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# Comparative study of Mental Time Travels in cephalopods

Lisa Poncet

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# THÈSE

Pour obtenir le diplôme de doctorat

Spécialité **PHYSIOLOGIE ET BIOLOGIE DES ORGANISMES - POPULATIONS - INTERACTIONS**

Préparée au sein de l'**Université de Caen Normandie**

## Comparative study of Mental Time Travels in cephalopods

Présentée et soutenue par  
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**Thèse soutenue le 02/05/2023**  
devant le jury composé de :

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# Publications

## Articles

Poncet, L., Desnous, C., Bellanger, C., and Jozet-Alves, C. (2022). Unruly octopuses are the rule: Octopus vulgaris use multiple and individually variable strategies in an episodic-like memory task. *Journal of Experimental Biology* 225, jeb244234. 10.1242/jeb.244234.

Poncet, L., Billard, P., Clayton, N.S., Bellanger, C., Jozet-Alves, C. (submitted to *Current Biology*). False memories in the cuttlefish.

Poncet, L., Roig, A., Billard, P., Bellanger, C., and Jozet-Alves, C. (submitted to the *Proceedings of the Royal Society B: Biological Sciences*). Different evolutionary pathways for episodic-like memory and future planning: insights from cephalopods.

## *Articles not included in this thesis*

Jozet-Alves, C., and Poncet, L. (2022). Conscience et mémoire : de la seiche au geai. *Société des Neurosciences* 63.

McGetrick, J., Poncet, L., Amann, M., Schullern-Schrattenhofen, J., Fux, L., Martínez, M., and Range, F. (2021). Dogs fail to reciprocate the receipt of food from a human in a food-giving task. *PLOS ONE* 16, e0253277. 10.1371/journal.pone.0253277.

## Oral communications

**50<sup>ème</sup> colloque de la SFECA** (Société Française pour l'Etude du Comportement Animal): May 31 – June 1, 2021 – Marseille, France (virtual). Poncet, L., Roig, A., Bellanger, C., Jozet-Alves, C. Exploration des capacités de planification du futur chez la seiche commune.

**23<sup>ème</sup> JEDnBISE** (Journées de l'Ecole Doctorale normande Biologie Intégrative, Santé et Environnement) : May 17 – 18, 2021 – Evreux, France (virtual). Poncet, L., Bellanger, C., Jozet-Alves, C. Mental Time Travel Abilities in the common cuttlefish. **Price of the public**

**51<sup>ème</sup> Colloque de la SFECA** (Société Française pour l'Etude du Comportement Animal): May 31 – June 2, 2022 – Clermont-Ferrand, France. Poncet, L., Bellanger, C., Jozet-Alves, C. Exploration des faux souvenirs chez la seiche.

**8<sup>th</sup> edition of ESCBC** (European Students Conference on Behaviour & Cognition): September 1 – 2, 2022 – Rovereto, Italy. Poncet, L., Bellanger, C., Jozet-Alves, C. False memories in the common cuttlefish.

### **Poster communications**

**CephRes 2020**, Biology and Life History of Cephalopods: September 16 – 21, 2020 – Virtual. Poncet, L., Roig, A., Bellanger, C., Jozet-Alves, C. Future planning abilities in the common cuttlefish.

**ASAB Virtual Winter Conference**: December 3 – 4, 2020 – Virtual. Poncet, L., Roig, A., Bellanger, C., Jozet-Alves, C. Future planning abilities in the common cuttlefish.

**ICN 2022** (International Conference for Neuroethology): July 25 – 29, 2022 – Lisbon, Portugal. Andouche, A., Baratte, S., Poncet, L., Durand, T., Jozet-Alves, C., Bellanger, C. Looking for immediate early genes as neuronal activation markers in the cephalopod mollusc *Sepia officinalis*

## List of abbreviations

<b>DMTS</b>	Delayed Matching To Sample
<b>DRM</b>	Deese-Roediger–McDermott associative memory illusion.
<b>fMRI</b>	Functional Magnetic Resonance Imaging
<b>GLMER</b>	Generalised Linear Mixed Effect Model
<b>MTT</b>	Mental Time Travels
<b>N</b>	Non-misleading condition
<b>O</b>	Octopus
<b>OV</b>	Olfactory and Visual misleading condition
<b>S</b>	<i>Sepia</i>
<b>ToM</b>	Theory of Mind
<b>V</b>	Visual misleading condition

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## Introduction:

Literature background and  
presentation of the studied  
species



# **Introduction: Literature background and presentation of the studied species**

This introduction presents the literature background of this PhD thesis. First, I will give an overview of Mental Time Travels Abilities, namely episodic memory, its counterpart in animals known as episodic-like memory, and future thinking. Then I will present an overview of the field of comparative cognition, and the hypotheses that try to explain the emergence of complex cognition, which will lead me to present the two cephalopod species studied during my PhD thesis.

## **Part I: Mental Time Travels**

- A. Episodic memory in humans: In this section are presented memory systems, and episodic memory is defined, with its specificities, its reconstructive properties and its roles.
- B. Episodic-like memory in animals: In this section are presented the criteria for studying episodic memory in animals, and various experiments conducted in animals are detailed.
- C. Future thinking: In this section is defined future thinking and various experiments conducted in animals are detailed.

## **Part II: Comparative study of Mental Time Travels**

- A. Comparative Cognition: In this section is defined comparative cognition, and the hypotheses emitted about the emergence of complex cognition are detailed.
- B. Studied animals: In this section are presented the cephalopod species studied in this thesis, to apprehend how the anatomical, ecological and behavioural specificities of both species influence their cognitive abilities.

## I. Mental Time Travels

Mental Time Travels (MTT) are the ability to travel mentally in one's personal past and one's personal future, in order to re-experience or pre-experience events (Suddendorf, 1994). The retrospective side of MTT is known as episodic memory, while the prospective side of MTT is generally called episodic future thinking.

### A. Episodic memory in humans

In humans, long-term memory is not considered as a single entity but rather as several types of memories mediated by different brain systems (Squire, 2004; Squire et al., 1993). It can be divided between the nondeclarative memory and the declarative memory which includes the episodic memory.

#### 1. *Nondeclarative and declarative systems*

The nondeclarative memory system acquires, retains and uses sensorial, cognitive and motor skills (Squire, 2004). This memory can be expressed through specific behaviours and can require practice (Griffiths et al., 1999; Tulving, 1984; Tulving, 1985). The nondeclarative system includes procedural skills and habits, simple classical conditioning, non-associative learning (*i.e.* habituation and sensitisation) and priming (*i.e.* improved ability to detect or identify stimuli based on the recent experience with them; Figure 1; Klein et al., 2002; Squire, 2004; Squire et al., 1993).

The declarative memory system receives information from different sensory and cognitive systems, retains this information and transmits it to other systems (Tulving, 1972; Tulving, 1984). Stored information is describable, thus it can be characterised as true or false (Squire, 2004). Retrieval interacts with other brain functions such as language, emotion and reasoning (Griffiths et al., 1999; Tulving and Markowitsch, 1998). The declarative memory system can be subdivided in two types of memory: the semantic memory, which corresponds to the knowledge of the world, and the episodic memory, which corresponds to the memory of personal past events (Figure 1).

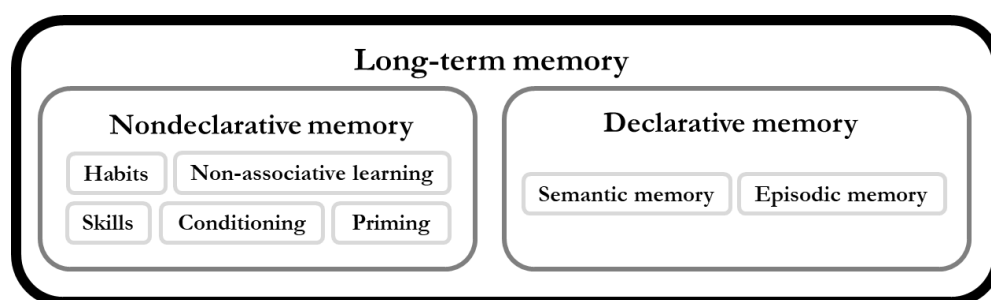


Figure 1: Taxonomy of long-term memory

## ***1. Episodic memory characteristics***

### *a. Episodic memory versus semantic memory*

Episodic memory represents personally experienced past events (Tulving, 1984; Tulving, 1985). It defines the identity of a person, is inherently believed to be true (*i.e.* we know the events in our episodic memory are true because we remember experiencing them), and is associated with the idea of “remembering” and “recollection”. This memory concerns a unique event (or episode) within a specific setting (time, “when”, and place, “where”, the event occurred), and a focal element (“what happened”; Tulving, 1984; Tulving, 1985).

The semantic memory corresponds to the knowledge of someone about the world. It is a network of facts, ideas, concepts, words, images, rules and relations. It is associated with the idea of “knowing” (Tulving, 1972; Tulving, 1985).

Semantic and episodic systems are generally considered as interlinked: semantic memory can function independently, but episodic memory is based on semantic memory (Suddendorf and Corballis, 1997; Tulving and Markowitsch, 1998). Encoding and retrieval of episodic memories rely on the semantic system, but the semantic system does not require the episodic system to function (Klein et al., 2002; Tulving and Markowitsch, 1998). This is observable in episodic amnesia, such as the case of “K.C.” described by Tulving (1985), or “D.B.” described by Klein and colleagues (2002): subjects lost their episodic but not semantic memory, they remembered their past in a semantic way, with language skills, knowledge of the world, knowledge of the time globally unimpacted. However, they could not remember their personal past experiences, such as what they did the day before (Klein et al., 2002; Tulving, 1985).

Episodic memory develops late, as shown with infantile amnesia, where episodic memories are unavailable until three years-old (Squire et al., 1993). Children develop the cognitive structures to re-experience their own past state around the age of four (Roberts, 2002; Suddendorf, 1994; Suddendorf and Corballis, 1997). Episodic memory also degrades with age, as seen with older adults who show a reduced ability to generate episodic events and episodic details (Addis et al., 2008; Schacter et al., 2007).

### *b. Anotoesis and chronesthesia*

Episodic memory is always associated with consciousness of self through time (Tulving, 1972). Anotoetic consciousness is the awareness of environmental stimuli, while noetic consciousness is the awareness of objects and events and their relations, in the absence of such objects and events

(“symbolic knowledge”). Auto-noetic consciousness is the awareness of one’s own existence and identity through time. It appears late in development, and is thus not present in young children, and can be selectively impaired by brain damage. Nondeclarative memory is auto-noetic, semantic memory is noetic and episodic memory is auto-noetic (Tulving, 1985).

Chronesthesia is the consciousness of the subjective time in which one lives that makes mental travels possible in such time (Tulving, 2002). Chronesthesia is distinct from chronognosia, which is the simple knowledge of time. Chronesthesia is essential in episodic memory, because it allows recollection while knowing that the event is not happening now, but happened earlier (Schwartz and Evans, 2001).

### *c. Temporal components*

Temporal components are an essential part of the episodic memory system. Memory for time can be encoded in various ways. Friedman (1993) elaborated three non-exclusive theories for the memory for time: distance-based, location-based and relative times of occurrence.

*Distance-based theories* correspond to ‘how long ago’ an event happened. This type of encoding might be based on the strength of the memory, which declines with the passage of time: stronger traces with more details are more recent than weaker traces with less details. It can also be encoded through chronological organisation, but also through contextual overlap: the context of the memory is compared to the present context, and the more similarities are shared between contexts (*e.g.* same season, same location), the more recent is the memory.

*Location-based theories* correspond to ‘when’ an event happened. This type of encoding might be based on encoding salient events, such as the beginning or the end of a trial. It might also be based on reconstruction, by encoding the general context, then interpret it with the knowledge of the patterns of time (*i.e.* seasons, course of the sun or life cycles): for example, when remembering a hot day at the beach, one can know it was during the summer holidays. Lastly, it might be based on time-tagging, based on an internal clock which attribute a time tag to each encoded memory.

*Relative times of occurrence or temporal order theories* correspond to the order of events. This encoding might be based on encoding the before-after relations between events, or by associating together events directly following each other. Overall, memory of time is based on general contextual information which allows inferences of location, associations, order or age of memories (Friedman, 1993; Friedman, 2007).

## ***2. Reconstructive and source monitoring processes of memory***

### *a. Reconstructive processes*

Episodic memory is not a continuous filmstrip with all details fused within each image as one can sometimes imagine. In fact, the features of our memories are split and stored individually. When they are remembered, all features are reassembled together to recreate the event. Memory is thus intrinsically reconstructive, as explained in the constructive memory framework (Schacter and Addis, 2007b; Schacter et al., 1998; Schacter et al., 2012). A constructive system allows to extract, recombine and reassemble events to a different form (Schacter and Addis, 2007a), and thus mentally imagine possible scenarios and reconsider the choices and possibilities of past experiences (Schacter and Addis, 2007b; Schacter et al., 2012; Suddendorf and Corballis, 2007). Constructive nature is also linked to the economy of storage by compressing information to avoid overload (Schacter and Addis, 2007b): instead of storing each experience with all its details as a whole, details are encoded separately and can be reused in various memories (*e.g.* the colleague in my office is the same colleague who went to the conference with me, thus the details about this colleague can be encoded once but remembered in various occasions).

### *b. Source monitoring*

The episodic memory reconstruction is verified by a source monitoring process (Johnson et al., 1993), which retrieves and evaluates the ensemble of contextual features (*e.g.* spatiotemporal, sensorial, emotional and physiological information) from a specific memory in order to determine the contextual bases (*i.e.* the source) of this memory and discriminate it from others (Crystal et al., 2013; Johnson et al., 1993; Zaragoza et al., 2007a; Zaragoza et al., 2019a).

### *c. False memories*

Source monitoring can fail, and in this case it generates source misattributions from a memory to another memory (Loftus and Hoffman, 1989; Zaragoza et al., 2019a). The misinformation effect is a misattribution of one or several features of a misleading post-event to the memory of an original event, forming false memories (Loftus, 2005; Pickrell et al., 2017; Tousignant et al., 1986; Volz et al., 2017; Wade et al., 2007; Zaragoza et al., 2007a). False memories are defined as an episodic memory impairment, where subjects remember events or features they did not experience. False memories are consequently a noteworthy indicator of source monitoring failures, and they are

therefore a circuitous way to study the source encoding and monitoring processes at the root of the constructive memory.

### ***3. Other cognitive abilities linked to episodic cognition***

Some authors, such as Suddendorf and Corballis (1994; 1997) consider that MTT require a concept of self and the others, also known as Theory of Mind. These authors state that if someone is unable to represent the mental state of another when it is opposed to their own present mental state, then they will not be able to represent their own earlier or later mental state. In the Machiavellian social intelligence hypothesis framework, the human ability to represent their past state might be a by-product of the ability to understand the states of others (Suddendorf, 1994). Moreover, Perner and colleagues (2007) noted that the development of the theory-of-mind parallels the development of episodic memory. However, it should be noted that human subjects lacking episodic memory were shown to possess a Theory of Mind, indicating that this ability can exist independently from episodic memory abilities (Rosenbaum et al., 2007).

For some authors (Roberts, 2002; Suddendorf and Busby, 2003; Suddendorf and Corballis, 1997; Suddendorf et al., 2009a), language favoured the emergence of MTT, as language allows to relate past stories to teach others, and to schedule future group actions. Thus, these authors argue that MTT might be uniquely human (Mahr and Csibra, 2018; Suddendorf and Corballis, 2008; Suddendorf et al., 2009a; Tulving, 2005). However, authors such as Corballis (2019) recently reconsidered the linkage between MTT and language, and concluded that it was more probably Mental Time Travels which favoured the emergence of language.

### ***4. Role of episodic memory***

Several hypotheses on the role of episodic memory have been made. A first hypothesis is that episodic memory would be useful for foraging in a patchy and predictable environment, to remember which sites have been visited and avoid their early revisit (Schwartz and Evans, 2001). Episodic memory function could also be social, to share information (Raby and Clayton, 2009) or to keep track of social relationships and remember friends from foes, situations which can vary in time, location and situation (Boyer, 2008; Schwartz and Evans, 2001). Episodic memory might serve to assess the veracity of a past information based on the reliability of its source (Mahr and Csibra, 2018), or episodic memory could be an “occasion specifier”, to identify events as being unique (Kouwenberg et al., 2009).

## B. Episodic-like memory in animals

In the absence of language, episodic memory is studied in non-human animals through its behavioural components. In the absence of behavioural indicators of auto-noetic consciousness, this memory is labelled “episodic-like” (Clayton and Dickinson, 1998; Griffiths et al., 1999). Behavioural criteria were set for episodic-like memory: 1) it possesses a specific content, 2) it is structured and 3) it is flexible (Clayton et al., 2003b). At first, researchers focused on 1) the content of the memory (*e.g.* Clayton and Dickinson, 1998a), and defined it as what happened during a past personal experience, where it happened and when it happened. It corresponded to Tulving’s original definition of episodic memory (Baddeley et al., 2001a; Tulving, 1972). The temporal component (“when”) is considered as the element which renders the memories unique: it allows to distinguish between two memories sharing the same what and where. Instead of “when”, some authors (Eacott and Norman, 2004; Eacott et al., 2005) consider that the context (“which”) can also be used to discriminate between memories. 2) In addition to the content, episodic-like memory must be structured (Clayton et al., 2003b; Griffiths et al., 1999), meaning that each episodic memory must be bound into an unique representation. This implies that episodic-like memory is a reconstructive process. 3) At last, episodic-like memories can be recalled flexibly, in various contexts, and can integrate novel information to adapt the behaviour.

Some authors (Friedman, 2007; Zentall, 2005) consider that these criteria are not sufficient to define a memory as episodic-like, as the studies exploring these criteria rely on training and expected tests, which favour the use of rule-based or semantic memory (Zentall et al., 2001; Zentall, 2006; Zentall et al., 2008). Instead, these authors consider unexpectedness as primordial (Friedman, 2007; Zentall, 2005), and encourage the use of unexpected questions rather than focusing on the what-where-when content. Indeed, in experiments using the what-where-when criterion, although each event is spatiotemporally unique, the subject might develop an expectation of the test and might voluntarily encode the information required later. Using unexpected questions prevents the animal to anticipate the test and thus ensure that the animal need to travel mentally back in time to retrieve memories.

### *1. Content*

#### *a. What – Where – How Long Ago: Temporal distance*

Using the spontaneous caching behaviour of western scrub jays, Clayton and Dickinson (1998) were the first to study episodic-like memory in an animal. Jays were shown to remember what food

item (peanuts or worms) they cached where (various locations on the left or the right side of a tray) and how long ago (4 h or 124 h prior; Figure 2). Prior to the experiment, jays learnt that wax worms, their preferred food, degraded in a few days while peanuts, a less favoured food, did not. During the experiment, jays could cache food during two successive caching phases, before recovering the cached items. In a first caching phase, jays cached one type of food (either peanuts or worms) in one side of a sand filled tray (the other side of the tray was inaccessible). In a second caching phase occurring 120 h later, birds cached the other type of food in the other side of the tray. Jays could recover cached items from the tray with both side accessible four hours later. If the worms were cached in the first phase, they would be degraded and unpalatable at recovery, but if they were cached in the second phase, they would still be palatable. Peanuts would be palatable in any case. 80% of jays were observed searching the worm side at recovery when worms were cached four hours earlier, and all jays searched for peanuts at recovery when worms were cached 124 h earlier. This behaviour was not dependant on smell or sight cues, as test trials were conducted by removing cached items. A control group showed that this behaviour was not spontaneous, but learnt: for the control group, the jays learnt prior to the experiment that the wax worms never degraded and always stayed palatable. In this group, during the experiment, all birds searched for worms whether they were cached 4 or 124 h earlier.

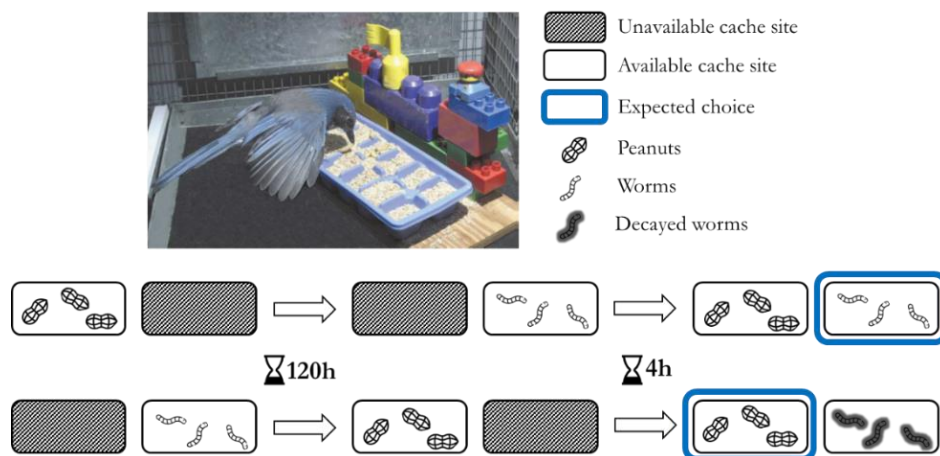


Figure 2: Procedure used by Clayton and Dickinson (1998) for their What-Where-When (temporal distance) task. Western scrub jays cached one type of food in a first caching phase, then after a delay of 120 hours, they cached the second type of food. They recovered their caches after a delay of 4 hours. When worms were cached last, they were palatable at recovery and thus preferentially recovered, while they were decayed and unpalatable when cached first, thus peanuts were recovered. Photograph from Clayton et al. (2003b).

These results were replicated several times, varying the modalities to study into more details the episodic-like memory ability of jays. Memory for content was explored in two other experiments.



In one experiment (Clayton and Dickinson, 1999a), worms were pilfered instead of decayed, and the results obtained were similar in both groups when worms were cached four hours before the recovery phase (*i.e.* search on the worm side). However, after a long interval, the preference was not reversed as in the decayed group. Different hypotheses have been stated: retrieving rotten worms might have a higher negative value than finding empty caches, or jays in the pilfered group maintained their searches on the worm side as finding empty caches might either reveal pilfering (which might not be systematic) or an inability to successfully locate the caches. In another experiment, three types of food with different degrading times were used. Jays quickly learn to recover their more preferred food (worms) at short delays, their second preferred food (crickets) at medium delays and their least preferred food (peanuts) at long delays (Clayton et al., 2001).

Several other vertebrates were tested using similar protocols to explore their what-where-how long ago memory (for a review, see Crystal, 2018). Similar results were obtained with magpies (Zinkivskay et al., 2009), black-capped chickadees (Feeney et al., 2009), hummingbirds (González-Gómez et al., 2011), rats (Babb and Crystal, 2005; Babb and Crystal, 2006) and great apes (chimpanzees, orangutans and bonobos in Martin-Ordas et al., 2010; but see Pladevall et al., 2020 for more conflicting results in gorillas, orangutans, bonobos and chimpanzees). Rhesus monkeys tested in a similar experiment were able to remember the spatial information but did not learn to use the temporal information (Hampton et al., 2005). Great apes were also observed in the wild travelling for trees bearing ripe fruits: Tai chimpanzees (Ban et al., 2014) and gorillas (observed by Tutin, from Suddendorf, 1994) seemed to remember which tree was where, and when to revisit it (depending on the maturation and depletion rates). Meadow voles were also shown to spontaneously remember the reproductive status of two females (what), the location of these females (where) and the delay elapsed since they encountered the females (when), to maximise their reproductive chances (Ferkin et al., 2008). Other vertebrates were tested in a variant of the what-where-how long ago experiment, where subjects were asked to separately retrieve the what, where and how long ago components. Mice were shown to remember which object was where and how recent their experience with the object was (Dere et al., 2005); pigeons could remember what, where and how long ago separately but failed to bound the three components together (Skov-Rackette et al., 2006); rhesus monkeys could remember what, where and how long ago separately, and the three components appeared to be bound (Hoffman et al., 2009).

Only one invertebrate was tested for its what-where-how long ago memory. Cuttlefish were shown to remember what they ate where and how long ago (Figure 3; Joze-Alves et al., 2013b). During the experiment, in a first phase, cuttlefish approached one of the two identical, randomly placed targets. A shrimp (their preferred prey) and a crab were placed in front of the targets and cuttlefish

could choose one prey. In a second phase, which happened one hour or three hours later, the targets were placed at the same location. After a delay of one hour, cuttlefish which approached the target associated with the crab were rewarded (the prey was replenished), while they were not if they approached the target associated with the shrimp (the prey was not replenished yet). After a delay of three hours, cuttlefish were rewarded for any target they approached (both preys were replenished). Cuttlefish learned to approach the target associated with crab after a delay of one hour, and they approached the target associated with their favoured prey, the shrimp, after a delay of three hours. Aged adults tested using the same protocol did not present an age-related decrease in episodic abilities (Schnell et al., 2021c).

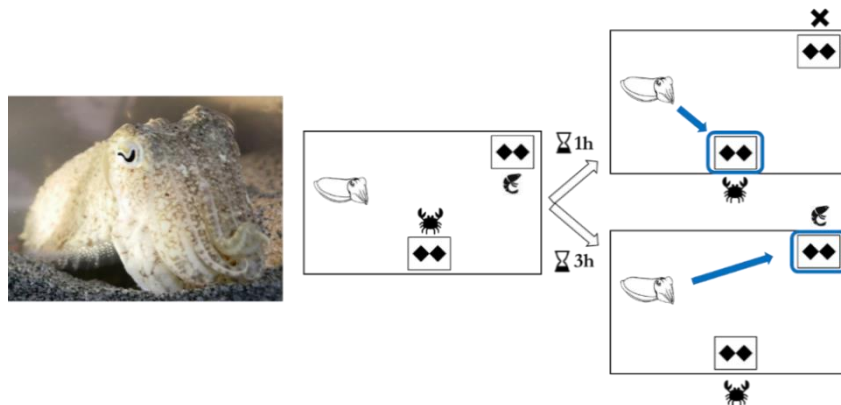


Figure 3: Procedure used by Jozef-Alves et al. (2013) in their *What-Where-When* (temporal distance) task. Common cuttlefish first obtained either a shrimp (their preferred prey) or a crab by approaching one target. Then, they waited for a varying delay. Shrimps replenished depending on the elapsed delay: after a one-hour delay, shrimps were not available, thus cuttlefish went after the crab, while after a three-hours delay, both shrimp and crabs were available, thus cuttlefish went after their preferred prey, the shrimp. Photograph from L. Poncet.

#### b. *What – Where – When: Temporal location*

Rats were tested on their ability to remember “when” (temporal location) an event happened. They first explored an 8-arms maze at 7 am and 1 pm (Figure 4). 4 arms were closed, 3 contained chow, and one contained chocolate, a preferred food. After a short delay, rats were tested in the maze. After a 7 am exploration, chocolate replenished in the same arm at test, while after a 1 pm exploration, it did not replenish anywhere. Chow replenished after 7 am and 1 pm explorations in locations which were previously closed, and arms previously containing chow were empty at test. Subsequent experiments showed that rats based their search for chocolate on the time of the exploration, and thus their choices were not impacted by shifting the light onset, by increasing the delay or by conflicting exploration and test times (Zhou and Crystal, 2009).

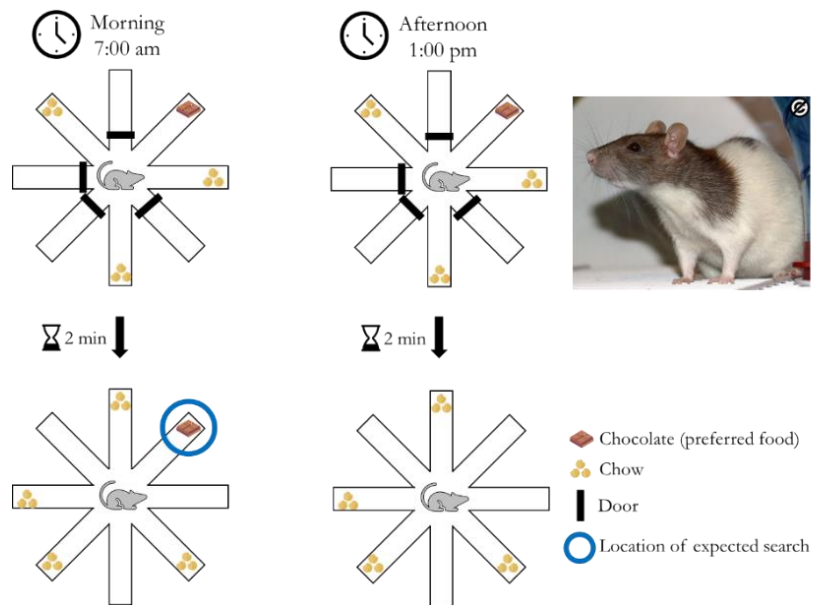


Figure 4: Procedure used by Zhou and Crystal (2009) in their *What-Where-When* (temporal location) task.

Rats were placed in an eight-arm maze either in the morning, at 7 am, or in the afternoon, at 1 pm. Four arms were closed, three arms contained regular chow, and one arm contained the preferred food (chocolate). After a short delay, rats were again placed in the maze. In this second phase, previously closed arms contained chow, arms previously containing chow were empty, and the chocolate arm was replenished only after a morning session, but was empty after an afternoon session.

Preference to use temporal location or temporal distance cues was studied in two species: rats and black-capped chickadees. Rats were tested in a similar procedure as before, and they could rely on temporal location cues (time of the exploration phase, ‘when’) or temporal distance cues (delay elapsed since the exploration phase, ‘how long ago’). Rats favoured temporal distance rather than temporal location cues to solve the task (Roberts et al., 2008). Black-capped chickadees were tested in a similar procedure, and were shown to use both temporal location and temporal distance cues, but they seemed to favour temporal location cues (Feeney et al., 2011a).

Other experiments also studied the ability to remember what, where and when an event happened, but in a semantic way. It means that instead of using unique events, information about content, location and time were kept constant throughout the training, thus subjects could rely on their knowledge of the rule instead of remembering their experience. Bees (Pahl et al., 2007), rats (Iordanova et al., 2008) and cuttlefish (Schnell et al., 2021c) were shown to remember what, where and when in a semantic way.

### *c. What – Where – When: Temporal order*

Memory for the order of elements presented in a sequence was explored in rats (Allen et al., 2014; Fortin et al., 2002), mice (DeVito and Eichenbaum, 2011) and rhesus monkeys (Templer and Hampton, 2013). These experiments were not episodic-like memory experiments but indicated a memory for temporal order. Rodents and monkeys were presented a sequence of five items (odours for rodents, images for monkeys) then had to choose between two items which item occurred the earliest in the sequence. Rodents and monkeys succeeded in the task.

