate and
133 spontaneous preferences. In cuttlefish, naïve individuals spontaneously respond to shrimp-like shapes
134 (*i.e.*, elongated shapes moving along a horizontal plane) and prefer shrimp over crabs. However, an
135 early exposure to crabs before or during the first hours after hatching can induce a reversal of their
136 'innate' preference for shrimp. Using a similar paradigm, an early exposure to light-coloured crabs
137 overrides their innate preference for dark-coloured crabs. It has been hypothesised that these food
138 imprinting processes allow a diversification of the diet of individuals without having to bear the
139 energetic cost of trial-and-error learning: *i.e.*, this type of learning requires several attempts,
140 potentially leading to less profitable prey and/or dangerous exploration.

141 Prey choice might change during the life course of individuals through learning from previous
142 unpleasant experiences: *e.g.* pain, unpalatability, toxicity. Food avoidance learning has been shown in
143 different species of octopus. For example, octopuses from the genus *Eledone* avoid catching hermit
144 crabs carrying sea anemones after they were stung. Common octopuses flexibly adjust their avoidance
145 behaviour when faced with different anemone species. Specifically, they avoid the more noxious
146 species, and display various kinds of cautious behaviours when exposed to them (*e.g.*, slow approach,
147 use of a single arm). Avoidance behaviour can also be driven by the perception of certain chemical
148 compounds. For instance, cephalopods can use contact chemoreceptors to discriminate between
149 edible and non-edible food items. In cuttlefish, individuals change their prey preference when their
150 preferred prey is rendered bitter with a coating solution made of quinine.

151 Decision-making processes during foraging not only depend on the apparent value of a food
152 item (*e.g.*, size, time required to catch and consume the food item) and state-dependent value (*e.g.*,
153 level of satiety) but also on previously learned valuation of food items. When presented with different
154 amounts of prey, cuttlefish spontaneously prefer the larger amount. However, they can learn to value
155 different amounts of prey through positive association. For instance, if cuttlefish are rewarded when
156 they chose one shrimp over no shrimp across several trials, they continue to choose one shrimp even
157 when the alternative choice is larger (*i.e.*, two shrimp) in subsequent trials. This demonstrates that
158 decision-making in cuttlefish was based on the relative value of prey items (learned valuation) and not
159 on their absolute value.

160 **Learning from others**

161 When living in a group, the capacity to learn by observing the actions of others undoubtedly
162 provides an adaptive advantage to rapidly acquire biologically important information. One would not
163 expect social learning to occur when minimal contact is observed between individuals within a species.
164 However, social learning has been demonstrated in several solitary species. Among cephalopods,
165 octopuses are generally considered to be the most solitary, the squids the most gregarious, and the
166 cuttlefish lie somewhere in between. While shoaling squids appear the more suitable candidates to
167 explore social learning abilities in cephalopods, the first evidence of observational learning has been
168 provided in the supposedly solitary octopus. Tested individuals appeared able to learn how to solve a
169 visual discrimination task by observing a conspecific demonstrator. The memory trace lasted at least 5
170 days after the observation learning phase.

171 Experiments carried out in cuttlefish were not as unequivocal. Individuals that observed
172 conspecifics preying on crabs without being nipped did not improve the efficiency of their own
173 predation tactics. By contrast, when cuttlefish observers were able to watch a conspecific participate
174 in the prawn-in-the-tube task, observers abstained from attempting to reach the unobtained prawn
175 more quickly than naïve cuttlefish. Cuttlefish used in a danger avoidance paradigm showed mixed

176 results when watching a demonstrator. Specifically, only some cuttlefish learnt to associate a threat
177 with a particular background by observing others, while some individuals did not show any sign of
178 improvement. Learning by observing others might not uniquely depend on the intrinsic imitative
179 capacity of cuttlefish but also on the level of attention, motivation, and tolerance (or lack thereof) to
180 other conspecifics.

181 While we can wonder why cephalopods would possess observation learning abilities, it is
182 important to state that being able to learn from others does not necessarily mean that individuals learn
183 from conspecifics. Cephalopods are known to dynamically change their appearance to resemble
184 specific features of their surroundings: *e.g.*, cuttlefish and octopus can change their posture to
185 resemble objects such as sea grass and rocks, as well as other animal species that are either venomous
186 or unpalatable. For instance, cuttlefish can mimic hermit crabs to catch more prey (Figure 3a), and
187 octopus can mimic lionfish, flounder, and banded sea-snakes to avoid being eaten (Figure 3b). Octopus
188 not only physically resemble these animals, but also learn to precisely imitate the way they move or
189 swim. Observational learning abilities in octopuses might not only result from the need to deceive
190 potential predators but also from the fitness advantages potentially provided by learning from other
191 species. For instance, the day octopus (*Octopus cyanea*) hunts with multiple fish species that have
192 complementary hunting techniques (Figure 3c). Learning from others might be paramount for this
193 form of collaborative hunting because it involves complex social interactions that likely require the
194 need to prevent exploitation (one hunter takes all the food) and ensure collaboration.

195 In summary, knowledge of cephalopod cognition has been propelled forward in recent years.
196 We have learnt a lot from learning and memory experiments couched within foraging contexts (*i.e.*,
197 using food rewards) but more knowledge can be gained about the flexibility of these capacities by
198 investigating such abilities across different contexts (*e.g.*, predator avoidance, mating). Uncovering
199 these cognitive details in cephalopods – an animal lineage far removed from the more traditionally
200 studied species (*i.e.*, social primates and corvids) – has the potential to provide a more comprehensive

201 understanding of the evolutionary patterns of intelligent behaviour. Indeed, these large-brained
202 invertebrates provide a unique opportunity to go further back in evolutionary time to pinpoint when
203 certain cognitive abilities emerged.