Episodic-like memory was also demonstrated using temporal order with rats (Ergorul and Eichenbaum, 2004; Panoz-Brown et al., 2016) and dogs (Lo and Roberts, 2019). To do so, subjects were successively presented four different odours in different locations, then they had to choose among two odours (what-when) or two locations (where-when) which one was encountered first in the sequence. However, contrary to other what-where-when experiments, subjects did not have to recollect the three components together (only what-when and where-when), thus binding of the three components could not be ensured.

### *d. What – Where – Which*

Some authors consider “which” as an “occasion-specifying context” which works similarly to “when” in an episodic-like memory task (Eacott and Norman, 2004; Eacott et al., 2005).

Eacott and Norman (2004) were the first to use context to explore episodic-like memory in rats without explicit training or food motivation. During the experiment, rats were placed in a context 1 and could explore an object A on the left side and another object B on the right side (Figure 5). They were then placed in a context 2 and could explore the object A on the right side, and the object B on the left side. After a delay, in the test phase, one of the contexts was presented with two copies of the same object (A or B) placed on the left and the right. Rats, which are neophilic, favoured exploration of the object associated to a novel location, showing that rats could remember which object they saw where in which context (Eacott and Norman, 2004). Pigs (Kouwenberg et al., 2009), hummingbirds (Jelbert et al., 2014) and zebrafish (Hamilton et al., 2016) were tested using the same procedure and successfully remembered what object they saw where and in which context.

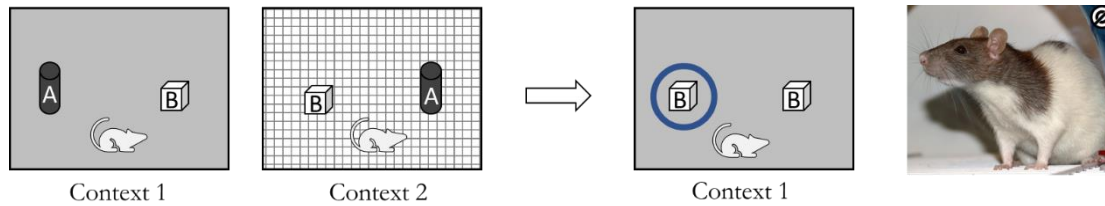


Figure 5: Procedure used by Eacott and Norman (2004) in their What-Where-Which task.

Rats could explore two objects in a first context then the two same objects but in reversed locations in a second context. Rats were then placed in one of the contexts with two copies of the one of the objects previously encountered, and they were expected to explore more the object in the novel location within that context.

Another experiment with rats was conducted to rule out familiarity, using an E-maze to make objects invisible from the starting location. After two exploration phases, as in the previous experience (*i.e.* two objects in reversed position in contexts 1 and 2), rats were allowed to freely explore one of the objects in an open field apparatus. At test, they were randomly placed in one of the previously encountered contexts and they successfully choose to enter the arm which contained the less familiar object according to the context (Eacott et al., 2005).

Another experiment with rats indicated they could remember the presence of numerous odours in a specific context: rats were successively presented with 8 odours in a first context, then they were presented 16 odours (including the 8 previously encountered odours) in a second context. They were then presented the same 16 odours in the first context, and rats had to remember which odour was novel in this context, thus remembering multiple events and the context in which they occurred (Panoz-Brown et al., 2016).

## 2. Structure

To study the structure of episodic-like memory, two experiments were conducted with western scrub jays. In an experiment, researchers used pre-feeding to manipulate which food would be recovered and they showed that scrub jays can remember the what and where in an integrated manner (Clayton and Dickinson, 1999b). To study the structure of jays' memory, jays were presented with two caching trays on two different days, then they could retrieve their caches. Jays searched for worms in the recent tray and peanuts in the one-day old tray. Given that there were two trays with similar content, jays had to remember for each tray what they cached where and when. Jays thus formed an integrated representation of their caches for each tray, and the representation of one tray was distinguishable from the representation of the other tray (Clayton et al., 2001).

Binding of memories into an integrated structure was also explored in rats: during the experiment, they were successively placed in two eight-arm radial mazes with two different contexts (Figure 6). In each maze, they could eat chow and chocolate in different locations. In a second phase, arms which provided chow before were empty, previously empty arms provided chow, and arms previously providing chocolate provided chocolate depending on a rule: during the first phase, if the rat was placed by the experimenter in front of the chocolate arm (experimenter-generated information), then it did not replenish, whereas if the rat found the chocolate arm by walking into it (self-generated information), then it replenished. Rats remembered the location of the “self-generated information” arm providing chocolate even if this location was reversed between the two contexts, showing binding of the information and strong source memory abilities (Crystal and Smith, 2014b).

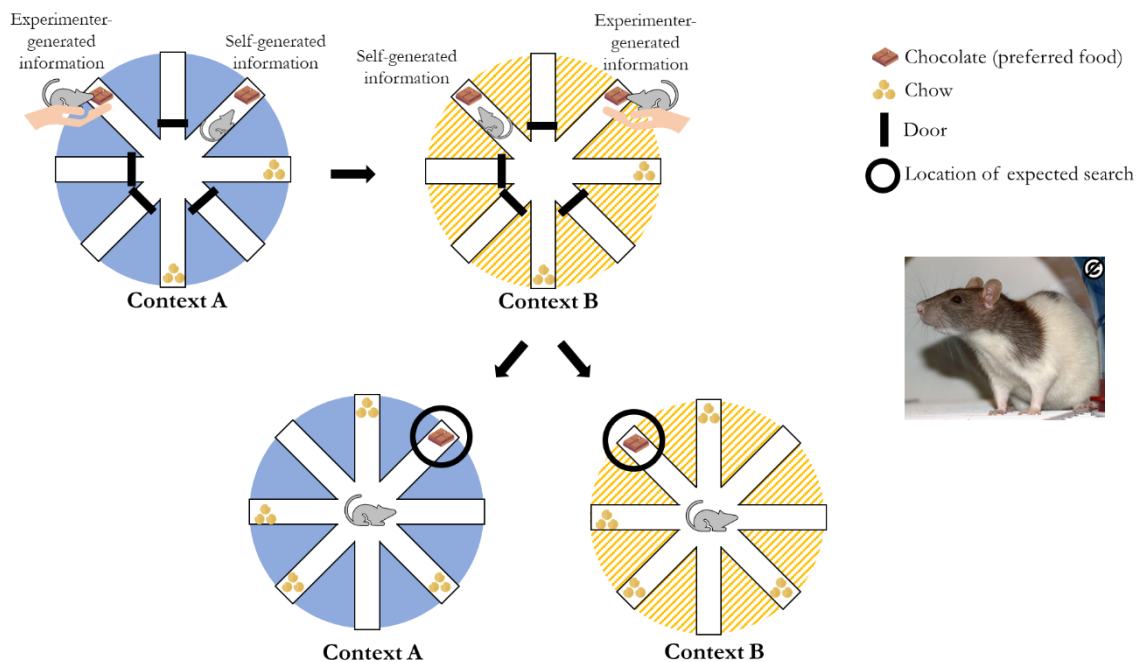


Figure 6: Procedure used by Crystal and Smith (2014b) in their binding task.

Rats were successively placed in two contextually different eight-arm mazes. Rats were positioned by the experimenter in one chocolate arm (experimenter-generated information), then rats explored the maze and found another chocolate arm (self-generated information) and two arms with chow. In a second phase, previously closed arms contained chow, arms previously containing chow were empty, and chocolate was replenished only when information was self-generated (and not when it was experimenter-generated).

### ***3. Flexibility***

Flexibility was explored in several experiments with western scrub jays. In one experiment, jays learnt only after caching the decaying rate of the cached food items. They subsequently integrated this novel semantic information into their episodic-like memories and subsequently recovered food items accordingly (Clayton et al., 2003a). Another experiment showed that caching is also sensitive to its consequences (state of the caches) at recovery. Jays reduced their caching of a food when that type of food was consistently degraded at recovery. It was not a simple conditioning, since jays did not reduce their caching when this food was not degraded after a short delay but was degraded after a long-delay (Clayton et al., 2005). In another experiment, jays were shown to learn a reversed procedure compared to the previously described experiments: worms were unpalatable after a short delay but palatable after a long delay. Jays performed well even in this ripening condition (de Kort et al., 2005). To sum up, these numerous studies show that western scrub jays present the three criteria of episodic-like memory: content, structure and flexibility.

### ***4. Unexpected question***

It can be considered that experiments using training and expected tests favour the use of rule-based memory or semantic memory rather than episodic-like memory (Zentall et al., 2001; Zentall, 2006; Zentall et al., 2008). Some authors such as Zentall (2005) thus consider that instead of focusing on the what-where-when content, episodic-like memory experiments should use unexpected situations and questions.

Zentall and colleagues (2001) studied pigeons' episodic-like memory using a test chamber with three aligned response keys (with projector behind; Figure 7): at first, pigeons were rewarded when they pecked a vertical line then a red light, or when they refrained to peck a horizontal line then pecked a green light. Pigeons were then presented a stimulus they tended to peck (lighted key) or not (unlighted key), then were unexpectedly asked "Did you just peck or did you just refrain from pecking?" using the red and green lights. Pigeons significantly chose the colour consistent with their previous behaviour, recalling what they did. Another experiment showed that pigeons could also report the location pecked on the screen (right versus left) when unexpectedly asked (Zentall et al., 2008).

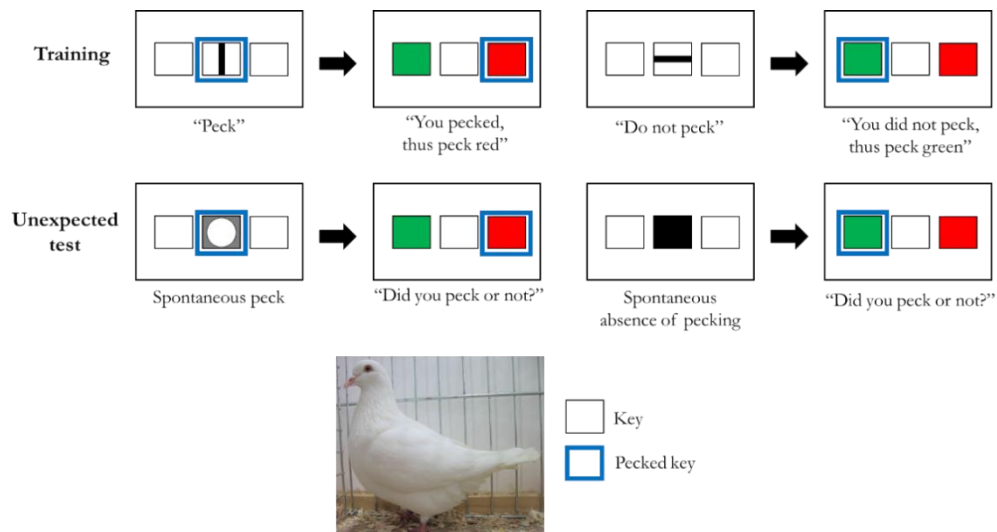


Figure 7: Procedure used by Zentall et al. (2001) in their unexpected question task with pigeons.

Pigeons were trained to peck a vertical line then peck a red key, or to refrain from pecking a horizontal line then peck a green key. They were then tested by showing them either a white circle they tended to spontaneously peck, or a black key they did not tend to peck. They were then unexpectedly presented the green and the red keys, and they were expected to retrieve what they just did, to peck the key accordingly. Photograph from D. Watteau.

Rats were tested using an incidental learning task, where they were unexpectedly asked if food was previously available or not (Zhou et al., 2012). To do so, rats were placed in an eight-arm maze which was divided into two tasks: an exploration task with five arms, and a T-maze task with the three remaining arms (Figure 8). In the exploration task, rats obtained food in some arms, then after a delay, the previously empty arms contained food while the others did not. In the T-maze task, rats were first given food, or not, then they had to go left when they had food and go right when they had not. The unexpected test consisted of presenting food (or not) in various arms during the exploration task, then unexpectedly opening the T-maze arms so rats had to indicate whether they had food or not. Rat successfully answered the unexpected question (Zhou et al., 2012).



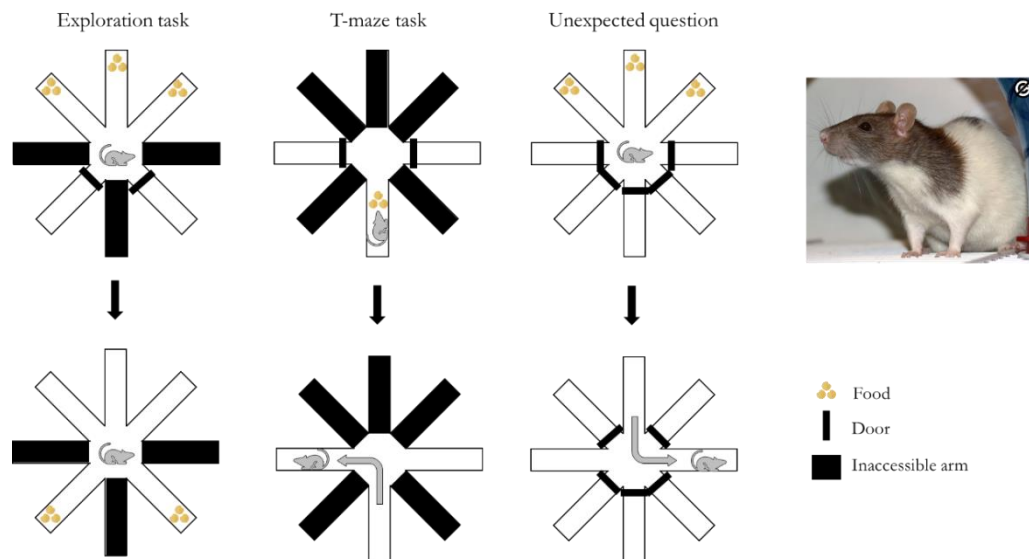


Figure 8: Procedure used by Zhou et al. (2012) in their unexpected question task with rats.

Rats were trained in two tasks: an exploration task, where they had to remember which arm previously contained food to avoid revisiting it; and a T-maze task, where they had to go left if they were previously given food, or go right if not. During the unexpected question, rats began an exploration task where arms contained food (or not), then they were unexpectedly given access to the arms of the T-maze and indicated whether they just had food or not.

Unexpected questions were also used with two bottlenose dolphins, which were trained to repeat the last behaviour performed in response to a gestural command. One of the dolphins generalised the rule and could repeat recently learnt behaviours and even repeat twice a behaviour, even when the command was unexpected (Mercado et al., 1998). Moreover, bottlenose dolphins recently showed episodic-like memory when they were unexpectedly asked an incidentally encoded information about where and who gave them a ball (Davies et al., 2022). Another experiment with chimpanzees and orangutans showed that great apes could remember where to find a tool and how to use it when unexpectedly asked, based on a prior experience that happened three years or two weeks prior (Martin-Ordas et al., 2013).

Unexpected questions are a valuable tool to explore whether animals can incidentally encode events and retrieve features of these memories, even though familiarity can sometimes explain the results. These experiments allow researchers to explore the flexibility of this memory and how subjects can recall memories in various contexts, an ability essential to qualify a memory as episodic-like.

## 5. Reconstructive processes

When defining animal episodic-like memory, Clayton and colleagues (2003) highlighted the need that such memory should possess a structured representation of an event, where features of the

event are bound together at encoding, to allow the complete retrieval of the memory. Although not mentioning it, their description fits within the constructive memory framework, which states that at encoding, features of memories are split and stored individually, and these features are reassembled together at retrieval to recreate the encoded event. Experimental studies on episodic-like memory rarely mention reconstructive processes, although some studies implicitly investigated reconstruction through features binding in scrub-jays (Clayton et al., 2001) and rats (Crystal and Smith, 2014a). Some studies focused on the source memory of an event, which is a way to explore the monitoring of reconstructive processes (for a review see Crystal, 2016). Rats were shown to recollect the source of an information (*i.e.* whether they encountered food by themselves or by being placed in front of it by an experimenter; Crystal and Alford, 2014; Crystal et al., 2013); rhesus monkeys remembered the source of an image, which was touched or categorised (Basile and Hampton, 2017); and cuttlefish remembered the sensory source of a prey, which was smelt or seen (Billard et al., 2020b).

Reconstructive processes can also be explored through their errors, using paradigms leading to the formation of false memories. Very few studies on false memories have been conducted in animals: in the early 2000s, Harper and Garry (2000, 2009) used the term false memories in their studies on pigeons and rats, however it remains uncertain whether tested individuals formed false memories or had recognition biases. Hunt and Chittka (2015) studied memories merging in bumblebees, and while the authors discuss their results in the light of false memories, the use of repeated reinforcement in their experiment rather suggest generalisation or extrapolation abilities. Schwartz and colleagues (2004) tested false memories on a gorilla, where the gorilla witnessed events, then was exposed to misleading pictures and had to choose the right event from picture. While misinformation occurred, the possibility that responses were based on familiarity could not be ruled out.

## **C. Future thinking**

### ***1. Definition and criteria***

Future-oriented behaviours are common in both humans and animals. We talk about our next holiday or buy groceries for our dinner, while squirrels hoard food for the winter or chimpanzees carry stone tools to crack nuts for their next meal. However, future-oriented behaviours can be divided in two classes: behaviours with no future awareness, and behaviours with prospective thinking, such as planning and future thinking (Raby and Clayton, 2009).

Anticipation corresponds to any behaviour that becomes meaningful in consideration of the following events. It can emerge without the need of a representation of the future, through learning or conditioning, innate stereotypical and inflexible behaviours (*e.g.* hibernation, or migration) or even coincidence (Suddendorf, 1994). On the opposite, episodic future thinking is defined as a projection into the future to pre-experience a hypothetical event that involves the self and which can be used flexibly to plan actions (Atance and O’Neill, 2001; Eacott and Easton, 2012; Szpunar, 2010). Future thinking relies on reconstruction, imagination, probability and evaluation processes (Suddendorf and Busby, 2005). Future planning is a type of future thinking where future needs are anticipated independently of current needs (Clayton et al., 2003b; based on the Bischof-Köhler hypothesis, from Suddendorf (1994), which states that animals cannot anticipate future needs and are bound to their current needs). Planning requires multiple skills, such as problem representation, goal selection, strategy choice, execution and monitoring (Atance and O’Neill, 2005). Future thinking and planning are used to increase future survival chances (Suddendorf, 1994; Suddendorf and Busby, 2005; Tulving, 2005); but also for motivation (Boyer, 2008; Suddendorf and Busby, 2005). Indeed, it can act as an emotional reward, by projecting oneself into a positive future state.

## ***2. Episodic memory and future thinking linkage***

A wide range of researchers accord on the hypothesis that Mental Time Travels into the past and the future are linked, and that episodic memory and its reconstructive processes evolved for future thinking, rather than for remembering (Addis et al., 2007; Boyer, 2008; Klein et al., 2010; Schacter et al., 2007; Suddendorf and Busby, 2003; Suddendorf and Corballis, 2007; Suddendorf and Corballis, 2008; Tulving, 1985; Tulving, 2005).

Several evidences support this hypothesis. First, retrospective and prospective MTT are both episodic abilities relying on auto-noetic consciousness (Atance and O’Neill, 2005). Secondly, subjects such as K.C. and D.B. who lost their episodic but not semantic memory lost as well the ability to anticipate their personal future but not the general future (Klein et al., 2002). Thirdly, episodic future thinking and episodic memory show the same age-related development: they emerge between three and four years of age (Suddendorf and Busby, 2005), slowly develop in the following years (Friedman, 2007) and they are both sensitive to physiological aging (Addis et al., 2008; Schacter et al., 2007) and to age-related diseases such as Alzheimer’s disease (Addis et al., 2009). Fourthly, episodic memory and future thinking share a common neural network, with mainly the superior frontal, prefrontal and medial temporal areas, and the left hippocampus (Figure 9; functional Magnetic Resonance Imaging, Addis et al., 2007 and Szpunar et al., 2007; Positron

Emission Tomography measuring cerebral blood flow, Okuda et al., 2003). It is worth noting that while no regions were found to be uniquely engaged in remembering (Addis et al., 2007), some areas are only involved in future thinking, such as the right frontopolar cortex, the left ventrolateral prefrontal cortex, the right hippocampus and the left parahippocampus (Okuda et al., 2003; Szpunar et al., 2007). These areas are thought to be linked with imagination and novelty (Szpunar et al., 2007).

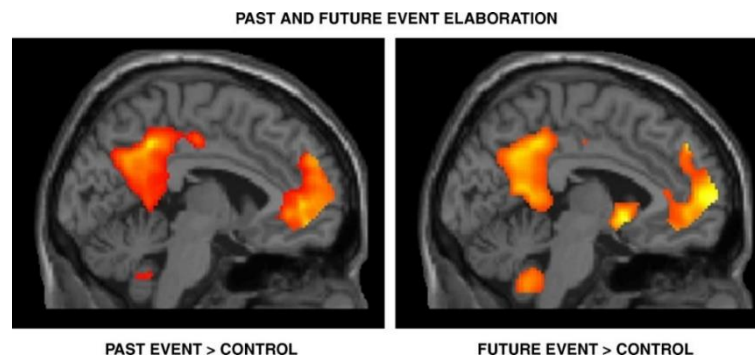


Figure 9: fMRI brain activity during thinking about personal past event (left) or personal future events (right; signal changes relative to a semantic control task; from Addis et al., 2007).

### ***3. Future thinking in animals***

Bischof and Bischof-Köhler claimed that animals cannot anticipate future needs or states and are bound to their current state, thus elaborating the Bischof-Köhler hypothesis (Suddendorf, 1994; Suddendorf and Corballis, 1997). In early 2000, Roberts concluded that no sufficient evidences were available to consider that animals could travel in time, especially in the future (Roberts, 2002), but several studies conducted since contradict these statements. The lack of evidences of planning abilities in animals may come from the underestimation of the costs associated with delayed rewards, the poor self-control and inhibition skills of subjects as well as the irrelevance of hoarding food in a social context in which pilfering occurs (Zentall, 2010).

In order to refute the Bischof-Köhler hypothesis, several criteria have been set to explore future representations in animals (Osvath and Osvath, 2008; Suddendorf and Corballis, 2010; Suddendorf, 1994; Suddendorf and Corballis, 2007; Tulving, 2005; Clayton et al., 2003b). To qualify a behaviour as future planning, animals must be able to plan for a future need independently of their current needs. The behaviour must not be instigated by a present need, nor cued by specific environmental stimuli (not a conditioned or learnt behaviour). A clear temporal-spatial separation between the action and its consequence should be used, and single trials should be favoured. The behaviour should not be innate, thus flexibility should be sought.

Other tests on future thinking are based on Tulving's spoon test (Tulving, 2005). The illustration of the spoon test is a young girl who dreamt of a cake, but could not eat it because she had no spoon. Thus, the next night, she went to sleep holding a spoon to eat the cake in her dreams. Spoon tests used with animals require the subject to select a tool that will be useful later to obtain food.

*a. Future-oriented behaviours observations*

Observation of animals in the wild can provide indications of future-oriented behaviours, but in the absence of an experimental framework, it is difficult to categorise them as future planning.

Observation of wild Tai chimpanzees showed that they could anticipate that a tree would bear valuable mature fruits by orienting their walk toward the tree long before it was in sight (Ban et al., 2014). Tayras (*Eira barbara*) cache unripe fruits, sapote and plantains, so they will ripen while hidden. This ability might come from innate predispositions, developed learning abilities or prospective thinking (Soley and Alvarado-Díaz, 2011). Captive western scrub jays which already pilfered caches of other individuals used their personal experience to re-cache food items when they had been observed during caching. Jays without experience did not re-cache (Emery and Clayton, 2001). Stone gathering and throwing of a captive male chimpanzee show indications of future planning: the gathering and manufacturing of stones using concrete was conducted calmly outside of opening hours of the zoo when he did not need to throw stones. When the zoo opened, the chimpanzee used the stones only to throw on visitors (Osvath, 2009).

*b. Inhibition by anticipation tasks*

In inhibition tasks, animals have to inhibit their desire to select or eat a larger quantity of food by anticipating they will obtain more food (or a more attractive type of food) later.

Squirrel monkeys learnt to choose counterintuitively the smaller quantity of peanuts instead of the larger one. In one experiment, a small and a large quantity of food were proposed to the monkeys. However, choosing the larger quantity of food led to the food being pilfered, thus the monkeys could eat very few of the peanuts. The smaller quantity was not pilfered, thus one of the monkeys learnt to favour the smaller quantity, and both monkeys began to hoard food. In the second experiment, monkeys preferentially chose the smaller quantity of food rather than the larger quantity when they learnt that they would obtain a lot more peanuts subsequently by doing so (McKenzie et al., 2004).

Black-capped chickadees learnt to consume less seeds or avoid seeds in a certain location to get more worms. In a first experiment, they could consume sunflower seeds, then waited before they could consume mealworms. Over the repeated trials, birds decreased their seeds intake. Birds probably showed anticipatory contrast, which corresponds to the suppressed intake of a lesser value food in a first phase in favour of a higher value food in a second phase. In a second experiment, chickadees were presented artificial trees, divided in a worm patch and a seed patch (Figure 10). In a first phase, sunflower seeds were available everywhere for the birds to eat. In a second phase, depleted locations were not replenished, and non-depleted locations were replenished depending on the patch they were in. The seed patch replenished with seeds, and the worm patch replenished with preferred worms. Birds associated consuming seeds in the worm patch in the first phase with future unavailability of the worms in the second phase, thus they learnt to inhibit their intake in this patch in the first phase (Feeney et al., 2011b).

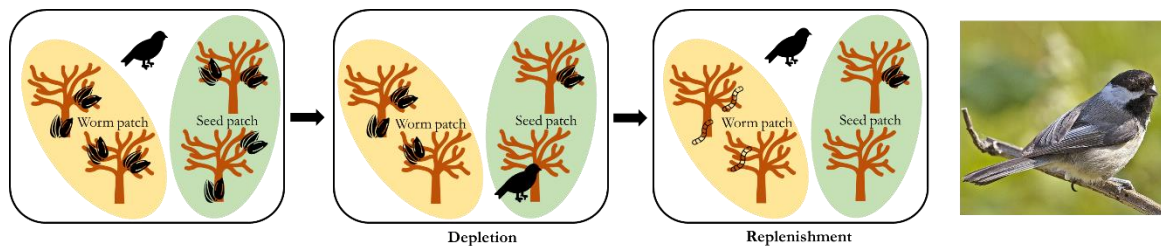


Figure 10: Procedure used by Feeney et al. (2011b) for their inhibition by anticipation task.

Black-capped chickadees were presented a worm patch and a seed patch both provided with sunflower seeds. After letting birds forage in the two patches, only non-depleted locations were replenished by the experimenters. Unconsumed seeds were replaced by preferred worms in the worm patch, and not in the seed patch. When tested again, birds showed anticipation by preferentially depleting the seed patch and avoiding the worm patch when allowed to forage (depletion phase). Photograph from A. D. Wilson.

In an experiment, cuttlefish were given crabs in the morning and shrimps in the evening. They quickly learnt to reduce their predation on crabs during the day when they knew shrimp would be available in the evening, but they ate crabs during the day when they could not predict the later availability of shrimps (Billard et al., 2020a).

### c. Spoon tests

In spoon tests, animals must select and carry a tool that will be useful later. Spoon tests can be ambiguous tests of future planning, since animals might have a desire in the present for the food and select and hold the tool for this present need, until it can be fulfilled, thus showing no planning (Suddendorf et al., 2009b).

Bonobos and orangutans were tested in a spoon test, where they chose a tool before going to a waiting room. One hour or half a day later, they could return to the test room, where was the apparatus containing a reward which could be obtained only with the tool. The subjects transported a tool out of the test room most of the time, and chose the suitable tool significantly more often than chance. They returned in the test room with the suitable tool more often than with an unsuitable tool (Mulcahy and Call, 2006; but Dufour and Sterck, 2008, got more ambiguous results). Chimpanzees and orangutans underwent the same experiment, and they were moreover tested on self-control: they selected the tool even in presence of a grape, a more immediate reward, and they selected the grape when they already had the tool in hand (Figure 11; Osvath and Osvath, 2008). This self-control task indicates that these apes can favour a future desire against an immediate reward, contradicting the Bischof-Köhler hypothesis. An equivalent experiment was conducted using an exchange task, where great apes could first collect a specific object, transport it and keep it, then exchange it later by giving it to the keeper to get a food reward. In some experiments, chimpanzees failed to select the right object, thus not planning for the exchange (Bourjade et al., 2014; Dufour and Sterck, 2008). However, in other experiments, chimpanzees and orangutans exchanged the right token with a human (Osvath and Persson, 2013), and bonobos and orangutans secured a token to exchange it later for food (Bourjade et al., 2014)

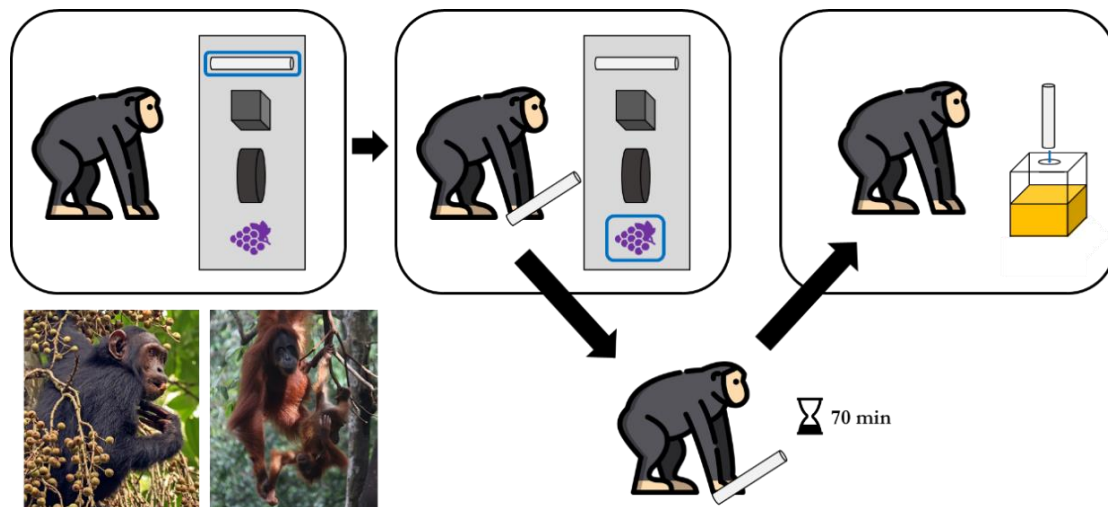


Figure 11: Procedure used by Osvath and Osvath (2008) for their spoon test task.

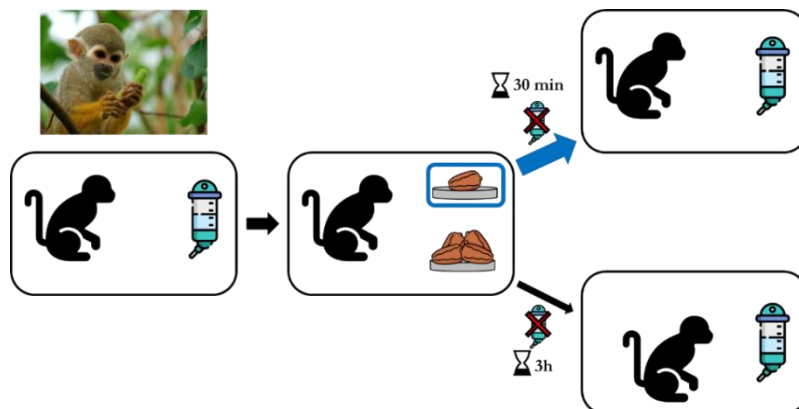
Chimpanzees and orangutans were presented a tray containing several objects and a small immediate reward (a grape). After selecting an object (most great apes chose the suitable tool, a hose), they were once more presented the tray, and all great apes chose the grape. Then they waited outside the experimental room for 70 minutes before gaining access to the reward apparatus containing juice, which was accessible only by using the hose. Photographs from C. J. Sharp and A. Zwegers.

Ravens were also tested on the tool task and the exchange task, and they selected, saved, and used a tool or an exchangeable token at a high success rate, even with delay of 17 hours. In the self-control experiment, ravens chose tokens or tools instead of immediate food in most of the trials (Kabadayi and Osvath, 2017).

#### *d. Future planning tasks*

Future planning experiments are constructed in order to refute the Bischof-Köhler hypothesis. Animals are tested on two conflicting needs, one present need and one future need, and have to act in other to insure the satisfaction of the future need.

Squirrel monkeys were tested using hunger and thirst (Naqshbandi and Roberts, 2006). In the experiment, nonthirsty monkeys had their water bottle removed and then they chose between a smaller and larger quantity of food (Figure 12). Consumption of the food induced thirst, and choice of the smaller quantity led to the return of the water bottle sooner than choice of the larger quantity. Monkeys reversed their baseline preference for the larger quantity of food, showing planning of their future need for water even if they were not thirsty. Rats tested in a similar experiment did not show any planning abilities (Naqshbandi and Roberts, 2006).



*Figure 12: Procedure used by Naqshbandi and Roberts (2006) for their future planning task.*

*Squirrel monkeys had ad libitum access to water prior to the experiment. The water was then removed and they were given a choice between half a piece and four half pieces of date. The smaller quantity led to the return of water after 30 minutes, while the bigger quantity led to the return of water after 3 hours. Monkeys subsequently learnt to select the smaller quantity to quench their thirst more quickly. Photograph from L. Viatour.*



Another experiment was conducted with western scrub jays. They were placed alternatively for six mornings in either a breakfast compartment, where they were given food, or a no-breakfast compartment, where they were not given any food (Figure 13). Then, they were given pine nuts one evening they could cache in both compartments. Jays stored more food in the no-breakfast compartment than the other one, planning for their future hunger. In a second experiment, jays were given kibble in one compartment and peanuts in the other. During the evening they could cache both food in both compartments. Jays cached more peanuts in the kibble compartment and more kibble in the peanuts compartment, planning for their future breakfast (Raby et al., 2007).

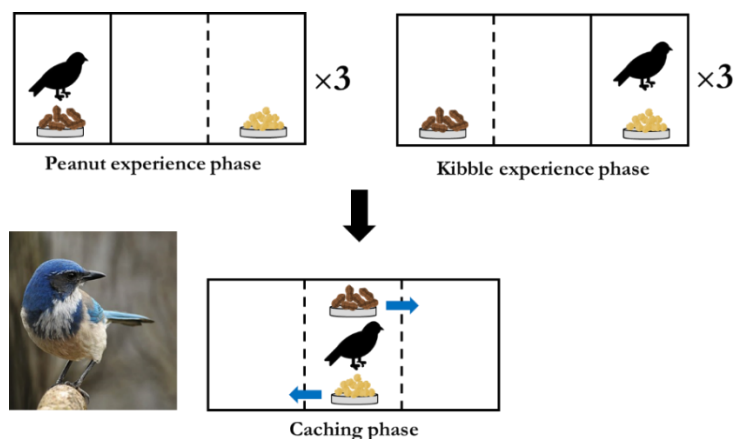


Figure 13: Procedure used by Raby et al. (2007) for their future planning task.

*Western-scrub jays were placed either in a compartment containing peanuts, or in a compartment containing kibble for three mornings each. Then, one evening, they could cache both types of food in both compartments. Jays cached more peanuts in the kibble compartment and more kibble in the peanuts compartment. Photograph from M. Layne.*

Western scrub-jays were also tested using specific satiety. It corresponds to the pre-exposure to one type of food which reduces the incentive value of that food and selectively reduces the subsequent consumption and caching of this food. During the experiment, in a first phase, jays ate either pine seeds or kibbles until satiety (prefed food), then they could cache the two types of food items. In a second phase, they were again fed until satiety with either the same type of food as the first stage (control) or with the other type of food (test), then they could recover their caches. While the control group continued to preferentially cache the non-prefed food, the test group switched their preference and cached the prefed food. Jays thus cached accordingly to their future state over their current one (Correia et al., 2007). In another experiment, Eurasian jays cached different types of food in trays (Figure 14). At first, they could cache food A and B in two trays. After a first delay, they were prefed with A then they could retrieve from the first tray. Then after a second delay, they were prefed with food B and could retrieve from the second tray. After a first experience where they cached equally both food in both trays, jays started to preferentially cache food B in the first

tray and food A in the second tray. Thus, jays distributed the cached food according to their future desires which were different from their current ones (Cheke and Clayton, 2012).

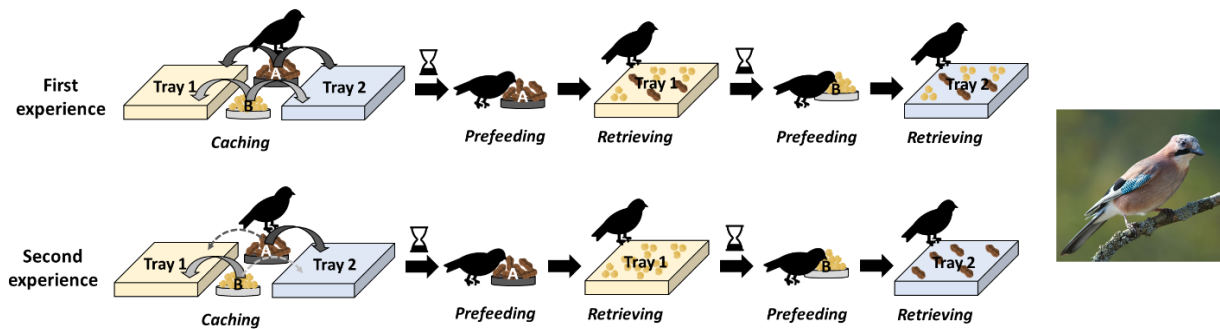


Figure 14: Procedure used by Cheke and Clayton (2012) for their future planning task.

During the first experience, Eurasian jays could cache two types of food (A and B) in two trays. After a delay, they were pre-fed with food A and retrieved the food cached in the first tray. Then, after a delay, they were pre-fed with food B and retrieved the food cached in the second tray. During the second experience, jays underwent the same procedure, but they cached food based on their previous experience and according to their future desire, and thus cached more items of food A in the second tray, and more items of food B in the first tray. Photograph from L. Viatour.

#### a. Neural investigation of future planning

As similar cerebral areas are activated by both episodic memory and future thinking in humans (Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007), a study explored whether the hippocampus of rats, known for its role in episodic-like memory, had also a role in future planning. The experiment showed that prior to navigation, the hippocampus of rats generates sequences corresponding to spatial trajectories from the current location to a known goal location, which are depicted in the brain prior to movement. These sequences flexibly predict immediate future navigational behaviour, and they are a recombination of previous episodes, similarly to humans (Pfeiffer and Foster, 2013).

## II. Comparative study of Mental Time Travels

### A. Comparative cognition

#### *1. Definitions*

Cognition corresponds to the flexible processes by which information from the environment are perceived, processed, stored, retrieved and used to take decisions and act (Chittka et al., 2012; Neisser, 1967; Shettleworth, 1998; Shettleworth, 2000). These information can be transformed or recombined to generate new information (Bayne et al., 2019; Chittka et al., 2012; Neisser, 1967; Shettleworth, 1998).

Comparative cognition research emerged from the idea that there are cognitive processes that are shared across species, notably between humans and nonhuman animals such as great apes (Beran et al., 2014; Bräuer et al., 2020; Wasserman et al., 2006). Comparative cognition tackles two questions: what are the cognitive processes of animals, and how cognition evolves and what selection pressures shape cognition (Clayton in Bayne et al., 2019; Chittka et al., 2012; Eaton et al., 2018).

Comparative cognition focuses on various fields of research, such as social cognition, and its multiple subcategories like communication, recognition, cooperation, social learning, deception or theory of mind, but also spatial cognition, tool use, causal relations, personality, numerosity, emotions or mental time travels (Beran et al., 2014; Shettleworth, 2010). It shows that complex cognitive abilities emerged multiple times independently, based on various neural substrates (*e.g.* cortex in mammals, nidopallium in birds, vertical lobe in cephalopods; Bayne in Bayne et al., 2019). Three main mutually non-exclusive hypotheses try to explain how cognitive abilities evolve: the social intelligence hypothesis, the ecological intelligence hypothesis and the predator-prey interaction hypothesis.

#### *2. Hypotheses on the evolution of cognitive abilities*

To understand what shapes the evolution of cognitive abilities, some researchers compare the brain size or the degree of encephalisation (*i.e.* the brain to body ratio) of different species (Barton and Dunbar, 1997; van der Bijl and Kolm, 2016), as well as the number of neurons in specific brain structures, and some considerate those values as a proxy for cognitive abilities (Herculano-Houzel, 2017).

Initially, an epiphenomenal hypothesis was elaborated. It stated that brain size was a by-product of body size (Dunbar, 1998). However, this hypothesis is unlikely, as different brain sizes were

observed for the same body size (hence the later use of degree of encephalisation). Since the brain consume a lot of energy (about 20% of the total energy expenditure), possessing a bigger brain must come from external demands selecting it (Dunbar, 1998). To determine these external pressures, comparative cognition compares brain size or encephalisation of different species with varying social or environmental complexity (Barton and Dunbar, 1997; van der Bijl and Kolm, 2016).

*a. Social intelligence hypothesis*

The social intelligence hypothesis emerged from the study of the large brains of primates, whose size is correlated with the social complexity of the species. Social complexity is notably visible through ‘Machiavellian’ strategies such as tactical deception, plotting and coalition-formation in fight for dominance (Barton and Dunbar, 1997; van der Bijl and Kolm, 2016). The observation of this social competition lead to the elaboration of the Machiavellian intelligence hypothesis (Barton and Dunbar, 1997; Dunbar, 1998). However, brain size and cognitive complexity is rather correlated with another type of social complexity: the group size, linked with the propensity of cooperative behaviour, social bonding and social learning (Dunbar, 1998; van der Bijl and Kolm, 2016). This thus led to the emergence of the social intelligence hypothesis (Dunbar, 1998).

*b. Ecological intelligence hypothesis*

The Ecological or foraging niche intelligence hypothesis states that large brains come from the need to find and extract food in a patchy and unpredictable environment (Barton and Dunbar, 1997). The hypothesis expects large brains to emerge because of the need of a complex memory and mental maps to remember the spatiotemporal location of ephemeral and patchy resources, and the ability to extract food (Barton and Dunbar, 1997; Dunbar, 1998). However, this hypothesis is not confirmed in primates (Byrne and Bates, 2007).

*c. Predator-prey interaction hypothesis*

The predator-prey interaction hypothesis supposes that the relation between preys and predators creates an arm race with a strong selection and a huge fitness cost, and this might impact cognitive strategies to avoid predators or find preys (Byrne and Bates, 2007). The predator–prey dynamic could be compared to the group members’ dynamics in dominance competition, as both require interactions with another individual pursuing personal gains (Amodio et al., 2019). This hypothesis

is plausible as there is a correlation between preys and predators brain sizes (van der Bijl and Kolm, 2016), as well as there is a link between predatory response and brain size in guppies (van der Bijl et al., 2015).

These three hypotheses are not mutually exclusive, and none reflects the reality better than the other, depending on the considered cognitive abilities or the studied species. Thus, primates fit well into the social intelligence hypothesis (Dunbar, 1998), while mammalian predators fit better into the predator-prey interaction hypothesis (van der Bijl and Kolm, 2016). Exploring multiple species living under various socioecological conditions is essential to better understand how cognitive abilities evolve.

## **B. Animals studied in the present thesis**

Comparative research is often biased by an anthropocentric view (Beran et al., 2014; Bräuer et al., 2020; Wasserman et al., 2006), thus the majority of comparative studies focuses on primates and looks for human-like cognitive abilities. Nevertheless, other species are also often studied, such as rats, pigeons and other birds in general, and dogs, bringing new insights into comparative cognition (Beran et al., 2014).

The focus on mammals and birds have brought the idea that the emergence of complex cognition comes from an omnivorous diet, socioecological challenges and a slow life history with a long developmental period paired with an extended longevity (Bayne et al., 2019; Schnell et al., 2021a). However, among invertebrates, complex cognition emerged in animals with an only carnivorous diet, a solitary lifestyle and a short life history: the cephalopods (Figure 15). These molluscs are defined by a rich, complex and flexible behavioural repertoire (Hanlon and Messenger, 2018). They predate upon a variety of dispersed preys, whose flesh needs for some to be extracted out of the shell or carapace. They live under strong predatory pressure, and their social interactions are mostly restricted to the reproductive period which occurs at the end of their one-to-two years life for most species. Cephalopods are thus the ideal candidates to challenge the social intelligence hypothesis and explore the ecological and predator-prey interaction hypotheses, to better understand the evolution of complex cognition (Schnell et al., 2021a).

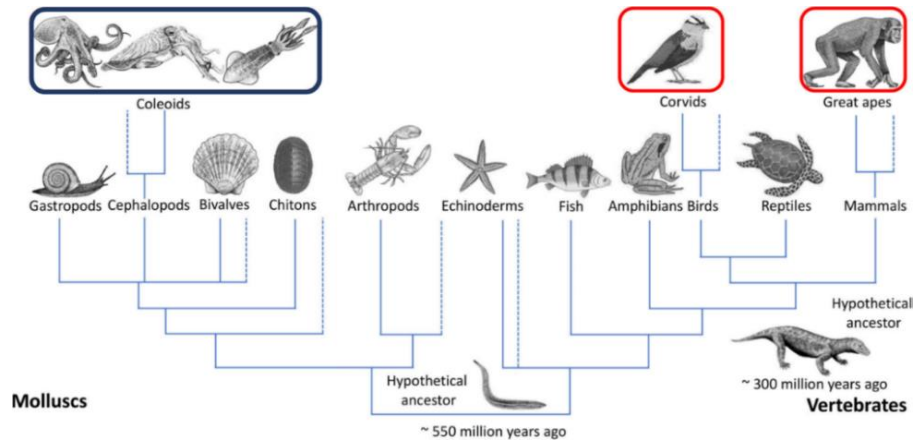


Figure 15: Phylogenetic tree showing commonly used species to investigate complex cognition (corvids, great apes), in parallel with molluscan coleoids, from Schnell et al. (2021a).

### 1. Generalities on cephalopods

Cephalopods are a class of the *Mollusca* phylum. The earliest cephalopods existed about 530 million years ago (Hanlon and Messenger, 2018), and the 700 species of cephalopods found today are only a small subpart of the 10,000 recorded fossil species (Boyle and Rodhouse, 2008).

Modern cephalopods, known as *Coleoidea* (or *Neocoleoidea* if we exclude the extinct taxon of the *Belemnoidea*) are divided between octopodiformes (about 200 species) and decapodiformes (about 450 species), which diverged 276 million years ago (Figure 16; Hanlon and Messenger, 2018).

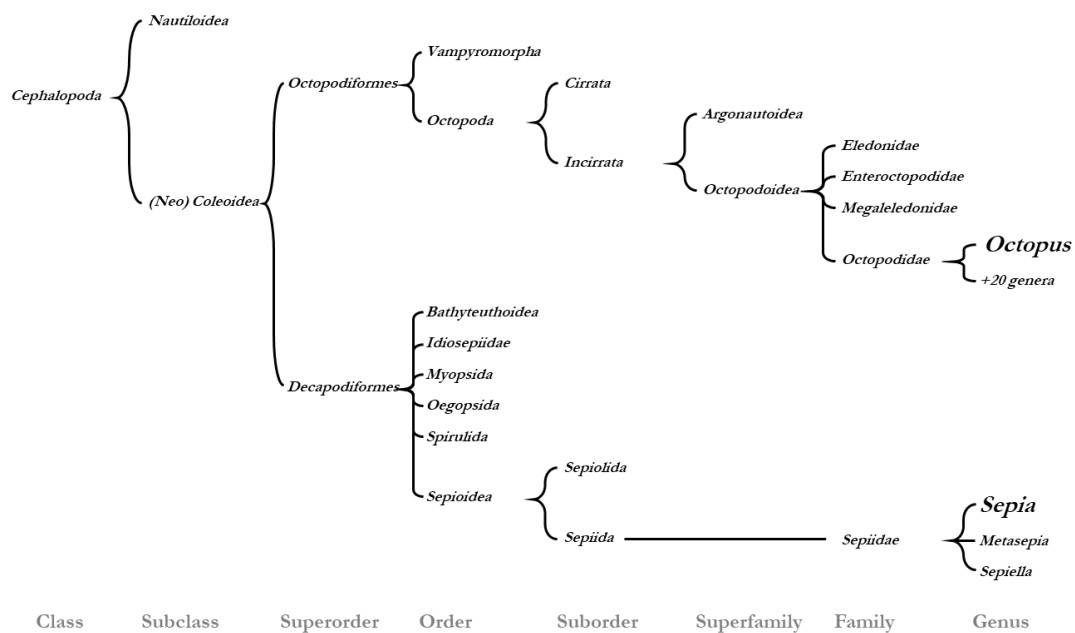


Figure 16: Phylogenetic tree of cephalopods.

Coleoids share a common anatomy, with a body divided between the cephalopodium and the visceropallium (Figure 17; Mangold, 1989). The cephalopodium comprises the head, the funnel and the brachial system with eight (in octopodiformes) or ten arms (in decapodiformes, two arms are modified in retractable tentacles). The visceropallium is constituted of an internalised shell, which is markedly reduced in octopods, a muscular mantle with fins, which are reduced or absent in octopods, and a paleal cavity containing the organs, such as the respiratory system, the digestive system, the circulatory system, the reproductive system and the ink sac.

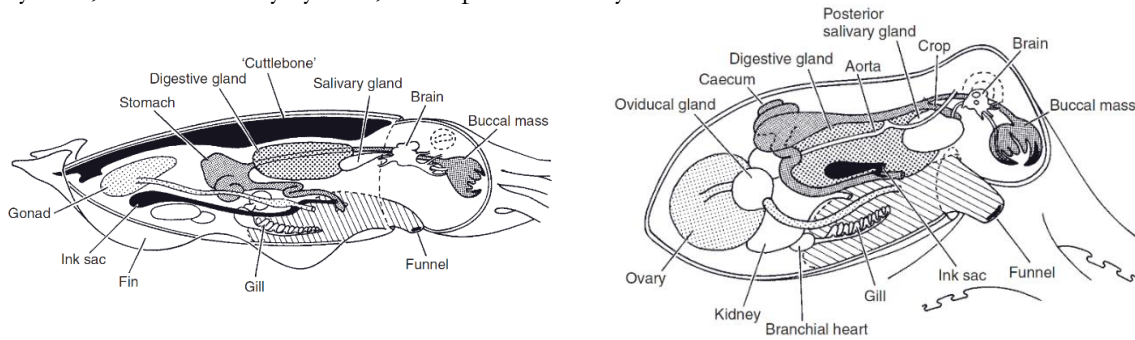


Figure 17: Representation of the internal organisation of cuttlefish (left) and octopus (right), from Boyle (2010).

## 2. Ecology

### a. Ecology of the common cuttlefish

Common cuttlefish (*Sepia officinalis*) are found only in western European and north African waters (Mediterranean Sea, northern-eastern cost of Atlantic Ocean, Channel Sea and North Sea; Figure 18; GBIF Backbone Taxonomy, 2021). They favour sandy and muddy bottoms in shallow waters, from the coastline to 100m depth, but can be found until 200m depth (Roper et al., 1984).

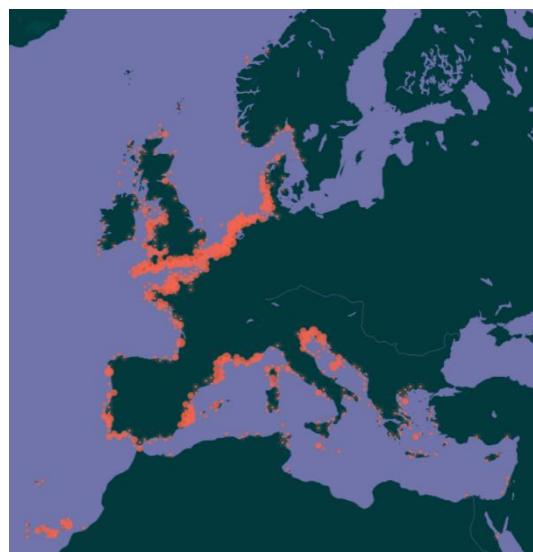


Figure 18: Map of the distribution of *Sepia officinalis* (GBIF Backbone Taxonomy, 2021a)

In the Channel Sea, cuttlefish show migration patterns linked to reproduction, but their life cycle is peculiarly consistent. Cuttlefish are semelparous and lay a few thousand eggs from February to July, and fully-formed juvenile hatch during the summer months (June to September). During the autumn, they migrate in deeper offshore waters where they spend the winter. The now subadults individuals return inshore in spring, where they begin to show signs of sexual development, even if most of them are not ready to reproduce. They again migrate in autumn to spend the winter offshore, and return to the coast in spring as fully-mature adult cuttlefish. Mating and egg laying happen shortly after their return, and cuttlefish enter a few-days-long senescence before dying at the end of their second year of life (Dunn, 1999).

Common cuttlefish are considered in between solitary and gregarious (Boal, 2006), as juvenile and subadult cuttlefish can be observed in group in the wild (Drerup and Cooke, 2021). Under captive conditions, they are socially tolerant, although sexually mature male display aggressive interactions towards other males (Hanlon and Messenger, 2018).

Cuttlefish feed on mobile preys, mostly on crustaceans of the infraorders *Brachyura* (“crabs”) and *Caridea* (“shrimps”), as well as on fishes (Table 1). Cannibalism can happen in the wild, and fragment of bivalves, gastropods and worms (annelids or nemerteans) have been found in stomach contents of cuttlefish (Alves et al., 2006a; Castro and Guerra, 1990; Le Mao, 1985; Najai and Ktari, 1979; Neves et al., 2009; Pinczon du Sel et al., 2000). Cuttlefish are considered as opportunistic predators, thus the species they consume vary greatly as they grow, and depend on the place and environment they live in (Neves et al., 2009; Pinczon du Sel et al., 2000). However, an experiment has shown that they can switch to a selective strategy depending on prey availability (Billard et al., 2020a).

Table 1: Comparison of composition of the food diet of cuttlefish and octopus. (Ajana et al., 2018; Alves et al., 2006a; Ambrose and Nelson, 1983; Anderson et al., 2008; Castro and Guerra, 1990; Le Mao, 1985; Najai and Ktari, 1979; Neves et al., 2009; Pinczon du Sel et al., 2000; Smith, 2003).

		Range of occurrence in diet (in %)	
		<i>Sepia officinalis</i>	<i>Octopus vulgaris</i>
<b>Fishes</b>		17-47	0-12
<b>Crustaceans</b>	<i>Brachyura</i>	26-35	12-38
	<i>Caridea</i>	1-25	<1
	<i>Anomura</i>	1-11	0-4
	Others	1-22	0-26
<b>Molluscs</b>	Cephalopods	0-14	0-5
	Bivalves	0-13	1-70
	Gastropods	0-3	1-72
<b>Worm-likes</b> ( <i>Annelida</i> , <i>Nemertea</i> )		0-2	0-8



### *b. Ecology of the common octopus*

Common octopuses (*Octopus vulgaris*) are found worldwide under temperate and tropical climates (Figure 19). In Europe, they are mostly found on the Atlantic coast and in the Mediterranean Sea (GBIF Backbone Taxonomy, 2021b; Luca et al., 2014). They are found from the coastline to 100m depth, even if some individuals can be found at 200m depth. They evolve in various habitats, from rocky reefs to grass beds (Roper et al., 1984).



*Figure 19: Map of the distribution of Octopus vulgaris (GBIF Backbone Taxonomy, 2021b)*

Octopuses show limited migration patterns, mostly linked with spending winters in deeper waters (Roper et al., 1984). In the Mediterranean Sea, common octopuses, which are semelparous, spawn all year round, but two spawning peaks are clearly identifiable, around mid-spring and mid-autumn (Katsanevakis and Verriopoulos, 2006; Roper et al., 1984), which generate two independent and parallel life cycles. Spring cycle octopuses lay a few hundred thousand eggs in February-March which develop in two to three months. Paralarvae hatch from these eggs and need two months to become fully-formed octopuses and settle, thus juveniles are found during summer. Adults mate during the next winter and die in the following months. Thus, the spring cycle is regular and create a bigger spawning than the autumn spawning. Autumn cycle octopuses lay their eggs from June to August, and paralarvae spawn from August to October. They settle after one month, from September to November, and adults mate at the end of the following spring, and die a few weeks to months after (Katsanevakis and Verriopoulos, 2006). Octopuses show a one to two years life cycle.

Octopuses are solitary in the wild, even if they can be occasionally found in dens close to each other (less than one-metre away; Guerra, 1981; Guerra et al., 2014). They show intolerance and

aggressivity toward conspecifics in restricted captive conditions (Hanlon and Messenger, 2018). Octopuses were found forming hunting associations with fishes such as groupers (Sampaio et al., 2021a). Fishes indicated the presence of preys to the octopus, and the octopus extracted the preys from crevices. Fishes could then eat the preys which escaped from the octopus. This behaviour thus enhances both the octopus' and the fishes' hunting success rate.

Octopuses feed on both sessile and mobile preys, mostly on *Brachyura* ("crabs"), bivalves and gastropods. They occasionally consume fishes, others crustaceans and annelids. Cannibalism is seldomly observed (Ajana et al., 2018; Ambrose and Nelson, 1983; Anderson et al., 2008; Smith, 2003). Octopuses are considered opportunistic at the species level, thus proportions of species consumed greatly depend on the place and environment octopuses live (Table 1). At the individual level, octopuses vary in their preferences, with some being opportunistic and other specialists of different types of preys (Anderson et al., 2008; Mather et al., 2012).

### *c. Anti-predatory behaviours of the coleoids*

Cephalopods are a prey of choice for many species, as they provide a lot of protein with few indigestible parts. Cephalopod predators vary as they grow, and can be found in various taxa: carnivorous teleosts and chondrichthyans, sea birds, seals and cetaceans (Boyle and Rodhouse, 2008). Juvenile individuals are particularly vulnerable to carnivorous fishes, while adults are hunted by marine mammals such as seals and toothed whales (Boyle and Rodhouse, 2008; Clarke and Clarke, 1997).

Most anti-predatory behaviours in cuttlefish and octopuses are based on primary defence, also known as visual camouflage. It prevents or delays the predator to encounter, detect or recognise the individuals (Hanlon and Messenger, 2018). Cuttlefish and octopuses thrive in crypsis thanks to their colour-changing skin. It allows cuttlefish and octopuses to finely match the environmental background. They can rely on disruptive patterning to impair recognition of their shape or their orientation, by exhibiting linear and squared shapes which create false edges and boundaries. They also extensively use masquerade by resembling objects such as rocks or algae (Hanlon and Messenger, 2018). This flexibility in camouflage come from specialized organs, the chromatophores. They are small organs containing red, yellow-orange or brown-black pigments and which can be expanded or contracted in the blink of an eye, thanks to their direct innervation from the brain. Their skin also possesses leucophores, which are "white cells" reflecting ambient light; they also possess iridophores which are reflective iridescent cells providing blue, green,

yellow, red and purple colours. Their camouflage also rely on papillae, which allow them to modify the texture and roughness of their skin (Mäthger et al., 2008). Moreover, they use their posture, the position of their arms, fins and body to enhance their camouflaging abilities, and octopuses also seem to rely on mimicry by shaping their body like other animals.

Cuttlefish are also known to present a freeze response when a predator approaches: they stop moving and sometimes inflate their mantle with water. This response may be involved in crypsis, notably bioelectric crypsis, as freezing cuttlefish are less likely to be detected by predators sensitive to electric stimuli such as sharks (Bedore et al., 2015).

When their camouflage fails and they are detected by a predator, cephalopods rely on secondary defence mechanisms. These mechanisms interfere with the approach or attack of the predator to allow the prey to escape. Cuttlefish and octopuses can rely on deimatic behaviour, using disruptive coloration, bright contrasts, increased body size or distractive markings such as false eye spots to threat or startle the predator. It can make the predator hesitates and allow them to flight by jet propulsion. In the case of a chase, they can use protean behaviour, an unpredictable sequence of colour changes combined with a flight with direction changes. Cephalopods also rely on the release of ink, in the form of an ink screen to mask their escape, or an ink pseudomorph to deceive predators (Hanlon and Messenger, 2018).

Concerning other type of defences, cuttlefish spend a significant time buried when they lay on a sandy or muddy substrate. Recent observations by Drerup and Cooke (2021) on shoaling behaviour of juvenile and subadult cuttlefish suggests the use of grouping behaviour to reduce the risk of predation, mostly during migration. Cuttlefish were observed forming linear-shaped groups with individuals as potential sentinels, or spherical-shaped groups with individuals facing outwards, both potentially increasing the likelihood to spot a predator. Octopuses spend most of their time hidden in their den. They arrange it with shells and rocks, and they can build a burrow in sand. Octopuses were seen relying on defensive tool-use: apart from the coconut octopus (*Amphioctopus marginatus*) known to transport coconut shell as a mobile shelter (Finn et al., 2009), other octopus' species such as *Octopus vulgaris* were seen collecting shells and stones and use them to cover their arms in order to wrap them around their body and create an "armour" against predators, but also transport them to their den to improve it (Mather, 1991b; Mather, 1994).