204 **Declaration of interests**

205 The authors declare no competing interests.

206 **Further reading**

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240 **Figures**

241 **Figure 1. Examples of different cephalopods**

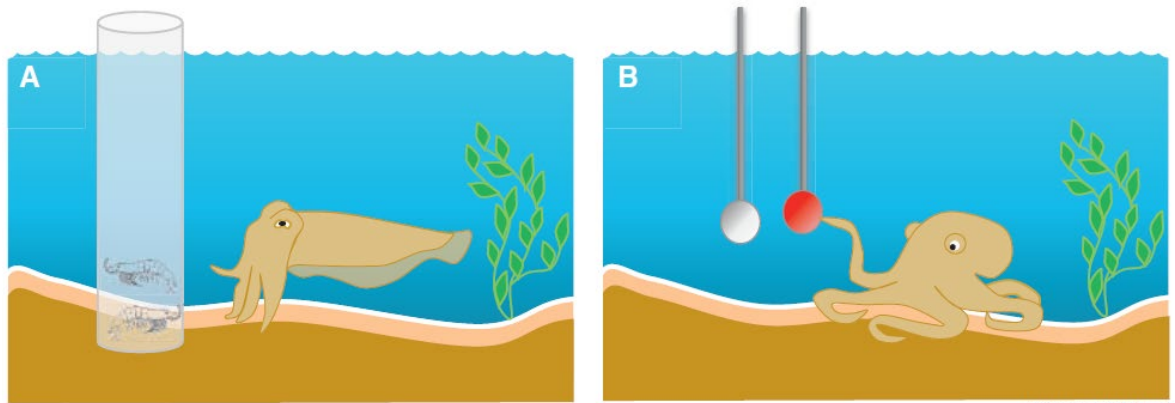
242 (A) A veined octopus, *Amphioctopus marginatus*, also known as the coconut octopus (photo:
243 adobe.stock.com); (B) a mating pair of giant Australia cuttlefish, *Sepia apama* (photo: A.
244 Izzotti/Getty); (C) a pair of schooling Caribbean reef squid, *Sepioteuthis sepioidea* (photo: A.K.
245 Schnell); (D) a chambered nautilus, *Nautilus pompilius* (photo: J.W.Alker/Getty)



246

247 **Figure 2: Graphic representation of memory tests in cephalopods**

248 (A) Paradigm called the 'prawn-in-the-tube' task. In this task, cuttlefish learn to inhibit catching
249 unobtainable prey enclosed in a glass tube; (B) Visual discrimination learning. In this task,
250 octopus learn to select one of two balls differing in colour.



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252 **Figure 3: Examples of different cephalopod behaviours**

253 (A) Two juvenile Pharaoh cuttlefish, *Sepia pharaonis*, mimicking the appearance of hermit crabs

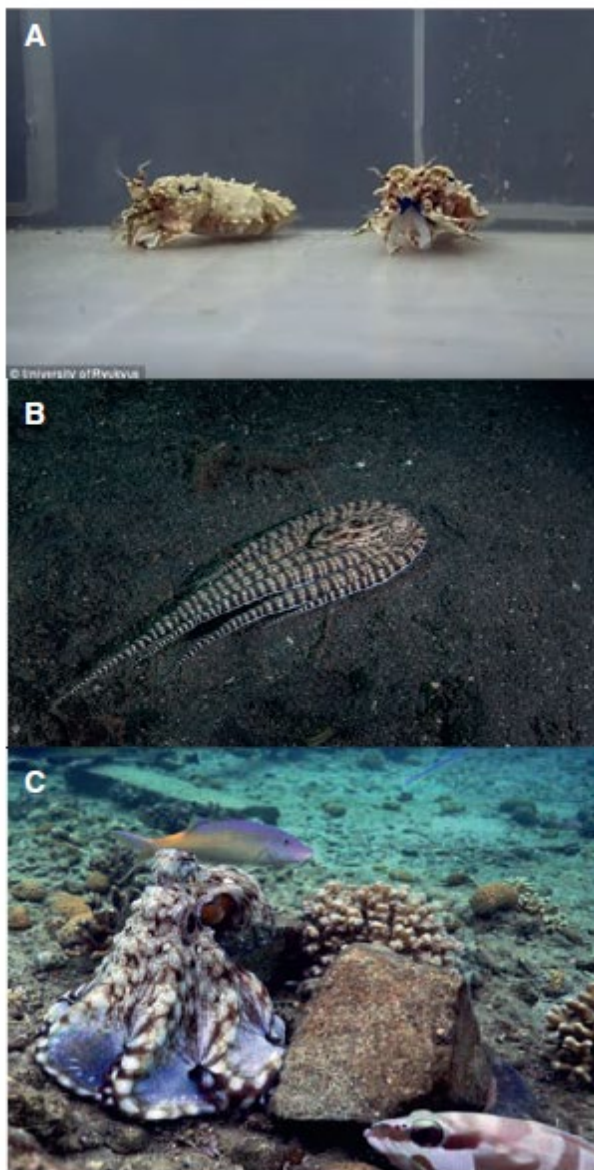
254 (image used with permission from Ryuta Nakajima); (B) a mimic octopus, *Thaumoctopus*

255 *mimicus*, mimicking the appearance and movement of a flounder fish (photo: Velvetfish/Getty;

256 (C) a day octopus, *Octopus cyanea*, forming a multispecific hunting group with a yellow-saddle

257 goatfish, *Parupeneus cyclostomus* and a blacktip grouper, *Epinephelus fasciatus* (image used

258 with permission from Eduardo Sampaio).



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