Cuttlefish and octopus can adapt their behaviour to the predator they face: in front of a bottom, sit-and-pursue predator such as black seabass, cuttlefish flighted and kept swimming in the water

column; with a bluefish, a pelagic (*i.e.* in the water column) searching fish, cuttlefish favoured crypsis and burying on the bottom (Staudinger et al., 2013). In front of a triggerfish, which hunts in the open, octopuses switched their activity phase so they would be hidden in their den when the fish was active; whereas they did not show this switch in front of a moray eel, which can hunt octopuses even in their den (Meisel et al., 2013).

### **3. Sensory systems**

Coleoids possess multiple sensory systems: photoreceptors (intra-ocular and extra-ocular), mechanoreceptors (statocysts, lateral line analogue and touch and pressure receptors), chemoreceptors, and probable nociceptors (Hanlon and Messenger, 2018). Only vision and chemoreception are developed below as they are the senses addressed in our experiments.

#### *a. Vision*

Coleoids possess eyes which look remarkably similar to marine vertebrates' eyes. They are constituted of a retina, a lens and a pupil (Gleadall and Shashar, 2004). The pupil reacts and contracts when exposed to light (Douglas et al., 2005). *Sepia* possesses thirteen eye muscles against seven in *Octopus*. The supplementary muscles in *Sepia* allow convergence of the eyes: cuttlefish fixates objects binocularly to estimate distance before striking with tentacles while octopus fixates monocularly. Octopus can move its eyes 60-80° in any direction (Budelmann and Young, 1993). The visual field of each cuttlefish eye is close to 180° wide, and the binocular overlap is about 75° (Budelmann and Young, 1993). Octopus shows a similar visual field, but the use of binocular vision remains uncertain (Hanke and Kelber, 2019).

Cephalopods are colour-blind, as they only possess one type of photoreceptors with one visual pigment, without any known filtering structures (Gleadall and Shashar, 2004). It was shown behaviourally that octopuses (Messenger, 1977) and cuttlefish (Mäthger et al., 2006) could not discriminate between colours of the same brightness. However, some researchers (Stubbs and Stubbs, 2016) made the hypothesis that they might be able to distinguish colours by relying on chromatic aberration detectable with their off-axis pupil. Coleoids are very sensitive to the polarisation of the light, meaning they can detect the *e-vector* orientation or the degree of polarisation of light stimuli (Gleadall and Shashar, 2004). It allows cuttlefish to detect more easily camouflaged preys such as transparent invertebrates (Shashar et al., 2002) or light-reflecting silvery fishes (Shashar et al., 2000). Polarisation might be used as an intraspecific channel for recognition and

communication (Shashar et al., 1996), as cuttlefish can display polarisation patterns with their skin by changing the arrangement of the iridophores (Mäthger and Hanlon, 2007). The *e-vector* of polarized light can also be used as a spatial cue by cuttlefish to orient themselves (Cartron et al., 2012).

Sensory systems develop early in the cuttlefish, with the visual system functional from stage 25 (three weeks before hatching at 18°C). The environmental features and prey seen in the egg influence the subsequent camouflage behaviour and the background preference (in *Sepia pharaonis*, Lee et al., 2012), as well as the shelter colour preference (Guibé and Dickel, 2011) and prey preference (Darmaillacq et al., 2008; Guibé et al., 2012) at hatching. Habituation to light stimulation already exists in the egg at stage 30 (one week before hatching, Romagny et al., 2012).

Coleoids' vision allows them to camouflage adequately by integrating visual information in order to finely match their environment. Octopuses select specific features of their environment to match with (Josef et al., 2012), and cuttlefish base their camouflage on multiple parameters of their background such as contrast, edges, size or intensity (Chiao et al., 2005; Chiao et al., 2007), and this matching vary between individuals (Darmaillacq et al., 2017). Moreover, cuttlefish attacks are visually initiated and controlled (Messenger, 1968), and octopuses can use vision to detect and identify preys (Hanlon and Messenger, 2018; Wodinsky, 1969).

#### *b. Chemoreception*

Chemoreceptors are dispersed on the suckers on the arms and around the beak (on the “lips”) of coleoids. Cuttlefish possess only about 300 receptors per sucker (Gleadall and Shashar, 2004), while octopuses possess 10,000 chemoreceptors per sucker, allowing them to explore their environment through the chemotactile abilities of their arms. Octopuses seem to favour chemical cues over visual ones during food choice. They use a temporal sensory hierarchy when evaluating food, relying first on visual, then tactile and lastly chemical senses (Maselli et al., 2020).

Octopus (Chase and Wells, 1986) as well as cuttlefish (Boal and Golden, 1999) possess distance chemoreception, which can also be labelled as olfaction. In coleoids, the olfactory organ is based on the skin behind each eye (Scaros et al., 2018). Olfaction develops early in the cuttlefish, as it is functional from the middle of the embryonic development (from stage 23, namely four weeks before hatching at 18°C; Romagny et al., 2012). It was shown that embryos innately react to visual and olfactory cues of predators from stage 25 (Mezrai et al., 2020), a predator odour perceived in the egg can influence visual laterality at hatching (Jozet-Alves and Hebert, 2012), and a prey odour

perceived a week before hatching can influence subsequent prey preference (Guibé et al., 2010). Moreover, cuttlefish can detect sexual pheromones: females can identify the sex of another cuttlefish based on chemical cues (Boal, 1997), and sexually mature cuttlefish are attracted by eggs pheromones (Boal et al., 2010). Octopuses use olfaction for prey detection (in *O. maya*; Lee, 1992), conspecific detection (in *O. bimaculoides*; Walderon et al., 2011) and in reproduction (Polese et al., 2015).

#### ***4. Learning abilities***

Studies described here were conducted on *Sepia officinalis* and *Octopus vulgaris*, unless otherwise specified.

##### *a. Associative learning*

Associative learning is the basis of learning: individuals form a connection between a stimulus and a response, and this connection is created when the response is rewarded (Pearce and Bouton, 2001). Cuttlefish can associate a light cue to food, and they spontaneously attack the cue (Purdy et al., 1999). Octopuses can associate food with a cue, but only if this cue is rewarded continuously; if a reward is given only half of the time, octopuses fail to learn the association (Papini and Bitterman, 1991). Both Cuttlefish and octopuses can associate a low frequency sound to an electric shock, and subsequently stop breathing or jet away when perceiving the vibration (Packard et al., 1990).

##### Avoidance learning

In cuttlefish, learning has been extensively explored with the prawn-in-the-tube task: a prawn is placed in a transparent glass tube, inaccessible to the cuttlefish. The cuttlefish attacks the tube to get the shrimp at first, but quickly learns to inhibit its predatory behaviour, showing avoidance learning (Agin et al., 2006; Cartron et al., 2013; Dickel et al., 2013; Purdy et al., 2006). Avoidance learning was also explored with taste aversion, where cuttlefish learnt to avoid a prey when it was made bitter with quinine (Darmaillacq et al., 2004).

Octopuses can learn to avoid attacking a crab when paired with a square, after receiving an electric shock. This memory lasts for several days (Boycott and Young, 1955). They also learn to avoid attacking crabs carrying stinging anemones (Boycott, 1954).

### Discriminative learning

Adult cuttlefish show discriminative learning when they learn to attack a plastic sphere or an image out of two based on brightness differences (Cole and Adamo, 2005; Schnell et al., 2021b). Moreover, numerous experiments use the ability of cuttlefish to discriminate targets based on their pattern or brightness to explore other abilities, for example spatial learning (Alves et al., 2006b; Jozet-Alves et al., 2008). Cuttlefish can also learn to discriminate between sensorial modalities (vision and olfaction): they successfully learnt to select one patterned target when seeing a prey and another patterned target when smelling a prey (Billard et al., 2020b).

Discriminative learning was extensively studied in octopus, and it was shown that they can learn to discriminate between two shapes differing in orientation, size or brightness (Boycott and Young, 1957; Mackintosh and Mackintosh, 1964; Messenger, 1977; Messenger and Sanders, 1972; Sutherland, 1957a; Sutherland, 1958; Sutherland, 1960; Sutherland et al., 1965). They can learn to attack or not based on the direction of polarised light (Moody and Parriss, 1961). Moreover, octopus can learn to discriminate two objects based on their tactile properties such as roughness (Robertson et al., 1994; Wells and Young, 1970a; Wells and Young, 1970b).

### Reversal learning

Reversal learning tasks consist in learning to select one correct response in a two-choice task, and the correct response is reversed when the learning is acquired. When discriminating between two shapes, octopus show improvement over series of reversals (Mackintosh and Mackintosh, 1963). However, most experiences on reversal learning were conducted with negative reinforcement and pretraining, and without it, reversal learning takes longer and few animals are successful (Bublitz et al., 2017). In a spatial reversal task (go left or right), octopuses can reverse the side several times, and they improve their ability to reverse, reducing the number of errors, but a high individual variability was observed (Bublitz et al., 2021).

### Conditional discrimination

Conditional discrimination is the ability to discriminate between elements depending on the context. Cuttlefish show this ability when they learnt to find an exit whose location depended on the contextual cues available in the apparatus (Hvorecny et al., 2007).

Octopuses (*O. bimaculoides*) show conditional discrimination abilities by learning to find the location of a burrow depending on the contextual cues available in the apparatus (Hvorecny et al., 2007). Moreover, octopuses learnt to touch an object only when aeration in the tank was activated (or not, depending of the group; Tokuda et al., 2015).

### Generalisation

Cuttlefish which learn to choose a specific image of a prey can generalise this learning to a modified image. Some individuals learnt to select the correct image even when the image size or contrast was reduced, or when the image was in form of a sketch, a black silhouette or a white silhouette. Partial masking did not impair the selection of the image for some cuttlefish, but individual variation was important (Lin and Chiao, 2017). Cuttlefish can also learn to discriminate between sensorial modalities (vision and olfaction), and they can generalise the discrimination rule to a novel prey not encountered during training (Billard et al., 2020b).

### Spatial learning

Cuttlefish show spatial learning by knowing which specific door to choose to escape. They show improvement over serial reversals (Karson et al., 2003). Moreover, they use landmarks and *e-vector* of a polarised light as spatial cues to orient themselves in a maze (Cartron et al., 2012). Cuttlefish rely on a motor response strategy (right/left turn) when distal cues are provided, while they rely on salient proximal cues when they are available (Alves et al., 2006b). The strategy used also depends on individual characteristics, since mature males rely on visual cues while mature females or immature individuals favour motor responses (Jozet-Alves et al., 2008). When tested with a vertical two-dimensional target, cuttlefish were able to extract the vertical or the horizontal spatial information (Scatà et al., 2016).

When returning to their den, octopuses generally follow major features of the landscape (Forsythe and Hanlon, 1997; Mather, 1991b). In captivity, they can learn the location of an accessible den in less than a day and retain it for at least a week (Boal et al., 2000a). Octopus can also learn to make detours to obtain a prey seen through a glass (Wells, 1964), or learn to go left or right to obtain a prey (Bublitz et al., 2021). Using only one arm, octopuses can learn to reach a specific compartment in a maze by visually guiding a single arm (Byrne et al., 2006; Gutnick et al., 2011).



### *b. Observational learning*

Observational learning is the ability of an individual to learn by observation of others' behaviour (Huang and Chiao, 2013). It is commonly considered that cuttlefish do not rely on observational learning. Indeed, it was shown that cuttlefish do not improve their technique for hunting crabs when watching conspecifics hunt without being pinched. They instead seem to rely on trial-and-error learning, by gradually increasing the number of attacks successfully avoiding claws (Boal et al., 2000b). However, in more recent experiments, cuttlefish showed some elements of observational learning. An experiment indicated that, after witnessing a conspecific being chased away from its favourite resting place, some cuttlefish (*S. pharaonic*) subsequently favoured the "safe" place (Huang and Chiao, 2013). Moreover, using the prawn-in-the-tube task, new-born cuttlefish were shown to learn more quickly to inhibit their predatory behaviour after witnessing other cuttlefish failing to catch the prawn in the tube (Sampaio et al., 2021).

Octopuses show rapid observational learning, by learning to attack a ball of a specific colour after watching a conspecific attacking one for four trials (Fiorito and Scotto, 1992).

### *c. Inhibition learning*

Cuttlefish learn to inhibit their predatory behaviour by waiting for 50 to 130 seconds to obtain a prey of higher quality instead of an immediately available prey of lesser quality (Schnell et al., 2021b). This ability allows them to adapt their foraging behaviour to the availability of preys. When the presence of a preferred prey (shrimp) was predictable in the evening, cuttlefish learnt to refrain from consuming a less preferred prey (crab) in the morning. If the presence of the shrimps was unpredictable, cuttlefish consumed the crab during the day, showing flexible and future-dependent foraging abilities (Billard et al., 2020a).

### *d. Problem-solving abilities*

Octopuses show problem solving abilities, such as opening the lid of pots (Fiorito et al., 1990). They can also be trained in several steps to solve a task of increasing complexity, where they have to retrieve a L-shaped container through a tight hole in an opaque partition, then open the container in order to obtain food (Richter et al., 2016).

### *e. Episodic-like memory*

Cuttlefish show episodic-like memory, remembering what prey they ate (crab or shrimp), where and how long ago (one or three hours earlier; Jozet-Alves et al., 2013). This memory is conserved even in old age (two-years old cuttlefish; Schnell et al., 2021a). Moreover, after being unexpectedly asked, cuttlefish can retrieve the modality of presentation of a prey encountered three hours earlier (*i.e.* was it seen or smelt?), a source discrimination ability which is linked with source memory (Billard et al., 2020b).

## **5. Neural substrates of learning and memory**

### *a. Coleoids' central nervous system*

Coleoids' nervous system shows a molluscan design with six pairs of ganglia, but their brains show a great centralisation, or cerebralisation, compared to other molluscs (Figure 20; Nixon and Young, 2003). Centralisation is observed through shortening of the connectives between lobes and ganglia. This reduces the time between stimulus detection and behavioural reaction, by decreasing the time for processing information (Budelmann, 1995).

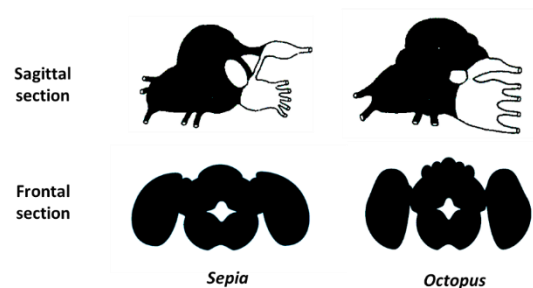


Figure 20: Schematic representation of the brains of cuttlefish and octopus, adapted from Bullock and Horridge (1965) and Shigeno et al. (2018).

Sagittal sections are oriented from the front (left) to the back (right). The white areas in the sagittal sections correspond to the superior buccal and brachial lobes. The black areas correspond to the supra- and sub-oesophageal masses in both sections (see Figure 21 for details). Optic lobes and perioesophageal mass are visible in the frontal section.

Coleoids share a comparable central nervous system, constituted of a pair of optic lobes on both sides of the central mass. This central mass is organised in a supra- and a sub-oesophageal mass, connected by perioesophageal lobes. The brain is subdivided into 37 lobes in octopods and 38 lobes in decapods (Figure 21; Budelmann, 1995). The optic lobes are primary sensory centres which are involved in higher-order visual processing. The sub-oesophageal mass is involved in the motor

control of chromatophores, viscera and appendages (Nixon and Young, 2003; Sanders and Young, 1940). The supra-oesophageal mass contains the higher centres, which operate integration and processing of sensory information (Nixon and Young, 2003; Sanders and Young, 1940)

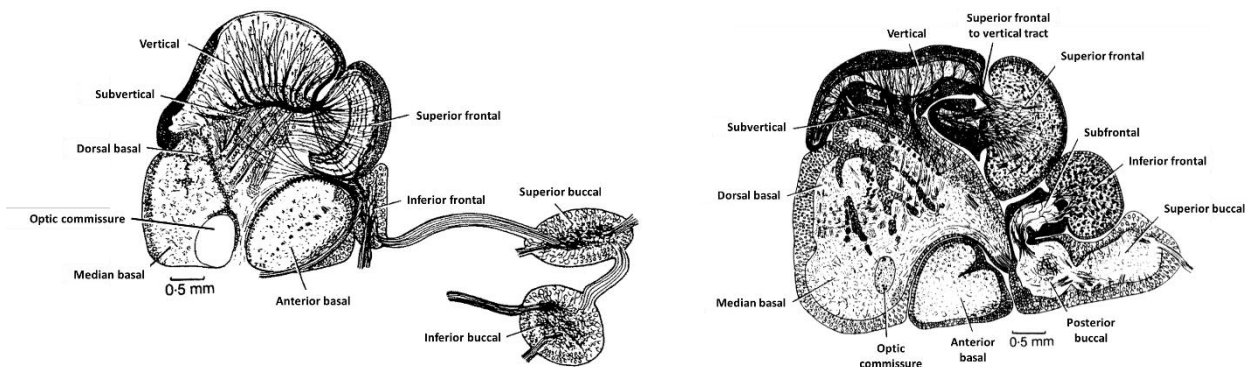


Figure 21: Drawings of sagittal sections of the supra-oesophageal masses of cuttlefish and octopus, from Maddock and Young (1987).

#### *b. The vertical complex*

In the dorsal part of the supra-oesophageal mass, the vertical complex is composed of the vertical lobe, the subvertical lobe and the frontal lobe (Table 2; Sanders and Young, 1940). Sanders and Young (1940) were the first to discover the implication of this complex in learning and memory abilities: the removal of the vertical complex impairs learning abilities of cuttlefish in the prawn-in-the-tube task. Using this task, Agin and colleagues (2001) showed the activation of the superior frontal lobe. The results of these studies were confirmed by Dickel and colleagues (2001) who showed that the development of learning ability during the task was correlated with the growth of both the superior frontal and the vertical lobes. More recently, using electrolytic lesions of the vertical lobe, it has been shown that the ventral and dorsal parts of the lobe are critical for the acquisition or the long-term retrieval of a spatial task, respectively (Graindorge et al., 2006). In octopuses, Young (1958) used discrimination tasks to explore the role of the vertical lobe. When this lobe was removed, octopuses lost their knowledge of the task, but could re-learn the discrimination, but with reduced speed and accuracy. Shomrat and colleagues (2008) showed that this lobe mediates both short-term learning and long-term memory acquisition. The vertical complex shows similarities with the mammalian hippocampus: both systems present crossing fibres and long-term potentiation, and both systems allow memory formation and consolidation (Gutnick et al., 2017; Shigeno et al., 2018).



*c. Other structures for learning and memory*

Along with the vertical complex, optic lobes might be involved in visual learning, as indicated by their activation after a prawn-in-the-tube task in cuttlefish (Bellanger et al., 2003). Moreover, octopods possess a chemo-tactile learning system which is mediated by the subfrontal, inferior frontal and posterior buccal lobes (Gutnick et al., 2017).

*Table 2: Brain size and lobes volumes for cuttlefish and octopus, from Nixon and Young (2003). Volumes are expressed in percent of the volume of the central nervous system without the optic lobes.*

	<b>Cuttlefish</b>	<b>Octopus</b>
<b>Central nervous system</b> (at mantle length = 8 cm)	164 mm <sup>3</sup>	93 mm <sup>3</sup>
<b>Supra-oesophageal mass</b>	46.4 %	33 %
<b>Vertical complex</b>	13.5 %	6.4 %
Vertical lobe	7.0 %	2.0 %
Subvertical lobe	2.2 %	0.8 %
Superior frontal lobe	4.4 %	3.7 %
<b>Optic lobe</b>	120.8 %	57.4 %

Table 3: Comparative summary of the ecological, sensorial and cognitive characteristics of the common cuttlefish and the common octopus. Photographs from L. Poncet.

	Common cuttlefish <i>Sepia officinalis</i>	Common octopus <i>Octopus vulgaris</i>
		
<b>World distribution</b>	European and north African waters	World-wide
<b>Depth</b>	Shallow waters, 0-100m	Shallow waters, 0-100m
<b>Habitat</b>	Sandy or muddy substrates	Various (rocky, grassy)
<b>Migration</b>	Inshore-offshore (Channel Sea)	Limited
<b>Life expectancy</b>	Two years (Channel Sea)	One to two years
<b>Life cycle</b>	One regular summer cycle (Channel Sea)	Two cycles: one regular spring cycle, one irregular autumn cycle (Mediterranean Sea)
<b>Eggs</b>	1000-5000 Laid in spring-summer  2-3 months of incubation	100.000-500.000 Laid in February-March or June to August  2-3 months of incubation
<b>Paralarvae stage</b>	No	Yes (1-2 months)
<b>Sociality</b>	Generally solitary in the wild, with some shoaling in juveniles and subadults  Socially tolerant in captivity	Solitary in the wild  Socially intolerant in captivity
<b>Food diet</b>	Opportunistic, but can switch to selective strategies Crabs, shrimps, fishes	Opportunistic, with specialist individuals Crabs, bivalves, gastropods Planktotrophic at paralarvae stage
<b>Anti-predatory behaviours</b>	Crypsis, masquerade, countershading, substrate burying Deimatic and protean behaviours Inking Shoaling?	Crypsis, masquerade, mimicry, motion camouflage Deimatic and protean behaviours Inking Den and burrows
<b>Vision</b>	13 eye muscles Visual field of 180° with 75° of binocular overlap Colour blind, polarisation sensitivity	7 eye muscles Visual field of 180° with uncertain binocular overlap Colour blind, polarisation sensitivity
<b>Chemoreception</b>	Tactile and distance chemoreception 300 chemoreceptors per sucker	Tactile and distance chemoreception 10,000 chemoreceptors per sucker

<b>Cognitive abilities</b>	Imprinting Associative learning Avoidance learning Discriminative learning Reversal learning Conditional discrimination Generalisation Spatial learning Observational learning in juveniles Inhibition learning Episodic-like memory Source memory	Associative learning Avoidance learning Discriminative learning Reversal learning Conditional discrimination  Spatial learning Observational learning Inhibition learning  Problem-solving abilities
<b>Nervous system</b>	Central brain divided in supra- and sub-oesophageal masses, divided in 38 lobes with two big optic lobes Vertical complex for learning and memory	Central brain divided in supra- and sub-oesophageal masses, divided in 37 lobes with two big optic lobes Vertical complex for learning and memory

### III. Objectives of this PhD thesis

This PhD thesis studies Mental Time Travels abilities in cephalopods from a comparative point of view. This work investigates which MTT abilities are present in two representative species of cephalopods, the common cuttlefish (*Sepia officinalis*) and the common octopus (*Octopus vulgaris*). The comparison of these species allows to explore which ecological pressures can lead to the emergence of MTT in these cephalopods, and more generally in animals.

Both retrospective and prospective MTT in cuttlefish and octopus will be studied:

(1) Retrospective MTT was previously studied in cuttlefish, indicating that they possess episodic-like memory abilities, and this thesis will explore the same memory in octopuses. We will also go deeper into the study of cuttlefish episodic-like memory by investigating its reconstructive processes.

(2) Prospective MTT will be explored in both octopus and cuttlefish to understand under which conditions they can emerge and what is the relation between retrospective and prospective MTT.

## IV. Manuscript organisation

Three chapters compose this PhD thesis.

### **Chapter 1: Spatiotemporal memory in octopuses**

This chapter investigates episodic-like memory abilities in octopuses, reproducing the procedure previously used with cuttlefish. Given the results obtained, we decided to explore the memory for time in octopuses, by studying specifically the memory for the temporal order of a sequence.

### **Chapter 2: False memories in cuttlefish**

This chapter firstly presents a review on the false memories in humans and animals. Cuttlefish propensity to form false memories is then explored, using a novel procedure promoting false memories formation, to better understand the reconstructive and source-monitoring processes at the basis of their episodic-like memory.

### **Chapter 3: Future planning in coleoids**

This chapter studies the ability to act in the present to plan for the future in juvenile cuttlefish, subadult octopuses and adult cuttlefish. Juvenile and adult cuttlefish were tested using the same procedure which explored whether they could plan for a future need to eat independently of their current need to hide, while octopuses were tested on their ability to plan for their future needs to eat and to hide.

A **General discussion** concludes this PhD thesis, by discussing the results obtained during the experiments, the limits of our studies and their perspectives.

Following the summary in French, a short annex explores the Theory of Mind in cuttlefish.

Articles published or submitted in international journals are incorporated in the thesis. To facilitate the lecture, the numbering of pages, tables and figures of the articles has been adapted to correspond to the present organisation of the thesis. A summary figure concludes each chapter.



**Chapter 1:**  
**Spatiotemporal memory in  
octopuses**

# Chapter 1: Spatiotemporal memory in octopuses

## Article 1:

Poncet, L., Desnous, C., Bellanger, C., and Jozet-Alves, C. (2022). Unruly octopuses are the rule: *Octopus vulgaris* use multiple and individually variable strategies in an episodic-like memory task. *Journal of Experimental Biology* 225, jeb244234. DOI: 10.1242/jeb.244234.

## Preliminary study 1:

Poncet, L., Bellanger, C., and Jozet-Alves, C. Memory for the temporal order of a sequence in octopus.

## Introduction of Chapter 1

### Part I: Exploration of episodic-like memory in octopus (Article 1)

Common cuttlefish show episodic-like memory abilities by remembering what they ate, where and how long ago (Jozet-Alves et al., 2013b; Schnell et al., 2021c; see Introduction I. B. 1.). To explore whether episodic-like memory abilities are common to all cephalopods or whether they have emerged specifically in cuttlefish, we reproduced the same experiment with common octopuses. Only one individual learnt the replenishing rates during the training and subsequently showed episodic-like memory abilities, whereas the other individuals favoured simpler foraging strategies, showing a high variability between individuals. We hypothesise that environmental constraints might be lighter in octopuses than in cuttlefish, which could be why octopuses did not rely as much on episodic-like memory. Another hypothesis is that octopuses may possess episode-like memory abilities, but may not be able to encode time in terms of temporal distance, thus they were not able to solve the task presented in this way.

### Part II: Exploration of the memory for time in octopus (Preliminary study 1)

Following the episodic-like memory study undertaken in octopuses, we investigated their ability to encode time differently from temporal distances. We conducted an experiment to explore whether octopuses can rely on relative times of occurrence, in other words remember the order of a sequence. Octopuses were presented a sequence of images of seashells, then they had to select between two images which image occurred the earliest in the sequence. All tested octopuses succeeded the task, showing that octopuses might be more likely to encode time in terms of relative times of occurrence rather than temporal distances.

## I. Exploration of episodic-like memory in octopus

### Unruly octopuses are the rule: *Octopus vulgaris* use multiple and individually variable strategies in an episodic-like memory task

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#### **Abstract**

Episodic-like memory has mainly been studied through experimental tasks in which subjects have to remember what they ate, where and when or in which context. Seemingly quite common in mammals and corvids, episodic-like memory ability has also been demonstrated in the common cuttlefish, a cephalopod mollusc. To explore whether this ability is common to all cephalopods or whether it has emerged to face specific ecological constraints, we conducted an episodic-like memory task with seven *Octopus vulgaris*. Only one individual learnt the replenishing rates during the training and subsequently showed episodic-like memory ability, whereas the other individuals favoured simpler foraging strategies, such as avoidance of familiarity and alternation, use of a win-stay strategy and risk-sensitivity. A high variability in the use of these strategies was observed between and within individuals throughout the training. As octopuses seem to live under lighter environmental pressure than cuttlefish, they may not need to rely on episodic-like memory ability to optimize foraging as cuttlefish do. These results highlight the differences in the use of complex cognitive abilities between cuttlefish and octopuses, which might be linked to different environmental and predatory constraints.

#### **Key-words**

Octopus, Episodic-like memory, Foraging strategies, Individual variability

## A. Introduction

Episodic-like memory is the ability of an animal to remember the content (“what”), the spatiotemporal context (“where”, and “when” or “which”) and the source (contextual details such as the sensory modality of the content, the emotional valence, etc.) of a single event (Clayton et al., 2003b). The ability to remember, in an integrated manner, the what, where and when (how long ago) of an event has been shown in several taxa, including corvids (Clayton and Dickinson, 1998; Zinkivskay et al., 2009), rodents (Babb and Crystal, 2006) and great apes (Ban et al., 2014; Martin-Ordas et al., 2010). Amongst invertebrates, common cuttlefish also show episodic-like memory ability (Jozet-Alves et al., 2013b). In this experiment, the cuttlefish’s ability to remember what they ate (shrimp or crab), where (position of the target) and how long ago (one or three hours) was tested. Identical targets at distinct locations (unique locations on each day) were associated with each prey type. Whereas the less preferred crab supply was replenished after any delay, the preferred shrimp supply was replenished only after a long delay (three hours). Cuttlefish quickly learnt to go to the target delivering the preferred shrimp after a long but not after a short delay. Cuttlefish showed great capacities for the task, understanding the rules of the task in about 20 trials (Jozet-Alves et al., 2013b). A subsequent study confirmed the impressive memory abilities of cuttlefish, showing that their episodic-like memory does not fade, even in old age (Schnell et al., 2021c). Another recent study showed that cuttlefish possess the ability to retrieve the sensory modality (seeing or smelling a prey) of a past event (Billard et al., 2020b), indicating that cuttlefish can bind the source of a memory in addition to remembering the content and the spatiotemporal context of their memory.

We can question why cuttlefish possess episodic-like memory abilities. The first hypothesis is that this ability is shared with other large-brained cephalopod species as the result of their shared phylogeny. The second hypothesis is that episodic-like memory has emerged in cuttlefish to cope with specific ecological challenges such as explained in the ecological intelligence hypothesis (Byrne, 1997; Milton, 1981) and in the predator-prey interaction hypothesis (van der Bijl and Kolm, 2016). Indeed, cuttlefish have to be constantly aware of predators while hunting, which requires time and energy and thus impact fitness. Their preys are often spatiotemporally dispersed in patches which often do not offer shelters. Thus, when cuttlefish cannot minimise their risks by hunting from a hide, they may have to use an array of cognitive skills to find preys at the right place and time, such as spatial memory (Jozet-Alves et al., 2014), value-based decision making (Kuo and Chiao, 2020) or overcoming immediate gratification in order to obtain better preys (Schnell et al., 2021b). However, rather than being a coping ability to ecological challenges, we can also hypothesise that episodic-like memory in cuttlefish could be a mere by-product of the evolution of

its complex cognition. It would have emerged from other abilities required by the cuttlefish to hunt and avoid predators, without any particular need for episodic-like memory itself.

Octopuses appear to be as worthwhile species in which to explore the evolution of episodic-like memory ability in cephalopods. Indeed, some species, such as *Octopus vulgaris*, live in a similar environment to that of cuttlefish, as they are both shallow-depth bottom dwellers (Hanlon and Messenger, 2018), but possess different means to handle their environmental constraints. Indeed, because of their lack of an internal shell and their highly prehensile arms, octopuses possess a wider range of defensive strategies. While cuttlefish mainly use crypsis for defence, octopuses can also hide in crevices, arrange a shelter, cover themselves in rocks and shells in order to avoid attacks, or defend themselves aggressively against predators (Hanlon and Messenger, 2018). Consequently, octopuses may wander more easily in the open instead of relying on strategies minimising the time spent out of safety as cuttlefish do. Moreover, thanks to their complex arms, the octopus diet is broader than that of cuttlefish as octopuses can consume bivalves and gastropods, in addition to decapods, fishes and other cephalopods (Anderson et al., 2008; Mather et al., 2012). Thus, while cuttlefish hunt moving preys living in patches, which may come back to suitable patches quickly, octopus, on the other hand, forage partly on sessile preys such as bivalves, which replenish over very long timescales. Whereas remembering what was eaten where and when might be useful for cuttlefish, it might be unnecessary for octopuses. Instead, octopuses might rely on simpler foraging strategies based on rules of thumb to optimise foraging efficiency. They could depend on the following strategies (Levine, 1959), such as: a) familiarity, a memory process which uses a signal-detection function whereby elements exceeding a fixed criterion are recognised as having been perceived before (Baddeley et al., 2001b) - while foraging, individuals relying on this strategy will favour places they have already visited rather than exploring new ones; b) risk-sensitivity, the foragers' response to variance in food reward rate when choosing what to eat (Young et al., 1990) - risk-averse individuals will favour food rewards that are always available but of less quality, while risk-prone individuals will look for food rewards of higher quality but random availability; c) spontaneous alternation, the tendency to explore places that have been least recently explored (Ramey et al., 2009); and d) win-stay/win-shift strategies, used when subjects either repeat (stay) or avoid (shift) their last choice, depending on whether the choice was previously rewarded (win) or not (Kamil, 1983).

In order to assess whether octopuses keep track of time when different food sources vary in space and time or whether they favour simpler foraging strategies, we first evaluated their ability to learn replenishing rates of preferred versus less-preferred food items (procedure adapted from Jozet-Alves et al., 2013). Octopuses succeeding this task were subsequently tested to assess their episodic-

like memory ability (what-when-where experiment, adapted from Jozet-Alves et al., 2013). Given octopuses' ecology, we expected them to favour simpler foraging strategies rather than relying on time tracking strategies as cuttlefish do, which could indicate that cuttlefish complex memory abilities might have arisen from their ecological and predator-prey interactions specificities.

## B. Materials and methods

### 1. Ethical statement

Experiments were conducted in accordance with the directive 2010/63/EU (European parliament) and with the French regulation applied to the protection and use of animals in research experiments. Procedures were approved (#22429 2019101417389263 v2) by the ethical committee of Normandy region (Comité d'Ethique de NOrmandie en Matière d'EXpérimentation Animale, CENOMEXA; agreement number 54).

### 2. Subjects

The subjects used in the experiments were sub-adult common octopuses (*Octopus vulgaris* Cuvier). Octopuses were collected in the Mediterranean Sea by specialised fishermen (Carrodano, Poissons vivants, La Ciotat, France) in September 2020 (batch 1, n=3) and January 2021 (batch 2, n=4) (see Table 4 for names and sex). They were transported to the marine station of the University of Caen (Centre de Recherche en Environnement Côtier, Luc-sur-Mer, France). Their size (dorsal mantle length) ranged from 5 to 10 cm at the beginning of the experiment, to 15 to 20 cm at the end. They were individually housed firstly in glass tanks of 50x50x50 cm and transferred to glass tanks of 100x50x50cm or 120x40x50cm as they grew. Octopuses were maintained in circulated semi-artificial seawater (salinity: 37 g/L, Instant Ocean Salt – Aquarium systems; temperature:  $17 \pm 1^\circ\text{C}$ ;  $7.8 < \text{pH} < 8.2$ ;  $[\text{NH}_3 + \text{NH}_4^+] < 0,25 \text{ mg/L}$ ;  $[\text{NO}_2] < 0,2 \text{ mg/L}$ ;  $[\text{NO}_3] < 50 \text{ mg/L}$ ), with artificial lighting following the natural light cycle. A sand bed, pebbles, shells and a shelter in the form of a terracotta pot or a PVC tube were provided in each tank. Octopuses were fed daily outside of the experimental trials with live crabs (*Hemigrapsus sanguineus* or *Carcinus maenas*), thawed or live shrimps (*Crangon crangon*), pieces of thawed fish (mackerel *Scomber scombrus*, pollock *Theragra chalcogramma*, herring *Clupea harengus* and whiting *Merlangius merlangus*). Mussels (*Mytilus edulis*) were always available in the home tanks.

### ***3. Procedure***

Experiments were conducted in the home tank of each animal. Octopuses were pre-trained and tested for food preference, before starting the replenishing rate training.

#### *a. Replenishing rate training*

Octopuses were trained to learn that two different prey types (preferred *versus* less-preferred prey types; determined for each individual during the food preference test) were available at specific locations and after specific delays (1h or 3h delay; Figure 22). Octopuses were tested five days a week, one trial per day, with each trial consisting of two presentations separated by either a short (one hour) or a long (three hours) delay. During each presentation, octopuses were simultaneously presented with two closed opaque pots. Each pot contained a different prey item. The position and the content of the two pots were kept the same throughout the trials (“where” and “what” components were fixed for an individual for all the replenishing rate training).

During the first presentation of a trial, the octopus could open and consume the contents of each pot, and the pots were removed after 30 minutes. At the end of this delay, if octopuses did not open or consume the contents of both pots (a partial consumption of the less preferred food item was tolerated), the experiment was postponed to the next day. The second presentation was conducted after either a short delay (1h) or a long delay (3h). Delays (either short or long) were pseudorandomised, so the same delay could not be repeated more than three days in a row. Pots were replenished according to the elapsed time since the first presentation. Following a short delay (1h), only the pot containing the less-preferred food item was replenished. Following a long delay (3h), both pots were replenished. The octopus could only consume the contents of one pot, the second pot being removed with a small net immediately after the choice. A choice was considered correct when an individual chose the pot containing the less-preferred food after a short delay, and the pot containing the preferred food after a long delay.

The acquisition criterion was fixed at eight correct choices out of ten consecutive trials, as per Jozet-Alves *et al.* (2013). The maximum number of training trials was set to 40, corresponding to the double the number of trials cuttlefish needed to reach the acquisition criterion during previously published experiments (Jozet-Alves *et al.*, 2013; cuttlefish learnt the replenishing rate in  $21 \pm 4$  trials). However, as the first batch of octopuses ( $n=3$ ) did not reach the criterion in 40 trials, a second batch of octopuses ( $n=4$ ) was subsequently created and the maximum number of training trials was set at 80. In the case of an octopus reaching seven correct responses out of ten

consecutive trials at its 40<sup>th</sup> (first batch) or 80<sup>th</sup> (second batch) trial, three supplementary trials were conducted to test whether the octopus would reach the learning criterion within this extended period of training.

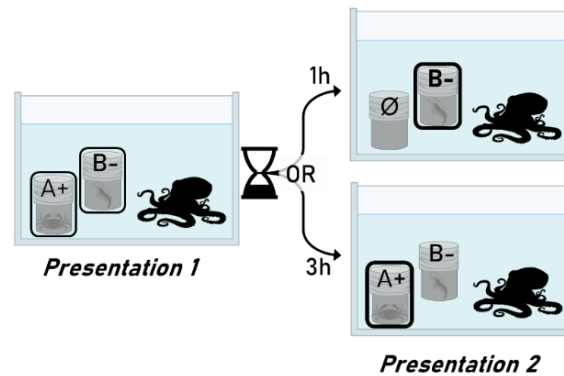


Figure 22: Organisation of a training trial.

During the presentation 1 of each trial, octopuses opened both opaque pots to consume their preferred food ( $A^+$ ) and their less-preferred food (B). After either a short (1h) or a long (3h) delay, both pots were presented a second time. After a one-hour delay, the pot previously containing  $A^+$  was empty, thus octopuses had to go to the pot containing B to realise a successful choice. After a three-hours delay, food was available in both pots, and choosing the pot containing  $A^+$  was considered a successful choice. The position of the pots remained unchanged within trials. The position was altered between trials for the episodic-like memory task, but not for the replenishing rate task.

#### *b. Episodic-like memory task*

Individuals which reached the acquisition criterion of the replenishing rate training within the pre-set number of trials were tested in the episodic-like memory task. This task was similar to the replenishing rate training task, except that the pots were randomly placed in any location in the tank and this location changed between each trial, while staying the same across the two presentations of a trial. During each trial, octopuses had to remember what prey was in each pot (what-where) and how much time had elapsed since the first presentation: the spatiotemporal information was thus unique. We considered that octopuses showed episodic-like memory ability when they realised ten correct choices out of twelve consecutive trials (binomial test,  $p=0.039$ ), with the maximum number of trials sets to 40 trials.

## **4. Analysis**

Data were analysed using R software (v. 3.5.1), using binomial tests for food preference tests and choices of octopuses. To investigate the favoured strategies, we analysed choices in the second presentation for both batches as well as individual choices of octopuses during the replenishing rate training. Only the first 40 training trials were considered and analysed as we wanted to compare



all octopuses, whether they were from the first batch (*i.e.* trained for 40 trials) or from the second batch (*i.e.* trained for 80 trials). Two-tailed Fisher exact tests were used to compare the use of one strategy between the first and the last 20 trials of training. It should be noted that for alternation and win-shift/win-stay strategies, the choice on the first trial was excluded from the analyses, as there was no previous reference trial. Therefore, we analysed 39 trials and compared the first 20 trials with the last 19 trials of training for these strategies. To simplify the understanding of the following sections, we will use the expressions “40 trials” and “first and last 20 trials” for all strategies.

In addition to replenishing rate learning, four strategies were explored in the second presentation of all trials: a) familiarity, b) risk-sensitivity, c) spontaneous alternation and d) win-stay/win-shift. They can be split into two subcategories: within trial strategies, where choices in the second presentation depend on the outcome of the first presentation, such as familiarity and risk-sensitivity; and between trials strategies, where choices in the second presentation of a trial depend on the outcome of the second presentation of the previous trial, such as spontaneous alternation and win-stay/win-shift. More precisely, each strategy was defined as the following: a) familiarity (Figure 23A) was observed when subjects chose the most familiar pot during the second presentation, which was the last opened (*i.e.* second opened) pot during the first presentation; b) risk sensitivity (Figure 23B) was observed when subjects chose preferentially one prey over the other during the second presentation of a trial. During this presentation, the less-preferred prey was always available no matter the delay, and hence was less risky, whereas the preferred prey was available half of the time (absent after a delay of one hour, and present after a delay of three hours), and was hence riskier. c) spontaneous alternation (Figure 23C) was observed when subjects alternated their choice between pots during the second presentation of each trial. and d) win-shift/win-stay (Figure 23D) was observed when subjects which won (obtained food in a given pot) during the second presentation of a first trial shifted their choice for the other pot (win-shift) or maintained their choice for the same pot (win-stay) during the second presentation of the next trial. The lose-shift/lose-stay counterpart of this strategy was not studied as instances of “lose” were statistically scarce (1/4 of the trials if subjects chose by chance).

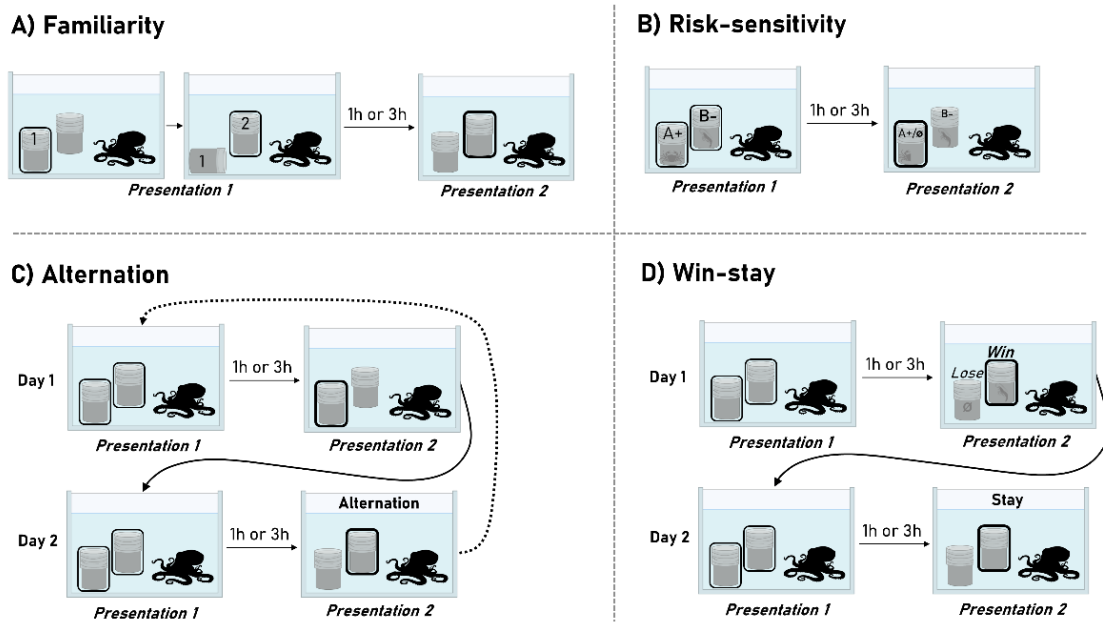


Figure 23: Representation of strategies used by octopuses during the replenishing rate training.

A) Familiarity. During the presentation 1, octopuses choose a first pot, then a second one. On the presentation 2, they choose the pot last visited. B) Alternation. Octopuses choose one pot on the presentation 2 of a trial (1), and then choose the opposite pot on the presentation 2 on the following trial (2). C) Risk-sensitivity. During presentation 2, the pot containing the less-preferred food is less risky (B-) than the pot containing the preferred food (A+ /  $\emptyset$ ), as the less-preferred food is always available whereas the preferred food is available randomly if delays cannot be discriminated. The representation shows the choice of a risk-prone individual. D) Win-stay strategy. On the presentation 2, pots can either be a “win”, when replenished, or a “lose”, when empty. When octopuses open a pot with food inside on the second presentation during a trial (1; “win”), then on the second presentation of the following trial (2) they choose the same pot as in the previous trial (“stay”), they use a win-stay strategy.

## C. Results

### 1. Food preference

All octopuses presented a significant preference for crabs (binomial test,  $p < 0.039$ ; Table 4). Less-preferred preys varied between individuals, with some octopuses tested with thawed fishes (whiting, mackerel or pollock), others with fresh shrimps or shelled mussels.

Table 4: Food preference of each octopus.

Food preference was assessed by presenting two different prey types to octopuses during 12 consecutive trials. Octopuses chose a prey item by grabbing it and eating it. Numbers within parentheses correspond to the number of times a prey item was chosen during the test. Asterisks indicate a significant preference for crabs (binomial test, \*  $p=0.039$  ( $<0.05$ ), \*\*  $p=0.006$  ( $<0.01$ )).

Subject	Suricate	Abe	Pipoune	Coquille	Rosy	Tickle	Teddy
<b>Batch</b>	1	1	1	2	2	2	2
<b>Sex</b>	Male	Female	Female	Female	Female	Female	Female
<b>Preferred prey</b>	Crab (10)*	Crab (10)*	Crab (11)**	Crab (10)*	Crab (11)**	Crab (10)*	Crab (11)**
<b>Less preferred prey</b>	Whiting (2)	Shelled mussel (2)	Mackerel (1)	Shrimp (2)	Shrimp (1)	Pollock (2)	Shrimp (1)

## 2. Replenishing rate training and episodic-like memory task

In the first batch (maximum number of training trials sets at 40), none of the three octopuses reached the established learning criterion (*i.e.* eight correct choices out of ten consecutive trials). In the second batch (maximum number of training trials sets at 80), only one individual (Teddy) out of four reached the learning criterion in 43 trials (Figure 27). One individual (Tickle) reached seven correct responses out of ten successive trials at its last trial (80<sup>th</sup>), but its performance did not improve in the three supplementary trials.

Only Teddy was subsequently tested in the episodic-like memory task. She reached the acquisition criterion and thus succeeded in the task in 21 trials.

## 3. Strategies

If we consider the first 40 trials of training of all individuals (Figure 24A), octopuses showed a significant avoidance of familiarity (109 familiarity choices out of 280 presentations, binomial test,  $p<0.001$ ); they showed significant constancy rather than alternation (114 alternations out of 272 presentations, binomial test,  $p=0.009$ ); and they significantly favoured a win-stay over a win-shift strategy (118 choices consistent with win-stay strategy out of 198 “win” presentations; binomial test,  $p=0.008$ ). However, no significant preference could be observed for the less or more risky option (154 choices of the risky option out of 280 presentations; binomial test,  $p=0.107$ ). Nevertheless, when distinguishing the first and the last 20 trials of training (Figure 24B), octopuses were significantly more risk-prone during the first 20 trials than during the last 20 (87/140 *vs* 67/140, two-tailed Fisher exact test,  $p=0.022$ ). We can note there that the preference for one prey

over the other was not significant for the first pot opened during the first presentation (149/280, binomial test,  $p=0.310$ ).

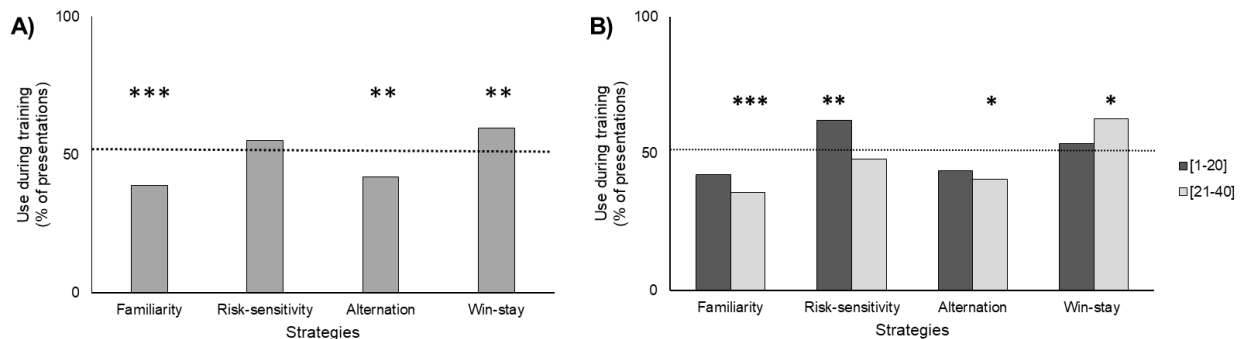


Figure 24: Percentage of octopuses ( $n=7$ ) using each strategy during the replenishing rate training.

See Materials and Methods and Figure 23 for description of these strategies. A) Use of each strategy throughout the 40 training trials. B) Use of each strategy throughout the training divided between the first and the last 20 trials. Risk-sensitivity is expressed in the number of risky choices. Over their training, octopuses significantly avoided the use of familiarity, favoured constancy rather than alternation, and favoured a win-stay rather than a win-shift strategy. Individuals did not seem to show risk-sensitivity when taking the 40 training trials together, but risk-proneness was observed in the first 20 training trials ([1-20]) then disappeared in the following 20 trials ([21-40]). The other strategies were not observed in the first 20 training trials, but they were employed in the following 20 trials. Asterisks represent a significant difference from chance (i.e. dotted line; binomial test, \*  $p<0.05$ , \*\*  $p<0.01$ , \*\*\*  $p<0.001$ ).

At the individual level, high variability in the strategies used was observed (Table 5, Figure 25).

**Suricate** showed no significant use of familiarity (23/40, binomial test,  $p=0.430$ ); but he presented a significant risk-aversion (10/40, binomial test,  $p=0.002$ ); he showed constancy by choosing the same pot for nine consecutive trials out of the last ten training trials (binomial test,  $p=0.004$ ); and he significantly used a win-stay strategy during training (24/35, binomial test,  $p=0.041$ ).

**Abe** showed significant avoidance of familiarity (12/40, binomial test,  $p=0.017$ ); she presented a strong risk-proneness (31/40, binomial test,  $p<0.001$ ), combined with a clear preference for her preferred prey even when choosing the first pot to open during the first presentation (29/40, binomial test,  $p=0.006$ ); she showed constancy by choosing the same pot for ten consecutive trials in the second half of its training (binomial test,  $p=0.002$ ); but she did not significantly use a win-stay nor a win-shift strategy during training (13/25, binomial test,  $p=1$ ).

**Pipoune** showed a significant avoidance of familiarity (13/40, binomial test,  $p=0.039$ ) which was delay-dependant: she avoided the familiar pot after a long delay but not after a short one (3/20 vs 10/20, two-tailed Fisher exact test,  $p=0.041$ ); she presented risk-sensitivity, with this sensitivity reversed between the first 20 and the last 20 training trials (16/20 vs 5/20, two-tailed exact Fisher

test,  $p < 0.001$ , Figure 25): she was risk-prone during the first 20 trials (16/20, binomial test,  $p = 0.012$ ), then risk-averse for the following 20 trials (5/20; binomial test,  $p = 0.041$ ); she showed constancy by choosing the same pot nine times out of ten consecutive trials in the second third of its training (binomial test,  $p = 0.021$ ); but she did not significantly use a win-stay or win-shift strategy during training (20/29, binomial test,  $p = 0.061$ ).

**Coquille** showed avoidance of familiarity, by choosing the unfamiliar pot nine times out of ten consecutive trials in the last ten trials of its training (binomial test,  $p = 0.021$ ); she presented a significant risk-proneness in the first 20 training trials (15/20, binomial test,  $p = 0.042$ ), but this seemed to disappear in the following 20 trials (15/20 *vs* 8/20, two-tailed Fisher exact test,  $p = 0.054$ , Figure 25), with no significant risk-sensitivity displayed anymore (8/20, binomial test,  $p = 0.503$ ); she showed alternation by choosing a different pot during ten consecutive trials in the second 20 trials of its training (binomial test,  $p = 0.002$ ); but it did not significantly use a win-stay or win-shift strategy during training (10/26, binomial test,  $p = 0.327$ ).

**Rosy** showed no significant use of familiarity (19/40, binomial test,  $p = 0.875$ ); neither did she present risk-sensitivity (25/40, binomial test,  $p = 0.154$ ); she showed constancy by choosing the same pot nine times out of ten consecutive trials in the second 20 trials of its training (binomial test,  $p = 0.021$ ); but she did not significantly use a win-stay or win-shift strategy during training (13/27, binomial test,  $p = 1$ ).

**Tickle** showed significant avoidance of familiarity (13/40, binomial test,  $p = 0.038$ ); she presented risk-aversion, by choosing the “safe” pot with her less-preferred food for 16 times out of 20 consecutive trials between her 10<sup>th</sup> to its 30<sup>th</sup> training trial (binomial test,  $p = 0.012$ ); but she did not significantly use constancy or alternation (19/39, binomial test,  $p = 1$ ); not did she use a win-stay or win-shift strategy during training (16/30, binomial test,  $p = 0.856$ ).

**Teddy** showed no significant use of familiarity (22/40, binomial test,  $p = 0.636$ ); but she presented risk-proneness (27/40, binomial test,  $p = 0.038$ ); she presented constancy by choosing the same pot 15 times out of 20 consecutive trials in the second 20 trials of its training (binomial test,  $p = 0.041$ ); and she significantly used a win-stay strategy during its training (19/26, binomial test,  $p = 0.029$ ).

Table 5: Strategies used by each individual (see methods and Figure 23 for description of the strategies).

The use of four different foraging strategies was analysed during the 40 training trials of each octopus: familiarity (“3h” indicates a significant use of the strategy only after the three-hours delay), risk-sensitivity (numbers in parentheses indicate use of the strategy during the first 20 or last 19 training trials), alternation and win-stay strategies. See Materials and Methods and Figure 23 for a description of these strategies.

Individual Strategy	Suricate	Abe	Pipoune	Coquille	Rosy	Tickle	Teddy
<b>Familiarity</b>		Familiarity avoidance	Familiarity avoidance (3h)	Familiarity avoidance		Familiarity avoidance	
<b>Risk-sensitivity</b>	Averse	Prone	Prone [2-21] Averse [22-40]	Prone [2-21]		Averse	Prone
<b>Alternation</b>	Constancy	Constancy	Constancy	Alternation	Constancy		Constancy
<b>Win-stay</b>	Win-stay						Win-stay

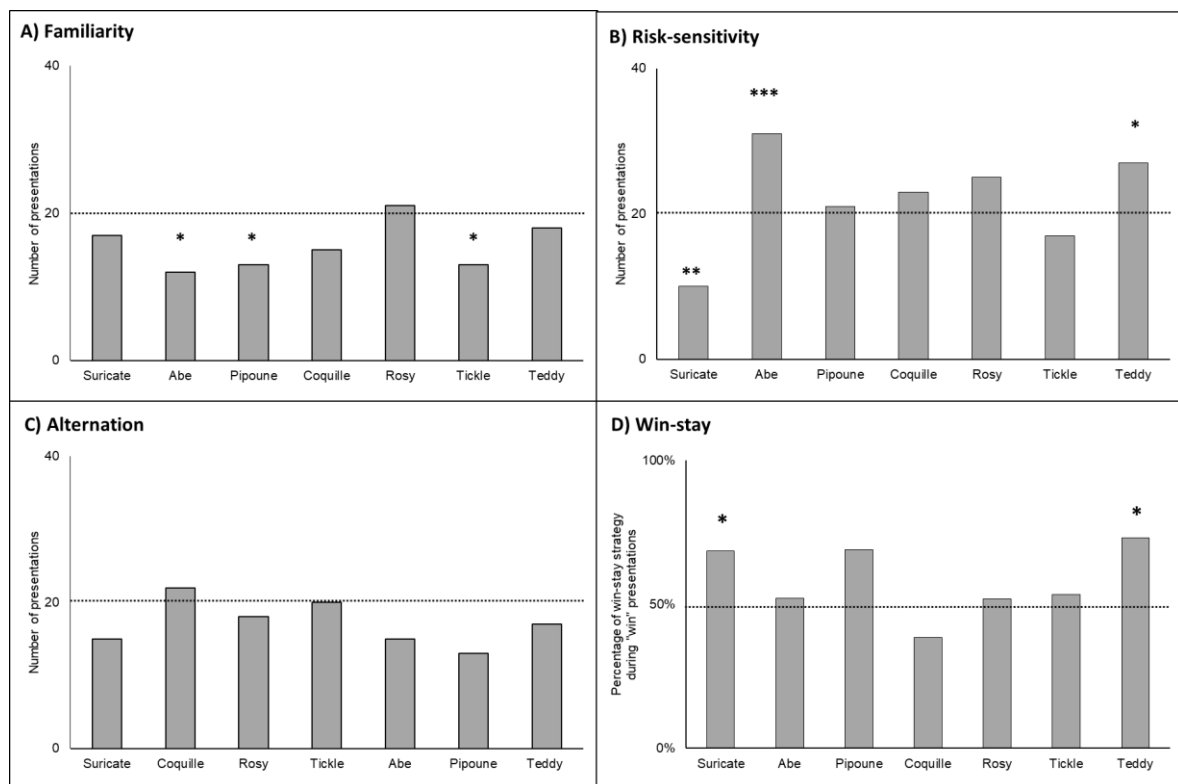


Figure 25: Individual use of each strategy during the replenishing rate training.

See Materials and Methods and Figure 23 for description of these strategies. A) Familiarity; B) Risk-sensitivity (number of risky choices); C) Alternation; D) Win-stay. During the 40 training trials, each individual favoured different strategies, with a high inter-individual variability. Asterisks represent a significant difference from chance (dashed line indicates chance level; binomial test, \*  $p < 0.05$ , \*\*  $p < 0.01$ ).

## D. Discussion

In our study, seven common octopus (*Octopus vulgaris*) were tested in a task requiring them to keep track of time with different food sources varying in space and time. Most octopuses (six out of seven) relied on less-cognitively demanding strategies than keeping track of time during the replenishing rate learning task. Only one octopus learnt the replenishing rates of different prey types and was able to use these rules to solve an episodic-like memory task. When analysing the strategies used by tested octopuses during the replenishing rate training, such as familiarity, risk-proneness, spontaneous alternation and win-stay, we observed above all a high interindividual variability.

We conducted this experiment to determine whether episodic-like memory is an ability shared by modern cephalopods, and thus present in both cuttlefish and octopuses, or whether it is instead a distinctive ability of cuttlefish to cope with specific ecological constraints. One individual (Teddy) learnt the replenishing rate of the different food items and subsequently succeeded in the episodic-like memory task. This may indicate that *Octopus vulgaris* possesses the neural prerequisites for episodic-like memory. Both cuttlefish and octopuses possess a central nervous system with similar brain shape and structures (Wang and Ragsdale, 2019). The vertical lobe is notably thought to be the place of higher cognitive functions (Shigeno et al., 2018), and it could be the basis of episodic-like memory ability for both species. If this is the case, we could hypothesise that episodic-like memory may be an ability shared by cephalopods in general. As stated in the ecological intelligence hypothesis (Byrne, 1997; Milton, 1981) and in the predator-prey interaction hypothesis (van der Bijl and Kolm, 2016), such cognitive skill might be necessary to cope with the ecological constraints shared by cephalopods. Indeed, as they all evolve under high predatory pressure without a shell to protect themselves, they need to sustain their exponential growth by finding substantial amounts of food. However, other complex cognitive skills might allow them to efficiently find prey and avoid predators, and we cannot rule out the possibility that episodic-like memory might not be necessary and might rather be a simple by-product of the evolution of other cognitive abilities.

Nevertheless, we have to note that only one individual relied on episodic-like memory ability whereas most octopuses relied on other simple foraging strategies. We can only speculate why most tested octopuses did not learn the replenishing rate task successfully. Firstly, we consider the inability of most octopuses to learn the replenishing rates was not due to an insufficient number of training trials. Indeed, with the first batch of octopuses, we conducted two times more trials (*i.e.* 40) than needed by cuttlefish to learn the replenishing rates in previous studies (*i.e.* 20 trials on average in Jozet-Alves et al., 2013 and Schnell et al., 2021b), and doubled this number of trials (*i.e.*

80) with the second batch. In this second batch, one octopus reached the learning criterion in 43 trials, but the three other octopuses which were given twice this number of trials did not show any signs of replenishing rates learning. Secondly, the fact that mussels were available at all times in the tank may have hindered the motivation to learn the replenishing rates. It might have lowered the pressure to find food, thus favouring random and simpler foraging strategies. However, this hypothesis is unlikely, as we observed that during the first months of the experiment, octopuses almost never consumed mussels, and while the quantity of consumed mussels slowly rose over the months, it remained quite a rare occurrence. Moreover, we observed that crabs always keenly drew octopuses' attention during our experiment, even when they had been fed shortly before. Indeed, cephalopods seem to possess strong hedonic motivation for their preferred food, like cuttlefish refraining from eating a less-preferred food available at all times when they know that their preferred food will be ensured at the end of the day (Billard et al., 2020a).

Thirdly, octopuses may not spontaneously encode the temporal component of their episodic-like memories in terms of "how long ago" or may, but with a low accuracy: they might not, or hardly, detect the difference in elapsed delays of one or three hours. "How long ago", known as temporal distance, is often used to study the temporal feature of episodic-like memory (*e.g.* Babb and Crystal, 2006; Clayton and Dickinson, 1998; Feeney et al., 2009), but it is not the only way to encode time. Indeed, time can be perceived in terms of temporal distance ("How long ago"), by evaluating the elapsed time between the encoding of an event and its retrieval; but also in terms of temporal location ("When"), by relying on information linked with the encoding time; or in terms of temporal order (or relative times), by retrieving the succession of events (Friedman, 1993; Friedman, 2007). While humans thrive in all these temporal perceptions, animals may favour one over the other. For example, black-capped chickadees rely more on temporal locations than distances (Feeney et al., 2011a), rats seem to have difficulty in using temporal locations (Roberts et al., 2008; Zhou and Crystal, 2009), but easily remember the temporal order of events (Fortin et al., 2002), and rhesus monkeys cannot perceive temporal distances (Hampton et al., 2005), but can recall the temporal order of events (Templer and Hampton, 2013). The possible absence of temporal distance perception in octopuses would not rule out their potential to use episodic-like memory, as it can be observed through other temporal modalities as well: indeed, episodic-like memory ability was tested in rodents using temporal distance (Babb and Crystal, 2006), temporal location (Zhou and Crystal, 2009) and temporal order (Dere et al., 2005). These different experimental approaches could be tested with octopuses to explore their episodic-like memory ability. They would offer an insight into time perception in octopuses, to observe whether



octopuses really do not keep track of elapsed time, or whether our experiment could not bring to light this ability.

Finally, our last supposition is that octopuses, instead of relying on episodic-like memory ability, rather favour simpler foraging strategies that do not require a heavy cognitive load. When exploring these foraging strategies in our two batches of octopuses, we observed a group-level avoidance of familiarity, with octopuses favouring the least familiar pot (i.e. choosing the same pot first during both presentations of a trial); a general risk-proneness at the beginning of the training, with octopuses favouring the pot containing the more preferred prey which was available half of the time; a general constancy, with octopuses favouring the same pot in the second presentation over trials; and a general win-stay strategy, with octopuses favouring the pot which provided them with a reward in the previous trial. Nevertheless, analysing the use of different strategies at the group level might not be ideal, as we observed a remarkable interindividual variability, with each octopus using and combining strategies in a different way from others. Coquille, for example, was the only individual using spontaneous alternation rather than constancy when choosing; Suricate and Teddy were the only ones significantly using a win-stay strategy; Rosy relied mostly on random choices; and Teddy was the only one to learn the replenishing rates. Pipoune showed even more distinctive traits: firstly, she used familiarity only after long delays, maybe because she favoured other strategies when the memory trace was stronger (*i.e.* after a short delay). Indeed, she used constancy, but also risk-sensitivity. Secondly, she shifted from risk-proneness to risk-aversion. Empirical studies on risk-sensitivity in vertebrates indicate that when risk comes from the variability in the amount or presence of a reward, animals are most frequently risk-averse or risk-indifferent (Kacelnik and Bateson, 1996). We can thus consider that Pipoune may have required 10 to 20 trials to learn that her preferred food was riskier than its less-preferred food, then she shifted to risk-aversion. To sum up, instead of using episodic-like memory ability to optimise their food intake and succeed in the task, octopuses rather relied on individually variable strategies which seemed equally relevant to satisfy their food needs.

In the wild, foraging strategies are a complex trade-off between predatory and starvation risk: risk-prone individuals may enhance their chances of finding more or better food but may also enhance the risk of finding no food at all, while risk-averse individuals may more easily find food but of a lesser quantity and quality; individuals which use familiarity, constancy or win-stay strategies may enhance their chances of finding food but may also enhance the chances of a predator predicting their arrival (Stephens and Krebs, 1986). Field studies show that common octopuses use different foraging strategies, with some being opportunistic and others selective, and interindividual variability is also observed among selective individuals as they are specialised in different types of

prey (Anderson et al., 2008; Mather et al., 2012). Interindividual variability in foraging strategies is in fact a common trait of various predatory species (*e.g.* seabirds (Ceia and Ramos, 2015), seals (Cherel et al., 2009), fishes (Szopa-Comley et al., 2020), squids (Lorrain et al., 2011)). The use of one strategy over the other is often considered to be linked to the physiological status of an individual and its prior experiences (Kacelnik and Bateson, 1996). However, the foraging specialisation of wild octopuses did not seem to be explained by environment or the status of the individual alone (Mather et al., 2012). This also seems to be the case in our experiment, as the observed differences were not explained by any physiological or behavioural parameters such as sex, size, batch or food preference. Differences in strategies may rather come from intrinsic parameters such as personality traits, as hypothesised by Mather and her colleagues (2012).

High individual variability, even outside foraging, seems to be common in, if not characteristic of, octopuses. Octopuses show clearly distinguishable personality traits, through differences in activity level, reactivity, boldness and aggressivity (Mather and Anderson, 1993; Pronk et al., 2010; Sinn et al., 2001). When looking at playful behaviour, octopuses demonstrate various interactions with objects, with some individuals showing possessiveness and playful interactions, and others simply ignoring them (Kuba et al., 2003; Kuba et al., 2006). The personality profile of each individual might affect its cognitive performances (Carere and Locurto, 2011), and thus individual differences are striking in cognitive tasks, such as in the number of trials octopuses need to reach a learning criterion in a discrimination task (*e.g.* 224 to 1463 ( $n=4$ , Bublitz et al., 2017)); in the number of successful reversals in reversal experiments (*e.g.* 4 to 13 (Bublitz et al., 2021)); or in the number of days to work out problem-solving tasks, such as retrieving through a hole and opening a container (*e.g.* in 3 to 24 days ( $n=7$ ; Richter et al., 2016)).

Inter-individual variability can be an advantage as it provides unpredictability, which is a major, although often overlooked, modulator of predator-prey interactions (Chang et al., 2017; Pettorelli et al., 2015). Indeed, variability in the foraging behaviour of octopuses may prevent prey from predicting their attacks, and also prevent predators from anticipating the arrival of their cephalopod prey. Individual variability seems to enhance the persistence of a species in an environment under predatory pressure (Morozov et al., 2013), but also seems to favour the dispersal and colonisation of new environments (Nanninga and Berumen, 2014), which might thus have promoted the development of *Octopus vulgaris* in diverse and world-distributed environments (Luca et al., 2014). In the common cuttlefish, variability in foraging strategies has also been documented. However, this variability seems mainly driven by age and environmental predictability: in the wild, juveniles appear more selective than adults, which present generalist and opportunistic behaviours (Neves et al., 2009; Pinczon du Sel et al., 2000). A lab-conducted experiment showed that cuttlefish have

a selective foraging behaviour when exposed to a predictable feeding schedule, and they switch to an opportunistic and less-risky strategy when the environment becomes unpredictable (Billard et al., 2020a). Unlike octopuses, cuttlefish seem to display a low level of inter-individual variability in foraging strategies under the same physiological and environmental conditions.

The need to optimise the time spent exposed to predators while foraging might have been the main driver of the emergence of episodic-like memory in cuttlefish, while octopuses seem to cope with their environmental constraints by displaying a wide range of foraging strategies varying both within and between individuals. Octopuses and cuttlefish have evolved different lifestyles and cognitive strategies to deal with the environmental challenges they are exposed to, while possessing the same fundamental brain architecture (Wang and Ragsdale, 2019). Comparative studies undertaken in cuttlefish and octopuses show how necessary it is to integrate ecological, cognitive and neurobiological data to understand how complex cognition has emerged.

## Supplementary material

### *Pre-training method*

The pre-training (constituted of five consecutive steps, Figure 266) consisted in training octopuses to open two pots within 30 minutes two times a day to obtain a food reward. Plastic pots (70mm x Ø35mm) opacified with grey tape (from step 2) and hermetically closed with Parafilm® (from step 3) were used during the experiment.

First step: Octopuses were presented with one open transparent pot containing a crab they should grab and eat. Two trials were conducted per day. When octopuses ate the content of at least one pot for three consecutive training days, they went to step 2.

Second step (no access to visual cues): Octopuses were presented with one open pot surrounded by opaque tape containing a crab they should grab and eat. Three trials were conducted per day. When octopuses ate the content of the three pots within a day, they went to step 3.

Third step (no access to visual and olfactory cues): Octopuses were presented with one pot surrounded by opaque tape and tightly covered with Parafilm®. Three trials were conducted per day. When octopuses opened the three closed opaque pots within a day, they went to step 4.

Fourth step (no access to visual cues): Two open opaque pots were simultaneously presented in the tank (random positions along trials). Each pot contained a different prey, from the two prey items used for the preference test. When octopuses retrieved food items from the two pots in less than 30 minutes, two times a day for at least four out of five consecutive training days, they went to step 5.

Fifth step (no access to visual and olfactory cues): The procedure used was the same than the one used during step 4, excepting that pots were closed with Parafilm®. The octopus had to consume the food of the two pots in less than 30 minutes, two times a day for at least four out of five consecutive training days to start the replenishing rate training.

### Food preference test

Prey preferences of each individual subject was tested between the step 3 and 4 of pre-training. General avoidance of certain types of food was noted during pre-training. Only preys which were not avoided were randomly tested two by two during the food preference tests. Two different prey types were placed at the tip of two steel wires and simultaneously presented at equal distances to the octopus (about 10 cm), with the right/left position of each prey type randomised between trials. The octopus chose a prey item by grabbing it and eating it. Preference was assessed when octopuses

choose one type of food over the other in at least 10 out of 12 consecutive trials (binomial test,  $p=0.039$ ).

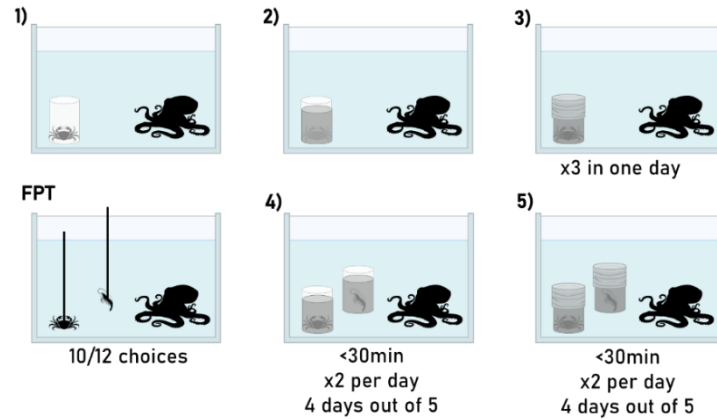


Figure 26: Sequence of pretraining steps and the food preference test.

1) Step 1: Octopuses learn to grab a crab inside a transparent open pot; 2) Step 2: Octopuses learn to grab a crab inside an opaque pot; 3) Step 3: Octopuses learn to open a closed opaque pot to eat a crab; FPT: Food preference test during which octopuses are given 12 times a choice between two types of food to determine their preference; 4) Step 4: Octopuses learn to eat preys out of two open opaque pots in less than 30 minutes two times a day, at least four out of five consecutive training days; 5) Step 5: Octopuses learn to eat the preys out of two closed opaque pots in less than 30 minutes two times a day, at least four days out of five consecutive days.

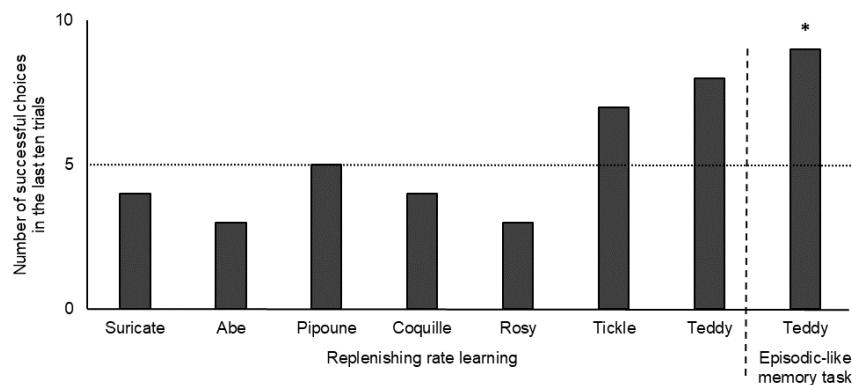


Figure 27: Number of successful choices in the last ten trials of the replenishing rate training and the episodic-like memory task.

None of the individuals, except Teddy, reached the learning criterion of eight successful responses out of ten consecutive trials during the replenishing rate training. Subsequently, only Teddy was tested in the episodic-like memory task, and reached the acquisition criterion of 10 out of 12 successive trials. The asterisk represents a number of success significantly different from chance (i.e. dashed line; binomial test,  $* p<0.05$ ).

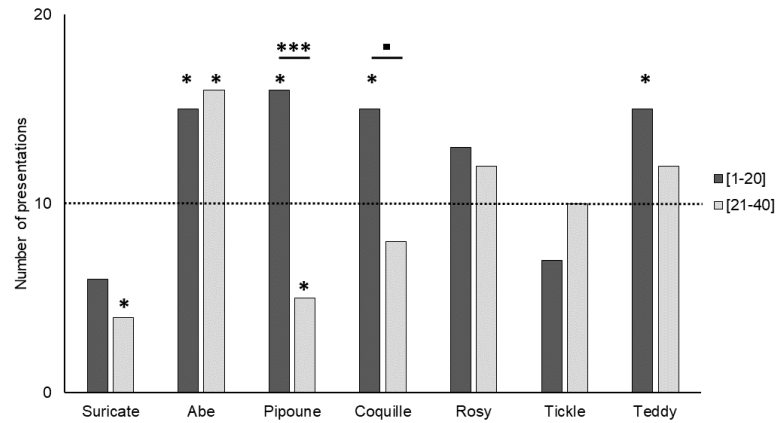


Figure 28: Individual use of risk-sensitivity (in number of risky choices) during the first 20 and the last 20 trials of replenishing rate training.

See Materials and Methods and Figure 23 for description of risk-sensitivity. High inter-individual and intra-individual variability in risk-sensitivity was observed: some individuals did not show any risk-sensitivity throughout the training (Rosy, Tickle), while other showed a steady risk-proneness (Teddy) or risk-aversion (Suricate); and some others showed risk-proneness during the first 20 training trials and reversed to risk-aversion or risk-indifference during the last 20 training trials (Pipoune, Coquille). Asterisks represent a significant difference from chance (i.e. dashed line; binomial test, ■  $0.06 < p < 0.05$ , \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

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## II. Exploration of the memory for time in octopus

### Memory for the temporal order of a sequence in octopus

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#### **Abstract**

Temporal information can be encoded in various ways, such as temporal distance (“How long ago?”), temporal location (“When?”) or relative times of occurrence (“Which order?”). While humans can equally rely on the three types of encoding, other animal species might not. A previous experiment indicated that octopuses could not discriminate elapsed delays, suggesting that they are unlikely to encode time in terms of temporal distance. That does not necessarily imply their inability to encode temporal information as they might use another type of encoding, such as relative times of occurrence. We here conducted an experiment during which octopuses were presented a sequence of images, then they had to select between two images which image occurred the earliest in the sequence. All tested octopuses succeeded the task and some subjects even transferred their learning to novel symbolic images, showing that octopuses can remember the order of information.

#### **Key-words**

Order, Sequences, Relative times of occurrence, Octopuses, Memory for time

## A. Introduction

In memory, time is an essential component, as it allows to discriminate between similar experiences and renders each event unique. Friedman (1993) theorised that time can be encoded in three non-exclusive ways: based on distance, based on location or based on relative times of occurrence. Distance-based theories correspond to “how long ago” an event happened, location-based theories correspond to “when” an event happened, and relative times of occurrence theories correspond to the order of events in a sequence, and the notion of “before-after”. Humans rely on these three types of time encoding, and it was shown that some animals can also rely on the three of them, such as rats, which can use temporal distance cues (Roberts et al., 2008), temporal location cues (Zhou and Crystal, 2009) and relative times of occurrence cues (Ergorul and Eichenbaum, 2004). However, it was observed that animals may perform better using some temporal cues than others. Hence, rats rather rely on temporal distance cues than on temporal location cues (Roberts et al., 2008), whereas black-capped chickadees favour temporal location cues over temporal distance cues (Feeney et al., 2011a).

Time encoding in animals has often been studied through episodic-like memory tasks, where subjects have to remember what they did, where and when. Such tasks allow to explore the encoding of temporal distance, as with western-scrub jays (Clayton and Dickinson, 1998), magpies (Zinkivskay et al., 2009), hummingbirds (González-Gómez et al., 2011), great apes (Martin-Ordas et al., 2010), meadow voles (Ferkin et al., 2008), rats (Roberts et al., 2008), or cuttlefish (Jozet-Alves et al., 2013b); but also the encoding of temporal location, as with rats (Roberts et al., 2008; Zhou and Crystal, 2009) or black-capped chickadees (Feeney et al., 2011a); and the encoding of relative times of occurrence, as with rats (Ergorul and Eichenbaum, 2004) and dogs (Lo and Roberts, 2019). Memory for relative times of occurrence has also been studied with tasks presenting sequences of items, such as odours or images, followed by a choice between two of the previously encountered items, where subjects have to select the item which occurred the earliest in the sequence. Rats (Fortin et al., 2002), mice (DeVito and Eichenbaum, 2011) and rhesus monkeys (Templer and Hampton, 2013) have been shown to succeed in such task.

Common octopuses have been previously tested in a replenishing rate learning task (*i.e.* temporal distance), but only one out of seven individuals succeeded the task (Poncet et al., 2022). Since failure in encoding one type of temporal cue does not preclude the successful encoding of another type of cue, we conducted an experiment to explore the ability of octopuses to rely on relative times of occurrence, or in other words the order of events in a sequence. To do so, we presented



octopuses with a sequence of four images of seashells, then asked them to choose between two images which was the one that occurred the earliest in the sequence.

## **B. Materials and methods**

### ***1. Ethical statement***

The experiment was conducted in compliance with the directive 2010/63/EU (European parliament) and with the French regulation applied to the protection and use of animals in research experiments. The procedure was authorised (#22429 2019101417389263 v2) by the ethical committee of Normandy region (Comité d’Ethique de NOrmandie en Matière d’EXpérimentation Animale, CENOMEXA; agreement number 54).

### ***2. Subjects***

Four female sub-adult common octopuses (*Octopus vulgaris* Cuvier, dorsal mantle length ranging from 6.5 to 10 centimetres at the beginning of the experiment) were tested in our experiment. They were collected in the Mediterranean Sea by specialised fishermen (Carrodano, Poissons vivants, La Ciotat, France) in June 2022. They arrived two months prior to the experiment at the marine station of the University of Caen (Centre de Recherche en Environnement Côtier, Luc-sur-Mer, France). They were individually housed in glass tanks of 100x50x50cm or 120x40x50cm, enriched with a sand bed, pebbles, seashells and a shelter in the form of a terracotta pot or a PVC tube. Octopuses were maintained in circulating natural seawater in a semi-closed system at  $15 \pm 1^\circ\text{C}$  with artificial lighting following the natural light cycle. Three weeks before the end of the experiment, octopuses were moved to another husbandry, where they were housed in the same glass tanks, with natural seawater in an open system at  $12 \pm 1^\circ\text{C}$  with natural lighting. Octopuses were fed daily with live crabs of suitable size (*Hemigrapsus sanguineus* and *Carcinus maenas*) and pieces of thawed shrimps (*Litopenaeus vannamei*).

### ***3. Procedure***

During the experiment, a pool of 15 laminated images (185x100 mm) of different coloured seashell on white background were used. At the start of a trial, four images were randomly selected out of the pool. The selected images were changed for each trial. Each trial was organised as follows: four

successive images presentation (constituting a sequence of images) and two successive choice tests. Images were presented one after the other (Figure 29A) by placing the image against the glass of the tank, in the middle upper part of it. Each image was visible for one minute, then an interval of one minute was conducted before presenting the next image. After the presentation of the fourth image, a ten-minute delay was conducted before the first choice test, followed by a ten-minute delay before the second choice test. A choice test consisted of the presentation of two images out of the four previously seen (two images were randomly attributed to the first choice test and the two others to the second choice test), which were presented at the surface of the tank. Each trial contained two choices. Octopuses spontaneously grabbed one of the images, and if the grabbed image was the least recently seen image, it was considered a correct choice and rewarded with a crab, while if the grabbed image was the most recently seen image, it was considered an incorrect choice and not rewarded. The chosen image was left to the octopus and was retrieved with a small net when the octopus let go of it.

Training ended when the acquisition criterion was reached: it was set to 12 correct responses out of 15 consecutive choices (*i.e.* 12 correct responses out of 8 trials, with two choices per trial). Two to four trials were conducted each day, five days a week, with a delay of at least one hour between each trial.

As none of the octopuses reached the acquisition criterion after 74 choices, we introduced a negative reinforcer in the form of a bright white light when octopuses made an incorrect choice, from the 75<sup>th</sup> until the 99<sup>th</sup> choice. As no improvement was observed and the light did not seem to be perceived negatively by octopuses, from the 100<sup>th</sup> choice until the end of the training, we used a negative reinforcer constituted of 1mL of alcohol vinegar (half diluted with tap water, final acidity of 4%) which was applied next to the base of the arms of the octopuses (chemoreceptors are present in the suckers), using a 3mL plastic Pasteur pipette. The positive reinforcer (crabs) remained unchanged throughout training.

#### ***4. Transfer test***

A transfer test was conducted when the acquisition criterion was reached by an individual (Figure 29B). Nine novel images of various black, grey and/or white symbols on a white background were used. The procedure was identical to the previous procedure. 15 consecutive choices (*i.e.* 8 trials) were conducted.

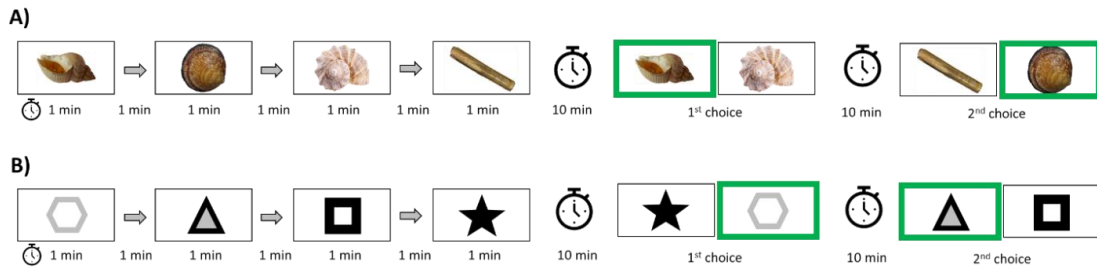


Figure 29: Representation of the procedure.

A) Training with images of seashells. B) Transfer task with symbolic images. Octopuses were successively presented four randomly selected images of symbols. After a ten-minutes delay, two images were presented, and selecting the image which occurred the earliest in the sequence was rewarded. After another ten-minute delay, a presentation of two other images was carried out.

### C. Results

All octopuses reached the acquisition criterion of 12 successful responses out of 15 consecutive choices (binomial test,  $p = 0.035$ ) in  $179 \pm 24$  trials (mean  $\pm$  SD; Octopus O1: 194 trials, O2: 194, O3: 184, O4: 143).

The light reinforcer did not have a visible effect (Figure 30) on the percentage of successful responses out of 25 consecutive choices: from the 50<sup>th</sup> to the 74<sup>th</sup> choice, the mean percentage of successful responses was 51% (individually ranging from 44 to 60%); when the light negative reinforcer was used (between the 75<sup>th</sup> and the 99<sup>th</sup> choice), it was 50% (ranging from 48 to 52%). When the vinegar negative reinforcer was used for the next 25 choices (between the 100<sup>th</sup> and the 124<sup>th</sup> choice), the mean percentage of successful responses was 48% (ranging from 40 to 56%), and it rose to 56% (ranging from 48 to 64 %) for the next 25 choices (between the 125<sup>th</sup> and the 149<sup>th</sup> choice).

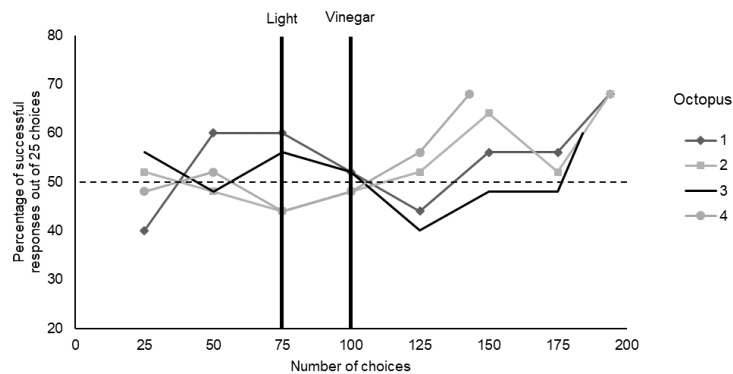


Figure 30: Percentage of successful responses for 25 consecutive choices throughout the training for each octopus. The dashed line corresponds to chance level, the two vertical lines correspond to the introduction of a negative reinforcer, either light or vinegar.

Only one octopus successfully transferred its learning to the novel symbolic images (O3: 12 successful responses out of 15 choices, binomial test,  $p = 0.035$ ), while the other octopuses did not significantly select more the correct image than the incorrect one (O1: 10/15, O2: 10/15; O4: 8/15).

## D. Discussion

All tested octopuses successfully learnt to select the image which occurred the earliest in a sequence of four images of seashells. At least one octopus was able to transfer this learning rule to novel and symbolic images.

Encoding time using the order of events rather than the temporal distance (*i.e.* elapsed time since the event) might have several advantages (Friedman, 1993). It might be valuable to encode the connections between events: such before-after relations might be useful for inferring causality. Moreover, recalling how events unfold might be more useful for octopuses than remembering how long ago these events happened: the ability to encode and retrieve sequences of events that generally happen in the same order might be useful during foraging and problem-solving. Octopuses might use specific series of behaviours that will allow them to catch a prey, open a seashell or avoid a predator (Hanlon and Messenger, 1996). It might also be useful for planning a potential hunt or a possible flight by preparing the sequence of behaviours that will allow them to find a prey or escape a predator, but also identify which behaviour in the sequence was the most useful or was the one which led to the escape of the prey, to optimise future behaviour.

The results obtained here show that octopuses are able to acquire and transfer a rule based on the order of a sequence, thus they might be able to use this type of temporal cues in an episodic-like memory task. Rats (Ergorul and Eichenbaum, 2004) and dogs (Lo and Roberts, 2019) have been tested in such a task by presenting them four different odours in different locations. Then they had to choose between two odours or two locations and select the one they encountered first. Octopuses could thus be tested in a similar experiment to explore their episodic-like memory abilities (what-where-in which order), as their inability to encode time in temporal distances prevented us to determine whether they do or do not possess such abilities (Poncet et al., 2022).

Another point to highlight is the use of negative reinforcement in our experiment. The majority of studies conducted on octopus cognition before the 2000s used negative reinforcement in the form of an electric shock which allowed them to obtain significant results within a limited number of

training trials (see for example Fiorito and Scotto, 1992; Sutherland, 1957; Wells and Young, 1970). In our experiment, as octopuses did not show improvement after 74 choices, we introduced a negative reinforcer in the form of a bright light. Cephalopods are known to favour dim lighted environments (Fiorito et al., 2015), thus we expected them to dislike the light stimulus and associate it with the false response. However, we did not observe any improvement in the following 25 choices. As we did not witness clear avoidance behaviours, such as turning the head or going away when exposed to the light, we hypothesised that light might not be aversive enough. We thus decided to replace the light by diluted vinegar. We chose vinegar as it was shown that injection of acetic acid induce pain (Crook, 2021). External application of diluted vinegar seemed to be perceived as a mild disagreement by octopuses. Indeed, they directed their funnel and sprayed water toward the area where vinegar was added, but they did not move away, and no lesions or pain-related behaviour were witnessed. Vinegar thus appeared to be mildly negative for octopuses, but its impact on learning was not clear: no improvement was noticeable in the first 25 choices following the use of vinegar, we needed to undertake 25 more trials to notice a performance improvement. The use of a mild negative reinforcement instead of a mere absence of positive reinforcement might be necessary to motivate octopuses to learn the task. It would be worthwhile to replicate our study and use vinegar as a negative reinforcement from the beginning to determine whether it accelerate the learning rate of octopuses.

## Conclusion of Chapter 1

Unlike cuttlefish, octopuses failed to use temporal distance to encode time, but they were able to encode time in terms of relative times of occurrence.

Three hypotheses can be raised from the result obtained with the episodic-like memory task: 1) octopuses do not have the ability to memorise the link between the three components of an event (focal element, place and time), thus they lack episodic-like memory abilities; 2) they need more trials or a negative reinforcer to understand the task; 3) they lack temporal distance encoding ability. The type of time encoding is a neglected aspect of the study of episodic-like memory in animals, and it would be beneficial to compare how various species encode time to better understand their successes and failures in episodic-like memory tasks. Thus, testing cuttlefish in the same task to explore whether they perform equally well using temporal distance or relative times of occurrences would bring valuable insights on the ecological and evolutionary pressures shaping the memory for time.

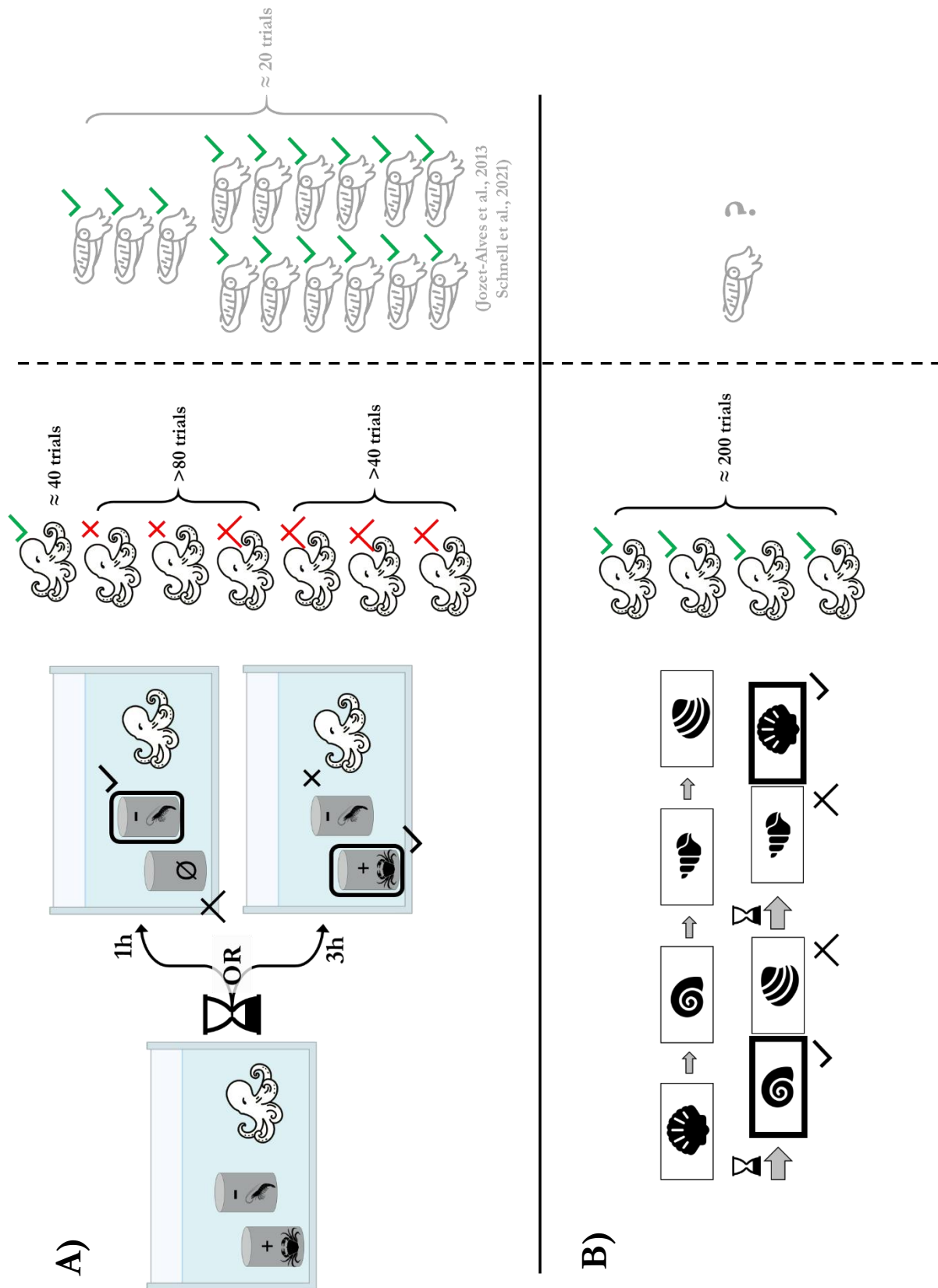


Figure 31: Summary of Chapter 1- Spatiotemporal memory in octopus and cuttlefish.

A: Episodic-like memory task with temporal distance; B: Memory for the temporal order of a sequence task

## Chapter 2:

# False memories in cuttlefish



## Chapter 2: False memories in cuttlefish

**Review 1: Poncet, L., Bellanger, C., and Jozet-Alves, C. (in preparation). Meaningful mistakes: Investigating false memories to explore the reconstructive nature of memory.**

**Article 2: Poncet, L., Billard P., Clayton Nicola S., Bellanger, C., and Jozet-Alves, C. (under revision). False memories in cuttlefish. Current Biology.**

### Introduction of Chapter 2

#### **Part I: Why studying false memories? (Review in preparation)**

False memories are episodic memory impairment reflecting reconstructive and source monitoring errors. They are extensively studied in humans, but infrequently studied in animals. Yet, studying false memories in animals would allow to better understand the processes at the basis of their memory. Setting clear criteria will allow to conduct valuable studies on false memories in animals.

#### **Part II: False memories in cuttlefish (Article 2)**

Cuttlefish are known to be able to remember specific events, namely episodic-like memories, but the processes underlying this ability are unknown. We elaborated a protocol promoting false memory formation in the cuttlefish, to explore the reconstructive processes of their memory. The results obtained suggest that cuttlefish do form visual false memories, and that this susceptibility is influenced by the level of sustained attention on the misleading event, which can be modulated by olfactory processes. These memory errors might be the first indication of the presence of reconstructive processes in memory of cephalopods.

## I. Why studying false memories?

### **Meaningful mistakes: Investigating false memories to explore the reconstructive nature of memory**

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#### **Abstract**

False memories are episodic memory impairments occurring when individuals remember events or features they did not experience. False memories fit within the constructive memory and source memory frameworks, which state that memories are constituted of multiple features stored separately. In order to remember a memory, its features must be bound together at encoding to be later retrieved together. The reformed memory is evaluated, through source monitoring, to verify whether it has been correctly retrieved and is thus plausible. However, source monitoring sometimes fails and misattribute a feature of a memory to another one, creating a false memory.

False memories are extensively studied in humans, with studies on rich false memories, with misinformation effect paradigms, or with Deese-Roediger-McDermott associative memory illusions. While the literature on human false memories is broad, studies on false memories in animals are peculiarly scarce. Studies trying to explore false memories in animals rather focused on recognition bias and context fear generalisation, and the few which used misinformation effect paradigms studied very few individuals. This lack of research is unfortunate, since false memory studies would bring valuable insights on episodic-like memory processes in animals, as well as the constructive and source-monitoring processes linked with it. We thus propose to set criteria to define the boundaries of this new field of memory studies in animals.

#### **Key-words**

False memories, animals, reconstructive memory, source-monitoring

## ***Glossary***

**Episodic memory:** Ability to remember personally experienced past events

**Event:** Set of several features which occurred together and form an integrated representation when encoded in memory

**False knowledge (false belief):** Semantic memory impairment, where subjects recall events or features they did not study, without any kind of recollection.

**False memory:** Episodic memory impairment, where subjects remember events or features they did not experience

**Misinformation acceptance:** Acknowledgment and belief that the misinformation was part of the original event

**Misinformation effect:** Memory impairment of one or several features of an original event resulting from exposure to misleading post-event information

**Semantic memory:** Knowledge of facts and general past events

**Source memory:** Ability to retrieve and evaluate the ensemble of contextual features from a specific memory in order to determine the origin of this memory and discriminate it from another one

**Source misattribution:** Erroneous attribution of the source (i.e. contextual features) of a memory to another memory

## **A. Reconstructive memory and false memories**

### ***1. Constructive memory framework***

Declarative memory is the memory used for conscious retrieval of facts and events. Tulving (1972) divided this memory in two types: the semantic memory, a knowledge (as opposed as recollection) of facts and generalities about past events, and the episodic memory, the ability to consciously recollect or remember personally experienced past events (i.e. episodic memories). Here, we define an event as a set of multiple features which occurred together and form an integrated representation (Johnson et al., 2012). Features can be various: objects and their characteristics (colour, size...), persons, actions performed, contextual features (location, time...), emotions, physiological parameters (thirst, cold...), etc (Crystal et al., 2013).

The constructive memory framework, elaborated by Schacter et al. (1998) explains how memories are encoded and retrieved in the brain. It is based on four essential mechanisms: feature binding, pattern separation, retrieval focus and source monitoring. In this framework, memories are presented as sets of features, with each feature representing an aspect of an experienced event.

Features are distributed across different parts of the brain, such as no particular location contains the whole memory. In order to be able to retrieve a whole memory, the features must be bound together at encoding (feature binding), without overlap between memories (pattern separation). This binding is reconstructed at retrieval: retrieval cues are compared with different subsets of features (retrieval focus), and when these cues match with a particular subset, the rest of the features are activated to form the entire memory, which is subsequently verified to insure its match with retrieval cues (source monitoring). False memories arise when one of these mechanisms is impaired.

## ***2. Source monitoring framework***

The last principle of the constructive memory framework – source monitoring – is based on the work of Johnson et al. (1993). Johnson and her colleagues elaborated the source monitoring framework (SMF), which is a ground work to explain false memories. The SMF is constituted of memory monitoring processes used for reconstruction. Memory monitoring processes evaluate memories based on their match with the expected characteristics of a given source. When an event is encoded into memory, the features of the event are bound. Later, some consolidation processes take place through reactivation. At retrieval, the bound features are retrieved, then evaluated with appropriate weights and criteria. The evaluation, or source monitoring, verify that the event is plausible in relation to general knowledge about the world and about oneself, in order to exclude improbable and unbelievable memories (Johnson and Raye, 1998; Wade et al., 2007). Source misattribution appears when there is a failure of source monitoring and/or a failure of reality monitoring, in other words a failure to distinguish between perceived information and internally generated information in memory (Johnson and Raye, 1998). Three main types of sources are known: external (*e.g.* information on television), internal (*e.g.* story constructed in one's mind), and both internal and external (*e.g.* reading a book produce both an external scenario and internal images such as faces and landscapes). External sources are rich in perceptual details, whereas internal sources are linked with cognitive processes (Steffens and Mecklenbräuker, 2007). Failure of reality monitoring can lead to misinformation effect, for example when a false memory is formed after reading an erroneous narrative about a previously witnessed event.

## ***3. False memories***

Defining false memories is a complex thing, as some authors already noted (Pezdek and Lam, 2007; Wade et al., 2007). On one hand, depending on the research team, the age of the study or the main

subject of the experience, the term ‘false memory’ does not have the same definition. On the other hand, different expressions such as ‘source confusion’, ‘source monitoring impairment’, ‘source monitoring failure’, or ‘source misattribution’ have the same meaning, thus confusing readers through synonyms. This section aims to draw clear definitions of the different terms necessary to understand false memories. We will try to use definitions commonly acknowledged in the psychology field, and to write them as clearly and unequivocally as possible.

Source monitoring can be impaired in distinct ways (Brainerd and Reyna, 2005), such as 1) memory loss, 2) source amnesia, 3) source misattributions. 1) Memory loss is the disappearance of a whole memory or most features of a memory which conduct to the inability to retrieve significantly the memory. When forcefully asked about this memory, subject will only have the option to acknowledge the absence of the memory and guess an answer (Rovee-Collier et al., 1994). 2) Source amnesia is the loss of only contextual features of a memory, thus memories retrieved without source cannot be distinguished from each other (Bornstein, 1999). 3) Source misattribution, often called source confusion, is the erroneous attribution of the source of a memory to another memory, thus confusing the context of two memories (Loftus and Hoffman, 1989; Zaragoza et al., 2019a). Among source misattribution, the misinformation effect is a memory impairment of one or several features of an original event resulting from exposure to misleading post-event information (Loftus, 2005; Volz et al., 2017; Zaragoza et al., 2007a). The memory impairment hypothesis supposes that the misleading post-event information hinders or prevents access to original event information, leading to source misattribution (Belli, 1989; Lindsay and Johnson, 1987). It can lead to either false knowledge or false memories (Lindsay and Johnson, 1987; Loftus and Hoffman, 1989). False knowledge, commonly termed false belief, is a semantic memory impairment, where subjects acknowledge and believe that the misinformation was part of the original event (*i.e.* misinformation acceptance, Belli, 1989), without any kind of recollection, and thus recall events or features they did not study. It is important to precise that we chose to use the expression *false knowledge* instead of *false belief* in order to avoid confusion with the *false belief* used in Machiavellian intelligence and theory of mind fields, where a false belief corresponds to the understanding by a subject that other individuals can believe in falsehoods, whereas the subject knows the truth (Byrne and Whiten, 1994).

False memory is an episodic memory impairment, where subjects remember events or features they did not experience (Pickrell et al., 2017; Tousignant et al., 1986; Wade et al., 2007). Subjects strongly believe in their false memories and claim to be sure they remember them (Norman and Schacter, 1997; Zaragoza and Lane, 1994).

Some authors, such as Pezdek and Lam (2007), define false memories in a stricter manner than stated here. They consider that false memories are only entirely new events which were never experienced by an individual but are nevertheless remembered by the individual. However, this is peculiarly restrictive and the study of false memory as defined by our more lenient definition would bring more valuable insights on episodic memory than the study of the narrow concept of Pezdek and Lam (2007).

Other authors, such as McCloskey & Zaragoza (1985), consider that false memories might not exist and might be instead based on misinformation acceptance. Suppose that in the population studied, 40% of the participants remember correctly the information of the original event whether they were in the control condition or the misled condition. For the control condition, the 60% which does not remember the event will choose by chance, leading the overall control group to have a success of 70 % (40% remembering + [ $\frac{1}{2}$  of 60% = 30% choosing the correct answer by chance]). For the 60% which does not remember the event in the mislead group, some of them will remember the misleading event, and accept this information. Let's say half of this group will remember the misleading event so  $\frac{1}{2}$  of 60% = 30% will choose the wrong answer. The last 30% of the group will use chance, thus  $\frac{1}{2}$  of 30% = 15% will choose the right answer. Thus, the misled group will answer the right answer 55% of the time (40%+15%), as in the misinformation effect studies. However, this theory cannot explain all the results found in rich false memory studies: some subjects can describe a whole "memory" which never happened to them before, without answering wrong or right questions and without using suggestions brought earlier by the interviewer.

#### ***4. Influencing parameters on the formation of false memories***

Studies on humans have highlighted that true memories are richer, clearer, more emotionally intense and contain more contextual and sensory details than false memories (Heaps and Nash, 2001; Norman and Schacter, 1997). However, multiple parameters can influence the perception of true memories and thus enhance the formation of false memories.

The **passage of time** has a great influence on the formation of false memories. When time passes, the memory for the event is weakened and loses details. It decreases the likelihood to detect the discrepancy between the misleading cue and the original event, as stated in the Discrepancy Detection principle (Loftus, 2005; Loftus et al., 1978). Moreover, during source monitoring, one

requires a lesser amount of perceptual details to recognise a memory as an actual old event compared to a more recent one (Frost, 2000).

The **age** of the subjects is an important factor in the suggestibility to the formation of false memories. Young adults are the less suggestible, and the suggestibility increases with aging. Old adults, especially the ones who are 70 years old and above, show a great suggestibility to misleading information (Karpel et al., 2001; Loftus et al., 1992; Mitchell et al., 2003; Norman and Schacter, 1997) and are more confident in their false memories than young adults (Mitchell et al., 2003). This suggestibility in old adults may be due to a reduced perception and encoding of information or an impaired decision process during source monitoring. Indeed, old adults are less confident in their overall source judgments compared to young adults (Mitchell et al., 2003). Children are also especially susceptible to misinformation, with the effect reducing as the children grow (Ackil and Zaragoza, 1998; Ceci and Bruck, 1993; Loftus et al., 1992; Otgaar et al., 2014). However, it must be noted that the inverse tendency is observed in Deese-Roediger–McDermott (DRM) associative memory illusion paradigms. This type of false memory paradigm is based on the presentation of a list of words which is constructed such as a target word come to mind without ever being told or read (see part B.1.c. for more details). In this paradigm, children show a stronger resistance to false alarm than young adults (Brainerd et al., 2010; Howe, 2008; see Otgaar et al., 2014 for a review).

The available **attentional resources** influence the resistance to misinformation: when attention is limited either at encoding or retrieval of misinformation, the misinformation effect is stronger, because the encoding or the retrieval of the source of the information is disrupted (Ackil and Zaragoza, 1998). A good memory of the actual source of the suggested item does not prevent the formation of false memories (Zaragoza and Lane, 1994). However, when subjects are asked to focus their attention on the source of their memories, it drastically enhances their ability to detect and subsequently eliminate false memories (Zaragoza and Lane, 1994; Zaragoza et al., 2019a).

The **repetition** of the misleading suggestion increases the likelihood to form false memories compared to false knowledge. Subjects repeatedly exposed to misleading cues form richer false memories, and place more confidence in them (Heaps and Nash, 2001; Zaragoza and Mitchell, 1996). The same trend is observed in DRM paradigms, when longer lists increase the likelihood to produce false memories, probably because the target word is repeatedly suggested (Robinson and Roediger, 1997).

The **contextual variability** has a negative influence on the performance of subjects to correctly remember events (Mitchell and Zaragoza, 1996). Indeed, the success of retrieving a memory, either true or false, depends greatly on how the retrieval context matches with the encoding context

(Pickrell et al., 2017). The context can be the environment where the experiment is performed (i.e. testing room, experimenter identity), but also the modality in which information was received. Increasing the number of modalities (read, listened, watched ...) in which original information or misleading information are presented enhance the likelihood to form false memories (Mitchell and Zaragoza, 1996). Matching an actual sound (Henkel et al., 2000) or an image (Braun-LaTour et al., 2004; Lindsay et al., 2004) with what is visually imagined also enhance the likelihood to falsely remember what was imagined. Moreover, misinformation is more produced when read in a narrative compared to seen in a video or an image (Kiat, 2018), probably because reading is both a source of external information and internally generated information through imagination. Through source misattribution, reading impair the recollection of the witnessed event which was also an external information.

Highly negative **emotional valence** (for example criminal activity or traumatic events) of false memories does not decrease the probability that subject will accept the memory as true (Porter et al., 1999; Shaw and Porter, 2015). In DRM paradigms, negatively-valenced lists increase the formation of false memories (Brainerd et al., 2010). Stress exposure can also enhance the formation of false memories after witnessing a neutral event, but not after witnessing a negative event (Payne et al., 2007).

**Social pressure** increases strongly the suggestibility to misinformation (Zaragoza et al., 2001): when the credibility of the source of misleading information is high (power, authority, attractiveness of the source), the likelihood to form false memory is enhanced. Moreover, when this highly credible source provides confirmatory feed-back, it doubles the probability to form false memories.

The **plausibility** of the misleading information has a great influence on the formation of false memories (Zaragoza et al., 2019a). When a discrepancy is detected between the original and the misleading event, it reduces the likelihood to form a false memory (Zaragoza et al., 2019a), but it does not completely prevent it (Greene et al., 1982; Zaragoza and Lane, 1994).

The **explanatory role** of the misleading information for a previously witnessed event impacts significantly the perception as a true memory of the misleading information (Chrobak and Zaragoza, 2013; Rindal et al., 2017). However, explanatory function is not a precondition for false memory development (Chrobak and Zaragoza, 2013).



### ***5. Why do false memories exist?***

After defining what a false memory is, we can wonder pertinently why false memories exist, and why memory errors were not eliminated through evolution. There seems to be a consensus among cognitive psychologists that no single process is responsible for all of the misinformation effects (Pickrell et al., 2017). Some authors think that memory preserves the individual's interpretations of their experiences. Since they are interpretations, they are influenced by anterior and posterior experiences and expectations, as well as inferences and interference drawn when remembering and understanding these experiences (Zaragoza et al., 2019a). The mechanisms producing errors observed through false memories may be the same mechanisms used to correct inaccurate memories (Loftus, 2005). Other authors, such as Suddendorf and Busby (2003), consider that it seems there is no advantage to conserve an exact copy of the past. Our memory is used as a mean of reconstructing events to use them in our present or to elaborate new construction for our future.

### ***6. Why studying false memories in animals?***

Studying false memories in animals could in fact bring valuable information in different domain of animal memory. False-memories would bring another approach to study source memory, and through it, episodic-memory, in animals. False memories may be a way to prove that information about an event obtained from various sources is integrated in memory into a single representation of the event (Loftus et al., 1978). Episodic-memory is defined by its content, its flexibility and its structure (Clayton et al., 2003b). Whereas content and flexibility can be observed through numerous What-Where-When memory experiments (Clayton et al., 2003b; Crystal, 2018), structure has been less studied. Structure can be explored through source memory experiments, since finding source memory indicate that the subject can discriminate between memories, which are thus individually bound into a single representation. Moreover, false-memories indicate failures of reconstruction processes, thus allowing the identification and the exploration of these reconstruction and retrieval mechanisms. Investigating false-memories would bring another approach and would highlight how encoded and bound features are in a memory and how resistant they are against overlaps of similar features from different memories. At last, since some authors consider the false-memories as a reflection of the memory updating and correcting processes (Loftus, 2005), studying them would highlight how flexible animal memory is.

The study of false memories in animals would also bring an insight on evolution of false memories and source memory. By studying various vertebrates and invertebrates which show different brain

structures, it would highlight what neural substrates are prerequired for false memory and its source memory counterpart. It would also bring valuable insight on why false memory exist, in order to deepen current theories on the subject, especially the role of linguistics in false memories. By studying the brain of mammals which form false memories, but also by creating and inhibiting false memories by direct stimulation of the brain, we could conduct medical studies and help the medical research on confabulation (*i.e.* automatically generated false memories; Johnson and Raye, 1998), memory loss and other pathological memory alterations (see Millin and Riccio, 2019 for a complete review).

## **B. Methodology of false memory studies**

### ***1. Human studies***

In humans, three main types of studies, or three groups as defined by Pezdek and Lam (2007), can be distinguished in false memories studies. The group A is constituted of rich false memories, the group B is the misinformation effect paradigm, and the group C is the Deese-Roediger–McDermott (DRM) associative memory illusion.

#### *a. Rich false memories (group A)*

The rich false memories, also called memory implantation or false autobiographical events, are based on the same principle (Heaps and Nash, 2001; Hyman Jr et al., 1995; Loftus and Pickrell, 1995; Mazzoni and Loftus, 1998; Ost et al., 2005; Porter et al., 1999; see Brewin and Andrews, 2017 and Loftus, 1997 for reviews): several childhood events are read by the subjects, and all but one are true events provided by family, whereas one never happened. Subjects then write or talk about what they remember over several weeks. The false event can depict the subject being lost in a mall, having spilled a bowl of punch at a wedding, having spent a night in an hospital ... The interviewer can ask neutral or misleading questions, or provide false-feedback by confirming false statements of the subject. The problem with this type of study is the possibility that a true memory resurfaced, and that the subject is describing this true memory, forgotten by their family. Moreover, the social pressure, or social desirability bias, can influence the report of the subject who want to please the interviewer. On average, a third of the subjects create full false memories, and half of the subjects create at least a partial memory (Scoboria et al., 2017). Some variants exist: implausible or impossible rich false memories or infancy memories use impossible events such as meeting Bugs Bunny at Disney resort or remembering the days after one's birth, in order to ensure that false

memories which are retrieved cannot be true memories (Braun et al., 2002; Braun-LaTour et al., 2004; Malinoski and Lynn, 1999; Spanos et al., 1999). Imagination inflation is another variant, where the subject is asked to imagine events that could have happened during their childhood. Over the weeks, the imagined event become a false memory (Garry et al., 1996; Goff and Roediger, 1998; see Garry and Polaschek, 2000 for a review). In this type of studies, false memories are formed due to source misattribution, where subjects unconsciously retrieve features of several other memories to create the false memory. It can also be attributed to familiarity, since subject are exposed to the false event several times. In some studies, false memories may also be formed by misinformation effect, where they integrate misleading suggestions of the interviewer to an old memory to create the false memory.

*b. Misinformation effect paradigm (group B)*

The misinformation effect paradigm, also called interference studies, is always constituted of a first original event, followed by a misleading post-event misinformation. The subjects must then answer a forced-choice test where original and misleading information are put against each other (Loftus, 1975; Loftus et al., 1978; McCloskey and Zaragoza, 1985). In the original study, the original event began with a car stopping at a stop sign, before it was involved in an accident. The misleading event was a text describing the accident where a yield sign was mentioned (Loftus, 1975). Variants were also used: in some, subjects generated themselves the misleading information through forced confabulation (Ackil and Zaragoza, 1998; Zaragoza et al., 2001); another variant was the illusory truth effect, where the misleading information was repeated several times (Begg et al., 1992); another variant used a misleading colour of an object, and proposed a choice between a range of several colours instead of only two choices (Belli, 1988; Loftus, 1977). In these studies, false memories occur because of a source misattribution, and are suggestion-based.

*c. Deese-Roediger–McDermott associative memory illusion (group C)*

In the Deese-Roediger–McDermott (DRM) associative memory illusion, a list of words is presented to a subject. This list of words is constructed such as a target word come to mind without ever being told or read (*e.g.* the list *bed, night, pillow, tired, dream* is linked with the target word *sleep*; Deese, 1959; Roediger and McDermott, 1995). It also works with images (Howe, 2008; Koutstaal et al., 1999) and phonetics of words (Sommers and Lewis, 1999). The false-memories are errors which are mostly by-products of normal associative and reconstructive memory processes. The

problem of the DRM paradigm is that they produce results which are not correlated with the results obtained in the misinformation effect paradigm (Ost et al., 2013), even though there is a correlation between suggestibility to DRM and false autobiographical memories (Gallo, 2010). Another point to consider is that this task is highly semantic, requires generalisation abilities and associative processes, which differ between subjects depending on age or socio-economic class. Moreover, the DRM paradigm relies on information and not a whole event, and make us wonder whether it should be considered in the same way as other false-memories.

#### *d. Brain studies*

The study of brain areas activated during encoding and retrieval of false memories is a growing field of research. We summarise here briefly the areas activated preferentially for true or false memories during their encoding and retrieval. In a nutshell, the frontal lobe, especially the prefrontal cortex, the medial-temporal lobe, especially the hippocampal and parahippocampal regions, and the temporal lobe are extensively used to encode and retrieve either true or false memories (Baym and Gonsalves, 2010; Budson et al., 2002; Cabeza et al., 2001; Darsaud et al., 2010; Dennis et al., 2008; Gallate et al., 2009; Gonsalves et al., 2004; Kiat, 2018; Kim and Cabeza, 2007; McDermott et al., 2005; Mitchell et al., 2005; Okado and Stark, 2003; Okado and Stark, 2005; Schacter et al., 1996). A stronger activation of these areas during encoding of either the original or the misleading event will respectively predict the subsequent report of true or false memories. The occipital cortex is involved only in encoding or retrieval of true memories (Baym and Gonsalves, 2010; Kim and Cabeza, 2007; Okado and Stark, 2003), whereas the cingulate gyrus and the cerebellum are only involved in encoding or retrieval of false memories (Baym and Gonsalves, 2010; Cabeza et al., 2001; Gonsalves et al., 2004; Okado and Stark, 2003; Schacter et al., 1996).

## **2. Animal studies**

### *a. Recognition bias*

The first mention of the effects of misinformation on animals is, to our knowledge, in the study conducted by Harper and Garry (2000) on pigeons. They used a modified version of a visual delayed matching-to-sample task to study the effect of a postevent cue on the performance of homing pigeons. During the experiment, the pigeons were first exposed to an original stimulus, a coloured light they had to peck on. It was followed by a post-event stimulus (PES), which also was a coloured light that pigeons pecked. At test, pigeons had to choose between 2 lights, one with the same colour as the original stimulus and a second colour. The PES was categorised as *misleading*

(inconsistent in the text) when the colour of the PES was presented at test along with the colour of the original stimulus; it was *reinforcing* (consistent) when the colour of the PES was the same as the original stimulus; and it was *neutral* when the PES was coloured in a third colour not presented at test. The results showed that performance decreased when the delay before or after the presentation of the PES increase. When the PES was presented right after the original stimulus, its category (misleading, reinforcing or neutral) did not have any influence on the performance of the pigeons. Opposite to this, when the PES appeared after a delay, right before the test, the performance of the subjects varied with the category of the stimulus. When it was a reinforcing PES, their accuracy was significantly better than trials with a neutral PES, and the accuracy of trials with neutral PES was better than trials with a misleading PES, where pigeons performed at chance level. The authors presented their experiment as a simplified version of the misinformation paradigm used with humans and claimed their results showed the same trends observed in human studies, and thus they concluded that animals were affected by misleading post-event cues. However, this study used an extremely simplified paradigm. Each event was one stimulus, and thus could not be accounted for the formation of a complex memory. Moreover, the delays used were peculiarly short, 2 to 20 seconds, thus animals probably used their working memory rather than their long-term memory for the task. Furthermore, the results are probably better explained with familiarity and misinformation acceptance. Indeed, the post-event cue may come to be accepted as the actual target stimulus, where the original memory is put aside whereas the new cue is accepted as the correct option. Indeed, the authors themselves recognise that pigeons may have treated the post-event stimulus as a new trial when it was presented to them after a long delay, and thus they would have expected this PES to be the correct response at test.

Thereafter, Garry and Harper (2009) conducted other experiments on what they consider false memories. Rats were placed in a response chamber with two levers. On the left, there was a light which was continuously light on when the left lever was inserted, and on the right, there was a light which was flashing on and off when the right lever was inserted. During the original event, one lever was inserted and the associated light was activated. After pressing on it, the lever was retracted and the light turned off. A PES was then presented to the rat: one of the lights was illuminated for a few seconds. If the illuminated light was the same as the one used during the original event, the PES was reinforcing; if the light was the opposite of the one used during the original event, the PES was misleading; the PES was neutral when no light was illuminated. Then at test both levers were inserted and the rat had to choose. As previously observed with pigeons, the type of PES had an influence on the performance of rats: they performed significantly better with reinforcing PES compared to neutral PES, and they performed significantly better with neutral PES compared to

misleading PES. The authors concluded that animals can report a response they did not experience due to the exposure of a misleading cue. However, they remain cautious and recognise that their experiment presents some differences with what is conducted with humans: the rats were exposed to a large number of repeated trials, contrary to humans; the delays used were very short, and working memory can be used for delays of a few seconds; and the events and cues were very basic, even though they were constituted of several features (two levers, two lights which illuminated differently depending on their position), as opposed to complex “real life” stimuli humans typically experience during misinformation effect experiments.

An experiment was conducted with bumblebees which explored memory merging (Hunt and Chittka, 2015). In a first phase, bees were rewarded on a homogeneously yellow stimulus then on a black and white concentric circle stimulus. After a delay, three stimuli were presented: the two previous stimuli and a combined stimulus, with yellow concentric circles. When the delay was short, then bees chose the last rewarded stimulus. When the delay was long (one to three days), bees chose in a first time the last rewarded stimulus, but then switched to the combined stimulus. Authors consider that retroactive interference was at work, meaning that newly learnt information impaired the recall of prior information. They compare their results to misattribution errors, but their experiment did not rely on episodic memories, thus their experiment might be more about generalisation and extrapolation than false memories.

#### *b. False context fear memory*

False context fear memory has been studied in rodents, such as the experiments conducted on rats by Bae and her colleagues (2015). They tested rats in three different contexts A, B and C. Context A shared features with B, such as size, shape, surfaces, whereas context C was fully different and placed in another room than context A and B. In the first experiment, a test group of rats was pre-exposed to the context A then shocked after a delay in context B. A control group of rats underwent the same experiment except the context A was replaced with the control context C. Control and test rats froze equally in context B but test rats froze more than control rats in A. A following experiment replicated the first experiment, except for the delay between the pre-exposition and the shock which was removed. In this case, tested rats froze in A but not in B or C, whereas control rats did not freeze anywhere. Authors conclude that rats feared a context (i.e. context A) in which they have not experienced pain, due to the formation of a false association between this context (A) and the context where pain was received (i.e. context B). They consider that this is due to an overlap of the features of the two contexts, activating the representation of

context A when shocked in context B. Another study, conducted by Ramirez and his colleagues (2013), used a similar paradigm but added an ontogenetical manipulation of the hippocampus neurons of mice. In their experiment, context A, B, and C were different, without overlapping features. Dentate gyrus neurons were labelled after being activated by exposure to a context A. Later, they were optically reactivated in a different context B involving fear conditioning. Mice showed increased freezing in the context A, but not in a new context C. The recall of the fear memory was context-specific and drove an active fear response. Authors state that this behaviour was not due to fear generalisation, since they did not display freezing in context C. However, other authors such as Jasnow and colleagues (2012) consider this experiment as context fear generalisation and not false memories.

These studies bring valuable insight to the understanding of the mechanisms of fear linked with context, but rather than calling what is observed *false memories*, we should use the term *transfer* (as Briggs and Riccio (2008), who use the expression “*Transfer of old ‘reactivated’ memory retrieval cues*”). Indeed, what is observed here is a transfer of the fear conditioning to a context A. Rats may consider elements of context B as pain-related, and when perceiving similar elements in context A, rats may express fear, anticipating pain linked with these elements. This transfer is rather normal and may not be due to any memory error.

### *c. Misinformation effect paradigm*

In a study conducted by Schwartz and his colleagues (2004), a gorilla witnessed unique events. There was either a familiar person engaging in a novel behaviour, a novel person engaging in a novel behaviour, the presentation of a novel fruit treat or the presentation of a novel object. After a few minutes, the gorilla saw three photographs, one depicting the correct person or object and two distractors (two others persons or two others objects). The gorilla returned the correct photograph significantly above chance. Then, the event was followed right after by misinformation in the form of a photograph of an incorrect stimulus. In this situation, the gorilla performed at chance level, and he was not more likely to choose the misinformation item than the additional distractor. When the photograph was consistent with the event, he performed significantly above chance level. This study is an example of a misinformation effect paradigm in non-human animals.

Adachi and Hampton (2011) used a delayed matching-to-sample procedure with two rhesus monkeys. Monkeys were trained to visually match a silent video of a familiar conspecific to a photograph of that conspecific, presented among four distractors which were other familiar

monkeys. During training, no auditory stimuli was used. During probe trials, the voice of a conspecific, either matching the video (reinforcing trials, or congruent trials in the text) or not (misleading, or incongruent, trials), was played during the interval between the video and the choice of the photograph. During control trials, no auditory stimuli was played. Each individual was tested on 75 congruent probe trials, 300 incongruent probe trials, and 75 control trials. The researchers wanted to study cross-modal access to visual memory for familiar conspecifics, and they were not looking for false memories, but they constructed an experiment corresponding to a misinformation effect paradigm. However, only one individual showed false memories effects: its performance in the Congruent condition was significantly higher than in the Incongruent condition, but neither condition differed from the Control condition. There were no significant differences for the second monkey. Both subjects picked the image of the vocalising monkey more often than expected by chance (25%) when committing an error. It is interesting to note that a visual delayed matching to sample is not commonly impaired by auditory interference such as classical music, it is only impaired by visual interference such as a flashing light (Colombo and Graziano, 1994). If the DMTS is auditory, then what is observed is exactly the opposite, the impairment is only done by auditory interference but not by visual interference. It shows the importance of the modality, and indicate that in the rhesus monkey study, the fact that the auditory modality impacted the performance is probably due to the link between the voice and the video presented (both were from familiar monkeys), thus if the different modality impacts the performance it is due to some shared characteristics with the initial stimulus.

### **C. Studying false memories in animals: criteria**

The listed experiments present various ways to explore false memories, with more or less successes. Several elements seem problematic to correctly explore false memories: original events that are reduced to only one element; delays that are particularly short, relying on the use of short-term working memory instead of long-term memory; numerous repetitions of the original event or of the whole procedure; favouring the use of familiarity and semantic memory instead of episodic remembrance; absence of a control or a control group.

In order to explore false memories in animals, we propose several criteria to define a false memory from a behavioural point of view. The best way to study them is by using misinformation effect paradigms, where four phases can be distinguished: 1) Original event, with at least 3 features encoded in memory. 2) Misleading event, which contain a modified feature from the original event 3) Delay of at least few minutes (before and/or after the misleading event) 4) Question about the



original event, where the effect of the misleading event can be observed. Single trials should be favoured, to prevent conditional learning and limit familiarity. A control group and a test group must undergo the same procedure, except for the misleading event which will be neutral for the control group. Successful creation of false memory will be observed if the test group perform below or at chance level whereas the control group perform above chance level. The impact of different parameters (age, delay, repetitions, modalities of presentation) must be monitored as they can strongly influence the formation of false memories.

## II. False memories in cuttlefish

### False memories in cuttlefish

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### Highlights

- Cuttlefish show false memories, indicative of reconstructive processes in episodic-like memory
- 80% of the cuttlefish remembered a previous event when not exposed to a misleading event
- Visual misleading events impaired memory retrieval ability, creating false memories, whereas olfactory ones did not due to more attentional salience of the olfactory cues

### Abstract

Episodic memory is a reconstructive process *per se*, which means that during an event, the features composing it are encoded and stored separately in the brain, then reconstructed when the event's memory is retrieved. However, because of this reconstruction, and even with processes monitoring the reliability of the memory such as source memory (e.g. did I see it, smell it, or hear it?), some mistakes can occur. These mnemonic mistakes happen especially when different events share several common features, producing overlaps difficult to discriminate, leading to the creation of false memories. The common cuttlefish (*Sepia officinalis*) is known to demonstrate an ability to remember specific events, namely episodic-like memory. In order to investigate whether this memory is based on reconstructive processes, we elaborated a protocol promoting false memory formation in the cuttlefish. The results obtained suggest that cuttlefish do form visual false memories, but not olfactory false memories, and this susceptibility might be influenced by the level of sustained attention to the misleading event. These memory errors might be the first indication of the presence of reconstructive processes in the memory of cephalopods.

### Key-words

Memory, Cephalopods, False memory, Reconstructive processes, Attentional processes

## A. Results and discussion

Episodic memory, or the memory of personally experienced events, is a reconstructive process (Schacter et al., 1998). Indeed, features of memories are split and stored individually at encoding, and reassembled together at retrieval to recreate the event. Reconstruction is verified by source monitoring processes (Johnson et al., 1993), but this monitoring can fail and generate source misattributions from a memory to another memory (Loftus and Hoffman, 1989; Zaragoza et al., 2019b). When one or several features of a misleading post-event are misattributed to the memory of an original event, false memories are formed (Loftus, 2005; Pickrell et al., 2017; Tousignant et al., 1986; Wade et al., 2007; Zaragoza et al., 2007b). They provide a noteworthy indicator of source monitoring failures, providing an indirect way to study source encoding and monitoring processes that lie at the root of the reconstructive memory.

The reconstructive mnemonic processes are rarely explored in non-human animals (Babb and Crystal, 2006; Hoffman et al., 2009; Martin-Ordas and Smulders, 2015), although some studies implicitly investigated reconstruction through features binding (Clayton et al., 2001; Crystal and Smith, 2014b), source memory (Crystal and Smith, 2014b; Crystal, 2016; Crystal et al., 2013) or re-ordering memories (Wang et al., 2020). Very few studies on false memories have been conducted in animals (Garry and Harper, 2009; Harper and Garry, 2000; Hunt and Chittka, 2015; Schwartz et al., 2004); some focusing on false context fear memory (Bae et al., 2015; Ramirez et al., 2013), but none have used false memories to explore the reconstructive nature of episodic memory. In order to explore reconstructive memory abilities, we studied common cuttlefish (*Sepia officinalis*), a cephalopod mollusc. Cuttlefish show episodic-like memory abilities, by remembering what they ate, where and how long ago (Jozet-Alves et al., 2013b; Schnell et al., 2021c). Moreover, it has been recently demonstrated that they possess the ability to retrieve the modality of perception, or source, of an event (Billard et al., 2020b). However, in this experiment, they had to retrieve only one contextual feature, while a reconstructive memory would need to retrieve multiple features and assess them in order to discriminate between memories. We thus elaborated an experiment to explore reconstructive processes in cuttlefish by inducing false memories using a misinformation effect paradigm (Loftus, 1975; Loftus et al., 1978; McCloskey and Zaragoza, 1985). As contextual variability, such as the variation of sensory modalities (*i.e.* seen or smelt) in which information is perceived, has been shown to enhance the likelihood to form false memories in humans (Mitchell and Zaragoza, 1996), we used both visual and olfactory misleading information in the experiment. In our experiment, we aimed to test whether cuttlefish would misremember that they had seen shrimps in a tube which was previously empty, after it had been encountered twice concurrently with a tube which previously contained shrimps.

To do so, we presented cuttlefish a first event where they visually witnessed different tubes (a netting partition not allowing them to choose one of the tubes): a tube containing a shrimp, their preferred prey, a tube containing a crab, a less preferred prey, and an empty tube (Figure 32; see methods for more details). Each tube was associated with a specific pattern. This was followed by a secondary event, where cuttlefish witnessed tubes (a front-back rotation of the tubes allowing them to see the pattern but not the content anymore) without choosing as previously. Cuttlefish were either presented with only a shrimp patterned tube, and shrimp odour (*non-misleading* condition; *N*), or they were misled by presenting an empty patterned tube, in parallel with either visual and olfactory information (a shrimp patterned tube and shrimp odour, *olfactory and visual misleading* condition; *OV*) or only visual information (a shrimp patterned tube with blank water, *visual misleading* condition; *V*). The goal of the misleading conditions was to create an overlap in memory between the content of the shrimp patterned tube and the empty patterned tube making cuttlefish subsequently think that shrimps were present in the empty patterned tube. After a one-hour-delay, cuttlefish could choose between two tubes whose content was not visible: the empty patterned tube, misleadingly associated with shrimps, and the crab patterned tube (non-preferred prey, but true memory).

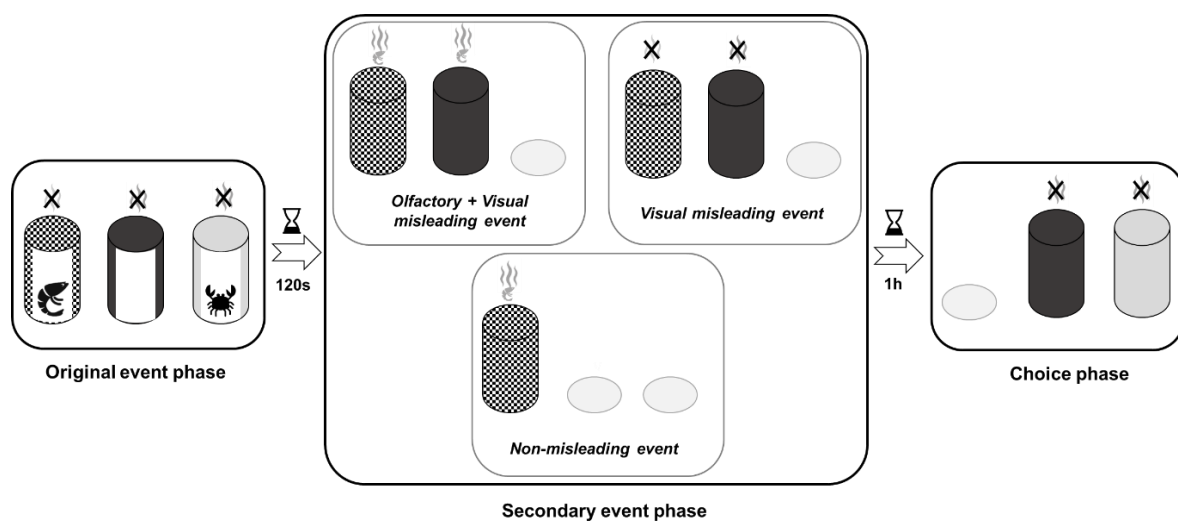


Figure 32: False memory experiment procedure.

Each condition of the experiment was divided in five phases, with one condition tested per day: the first and last motivational phases (not represented here), and in between, the original event phase, with the content of the three tubes visible, followed by a delay of 120 seconds; then the secondary event phase, with the content of the tubes not visible: it could be the olfactory and visual misleading event (*OV* condition: a shrimp patterned tube, originally containing shrimp, and an empty patterned tube, with shrimp odour), the visual misleading event (*V* condition: shrimp patterned tube and empty patterned tube with blank water), the non-misleading event (*N* condition: shrimp patterned tube with shrimp odour), all followed by a delay of an hour; then the choice phase, with the cuttlefish allowed to choose between an empty patterned tube and a crab patterned tube.

Cuttlefish significantly favoured the crab patterned tube over the empty patterned tube in the *non-misleading* condition (binomial test, N: 12 crabs out of 15 choices,  $p=0.035$ ; Figure 33), whereas no significant preference was observed in the two misleading conditions (OV: 10/14,  $p=0.180$ ; V: 7/14,  $p=1$ ). When comparing choices between each condition, a statistical trend was observed between the *non-misleading* and the *visual misleading* conditions (binomial GLMER,  $SD=0.827$  z-value=1.837,  $p=0.066$ ). Latencies to choose did not differ between conditions (Fligner test,  $N=15$ , median  $\pm$  IQR; OV:  $55\pm 132.5$ s; V:  $43\pm 74$ s; N:  $53\pm 73.5$ s;  $p=0.443$ ), nor when choosing the crab or empty patterned tube (Fligner test,  $N=15$ , crab:  $53\pm 70$ s; empty:  $36.5\pm 72$ s;  $p=0.169$ ), nor with the interaction of conditions and choices (Linear mixed-effect model,  $N=15$ ,  $df=3$ , F-value=1.030,  $p=0.392$ ). It is important to note that two individuals did not choose any tube in one of the two misleading conditions: either the *visual misleading* condition or the *olfactory and visual misleading* condition. During the ten minutes of the choice, rather than laying still in their tank, they showed a clear interest for the tubes by looking at them, moving closer and oscillating between them, without making any final choice. These two cuttlefish successfully approached a single tube presented before and after this unsuccessful choice phase, and made a choice in all the other testing conditions.

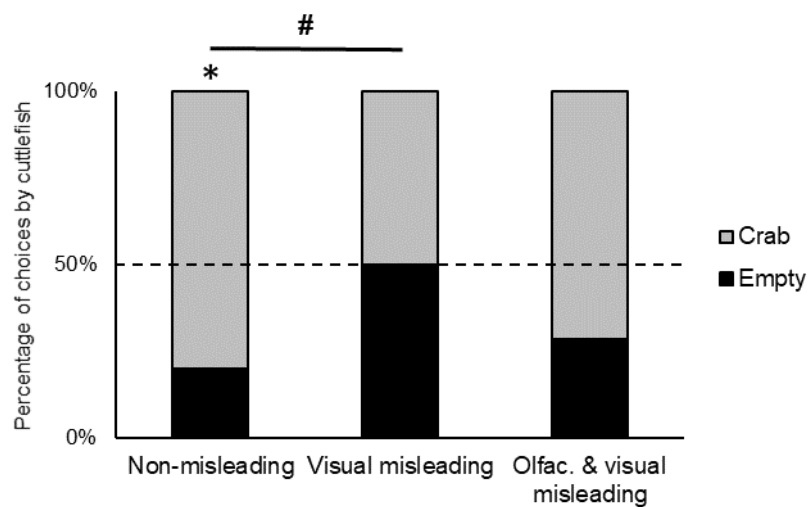


Figure 33: Tubes chosen by cuttlefish for each condition in the false memory experiment, each cuttlefish being tested once per condition ( $N=15$  for N condition, and  $N=14$  for V and OV conditions as one cuttlefish did not make any choice; see Methods and Figure 31 for a description of the protocol).

In the *non-misleading* condition (N condition), cuttlefish significantly favoured the crab patterned tube, whereas they did not in to the other conditions. Cuttlefish tended to choose the crab patterned tube more in the *non-misleading* condition compared to the *visual misleading* condition (V condition), but this difference was not noticeable when compared with the *olfactory and visual misleading* condition (OV condition). The black asterisk indicates a significant difference from chance (i.e. dotted line; binomial test,  $*p<0.05$ ), and the black square a trending difference in choices between conditions (binomial GLMER,  $\#p=0.066$ ).

Following the false memory experiment, we conducted a complementary experiment to explore the influence of an odour on the attentional processes of cuttlefish. A subgroup of cuttlefish was presented a tube while either shrimp odour or blank water was poured in the tank (each cuttlefish was tested once per condition: *i.e.* shrimp odour versus blank water; Figure 34). After a short delay, a second tube with shrimps visible inside was added, and the cuttlefish could choose between the two tubes.

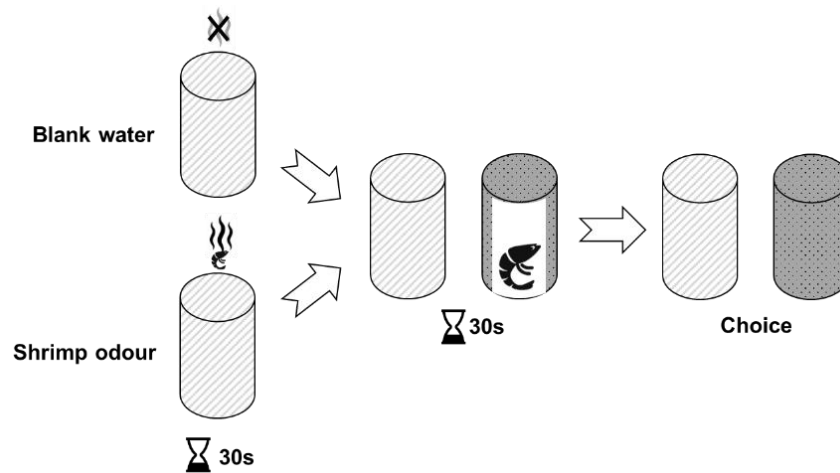


Figure 34: Complementary experiment procedure.

*Cuttlefish were firstly presented one opaque tube. Right after, either blank sea water or shrimp's odour was added in the tank. After 30 seconds, a second tube with shrimps visible inside was added next to the first tube. After 30 seconds, the content of the second tube was covered, and the cuttlefish chose between tubes.*

When shrimp odour had been added, four out of five cuttlefish chose the opaque tube, while when only blank water had been added, all five cuttlefish chose the tube with the shrimp inside (Figure 36). When the shrimp odour was present, in the 30 seconds where shrimps were visible inside the shrimp tube, the four cuttlefish did not orient their body nor their eyes toward this tube, while the fifth cuttlefish did. When only blank water had been added, in these 30 seconds, all cuttlefish oriented themselves toward the tube with shrimp visible. Due to the small sample size, statistical analyses could not be performed.

To sum up, when exposed to misleading information, cuttlefish did not choose the crab significantly more than chance, while they successfully retrieved the location of the crab when they were not exposed to misleading information. While the choices made during the visual misleading condition tended to be statistically different from the choices made during the non-misleading condition, it was not the case when both olfactory and visual information was provided. A

complementary experiment suggested that the presence or absence of a prey odour influences the level of attention of cuttlefish towards an opaque tube.

Only one tube was presented during the secondary event of the non-misleading condition, while two tubes were used in the two misleading conditions. The presence of two tubes instead of one might have an interference effect during the secondary event. However, it does not explain why cuttlefish formed false memories in the visual misleading condition and not in the olfactory and visual misleading condition.

The false memory experiment likely indicates that cuttlefish were impacted by a misleading event presented after an original event. The similarity of both events might have created an overlap at encoding or retrieval of the memories. There are at least two hypotheses that might explain the absence of a preference for either the crab or the empty patterned tube during the misleading conditions, both being the consequence of the formation of false memories. The first possibility is that cuttlefish relied on chance as they were not able to determine with certainty whether shrimps were or were not previously seen inside the empty patterned tube. This is consistent with the fact that some cuttlefish (while motivated) were not able to make a choice in the misleading conditions. Similarly, in a false memory study with humans (Ackil and Zaragoza, 1998), participants preferred to refrain from answering rather than guessing a response. The other possibility is that some of the cuttlefish were not misled and rightly retrieved the position of the crab, while others may have integrated the misleading information and deliberately chose the empty patterned tube, remembering falsely it previously contained shrimp. Indeed, susceptibility to false memories varies between individuals in humans (Loftus, 2005). These two explanations are not mutually exclusive: in misinformation effect experiment in humans, it is commonly observed that about a third of the misled subjects remember a false memory, while another third remember the original event, and the last third rely on guesses (Okado and Stark, 2005; Zaragoza and Lane, 1994; Loftus et al., 1995). While an increase in decision time (*i.e.* choice latencies) could have been expected in the misleading conditions, no difference was found. A potential effect might have been masked by variability within individual responses.

Another point to draw is that when cuttlefish were tested with visual misleading information only, they seem much more impacted than when both olfactory and visual misleading information were provided in comparison with the non-misleading condition (V: 50%, OV: 29% and N: 20% incorrect choices, respectively). Cuttlefish favoured the crab patterned tube in the olfactory and visual misleading condition, almost at the same level than in the non-misleading condition. In humans, varying the sensory modalities (auditory or visual) when repeatedly presenting the

misleading event usually produce a stronger misinformation effect (Mitchell and Zaragoza, 1996), and the same is observed when adding a matching sound to an imagined misleading event (Henkel et al., 2000). Two hypotheses can explain our results: either the propensity to create false memories was lower in the olfactory and visual misleading condition than in the visual misleading condition, or exposure to an odour had a resistance effect against the formation of false memory induced by visual misleading information. In the first case, this might be explained by the fact that the overlap between the original and the secondary event was higher in the visual misleading condition as no shrimp odour was available during the original event. As the match was stronger, this might have made cuttlefish more likely to create false memory. This prediction would be in accordance with the encoding specificity principle described by Tulving and Thomson (1973). However, studies conducted in humans were usually not consistent with this hypothesis, as no difference or opposite results were observed in literature (Gallo et al., 2001; Zaragoza and Lane, 1994). According to the second hypothesis, cuttlefish would not only be resistant to olfactory misleading information, but exposing them to prey odour might have even created resistance against the formation of a visual false memory. It was empirically noticed that during the misleading event phase, after detecting the shrimp odour, some cuttlefish placed themselves in front of the shrimp patterned tube and focused on it, showing no interest for the empty patterned tube nearby. This might have narrowed the scope of cuttlefish's attention to the shrimp patterned tube during the secondary event, strikingly lowering the salience of the empty patterned tube nearby, making cuttlefish less likely to form false memory.

Our complementary experiment suggests that in presence of prey odour, cuttlefish are focusing on its probable source (*i.e.* the tube placed in the tank concurrently with the prey odour) to the point of omitting other elements around them, such as a tube actually containing moving shrimps. When no additional odour was provided (blank water), the same individuals successfully chose the tube containing a shrimp. Cuttlefish are known for being a visual predator (Hanlon and Messenger, 2018), but they can also detect preys by their smell (Billard et al., 2020b; Boal and Golden, 1999), although the extent of their use of odours when hunting is not known. This multimodal prey recognition might be particularly important in the common cuttlefish considering the relative size of the brain substrates underlying chemosensory perception in comparison with cuttlefish tropical species (Chung et al., 2023). The results obtained with this experiment could explain the seeming resistance against false memories in the olfactory and visual misleading condition: one possibility is that during the olfactory and visual misleading event, cuttlefish focused on the shrimp odour, which limited the attentional resources toward the tubes. However, this is unlikely, since limited attentional resources enhance the probability of source misattribution in humans (Ackil and



Zaragoza, 1998). If we consider that cuttlefish in the complementary experiment chose the opaque tube because they focused only on it and did not see the tube with shrimp, then cuttlefish during the false memory experiment may have particularly focused their attention on the shrimp patterned tube during the olfactory and visual misleading event and may have not seen the empty patterned tube next to it, preventing them from forming false memories.

Nonetheless, some could say that our study does not indicate false memory formation in cuttlefish, but rather simpler memory mechanisms such as familiarity as cuttlefish were exposed twice to the empty tube in the misleading conditions, or even a simple memory loss. We cannot refute that some familiarity mechanisms may be at work in our experiment, however in this case we would have expected the two misleading conditions to affect the choices made in the same order of magnitude in comparison with the non-misleading condition. We also consider memory loss unlikely, as the non-misleading condition indicates that cuttlefish could remember well the position of the crab even when exposed to the shrimp patterned tube between the original event phase and the choice phase.

False memories thus seem to exist in cuttlefish when they are exposed to a visual event sharing features with a previous event. This could be due to the absence of source monitoring processes, but it is unlikely since memory of the source of an event was previously demonstrated in cuttlefish (Billard et al., 2020b). Instead, source monitoring impairment through misinformation effect is more likely (Johnson et al., 1993; Mitchell and Johnson, 2000). The observed false memories might be due to binding impairments during encoding or reconstruction errors during retrieval of the memory, whose source was not successfully monitored (Johnson et al., 1993; Zaragoza et al., 2007b).

Our study is the first to use false memory to explore reconstructive processes in memory of specific events. Studies on false memories in animals are scarce (Garry and Harper, 2009; Harper and Garry, 2000; Hunt and Chittka, 2015; Schwartz et al., 2004), even though they seem promising, as they highlight impairments in source monitoring and reconstructive processes. Moreover, our study is the first to indicate the presence of reconstructive processes in cuttlefish's episodic-like memory. Reconstruction may be necessary to alleviate cognitive demands, but it may also be used to recombine past scenarios to create and plan for future events (Schacter et al., 2007), an ability which still needs to be explored in cuttlefish.

## B. Methods

### 1. *Experimental model and subject details*

Cuttlefish rearing and experiments were conducted in compliance with the French regulation for the protection and use of animals in research and the directive 2010/63/EU of the European parliament. Experimental procedures were authorised (#22429 2019101417389263 v2) by the ethical committee of Normandy region (Comité d’Ethique de NORmandie en Matière d’EXpérimentation Animale, CENOMEXA; agreement number 54).

15 sub-adult cuttlefish (*Sepia officinalis*; three to nine months-old; 3 to 10 cm long, respectively; 8 males, 6 females, 1 undetermined) were trained and tested between September 2021 and March 2022 (False memory experiment). Eggs were collected in the English Channel, cuttlefish hatched and were reared for two months at the SMEL (Synergie Mer et Littoral, Blainville-sur-Mer, France) before being transferred to the rearing facilities of the CREC (Centre de Recherches en Environnement Côtier, Luc-sur-Mer, France) for the following months. Five individuals from the initial group were also included in the complementary experiment ran in March 2022.

### 2. *Methods details*

#### a. *Materials*

Cuttlefish were reared individually for the duration of the experiment in a semi-closed system of several cube meters of natural seawater with central filtration, at  $17 \pm 2^\circ\text{C}$ , under natural light conditions. They were housed in grey squared plastic tanks (20 x 20 x 8 cm) until they reached five centimetres in total length, and then in white rectangular plastic tanks (37 x 28 x 8 cm), enriched with pebbles and plastic algae. They were fed daily with live shrimps (*Crangon crangon*) or crabs (*Hemigrapsus sanguineus*) of suitable size.

Cuttlefish were trained and tested in their home tank. During the experiments, glass tubes (8 cm high x 4 cm in diameter, Figure 35) were used as targets. The inside surface of the tube was almost entirely covered with an opaque laminated paper, with a vertical window (about 2 cm wide x 8 cm high) remaining transparent. The paper was printed with various black and white patterns identical on both sides (13 patterns were used; *i.e.* solid grey, black or white, grey and black checked, black and white striped). By doing so, the cuttlefish could see the content of the tube by looking through the transparent window, and when the tube was rotated, the content could not be seen anymore. The content of the tubes could not be smelt by tested individuals, as the tubes protruded above water, preventing the water inside the tubes to mix with the tank water. When several tubes were

used in parallel, each tube presented a different pattern. To prevent immediate access to the tubes, a green rigid plastic netting was placed between the tubes and the cuttlefish, about ten centimetres away from the tubes. The shrimp odour, poured in the tank during the experiments, was made of 250 mL taken from of a bucket which contained ten live shrimps (*Crangon crangon*) per litre of seawater during at least ten minutes. All the tubes were thoroughly cleaned between each phase.

### *b. Training*

Cuttlefish were first trained to spontaneously approach an opaque and patterned tube. They subsequently learn to choose one tube out of three, one containing a shrimp, one containing a crab and one being empty. To do so, tubes were presented one after the other, with their content visible for 15 seconds each. Cuttlefish had then the opportunity to choose one of the tubes to be rewarded with its content (see Supplementary Material for detailed procedures).

### *c. False Memory experiment procedure (Figure 32)*

The false memory experiment was constituted of three different testing conditions: two misleading and one non-misleading conditions. Each cuttlefish was tested once in each of the three conditions. The misleading conditions were designed to promote the formation of false memories of shrimp presence (preferred prey), by using only the visual modality (V) or using both olfactory and visual modalities (OV). The non-misleading condition (N) was designed to control cuttlefish ability to remember the position of the crab (non-preferred prey). Cuttlefish were tested on each condition, one condition per day, in a randomised order.

All conditions followed the same procedure. Five phases could be distinguished: a first motivational phase, an original event phase, a secondary (misleading or non-misleading) event phase, a choice phase, and a last motivational phase.

The first motivational phase was conducted each day to assess and maintain the motivation of cuttlefish to reach for a tube to obtain a reward. During this phase, an opaque tube (with a pattern different from the ones used in the following phases) was placed in the tank and the cuttlefish obtained a shrimp by choosing the tube in less than 120 seconds. Throughout the experiment, we considered that cuttlefish made a choice when they oriented their body and eyes toward one tube while staying at a distance lower than ten centimetres from the tube, or by circling around it, for at least ten seconds. If the motivational procedure failed a first time, it was done a second time a few

minutes later, and if it failed a second time, the rest of the experiment was rescheduled until the next day (experiment was rescheduled one time for three cuttlefish).

In the original event phase, three tubes were used. They were covered with three different patterns (out of the 13 used during the training and testing) which changed randomly between conditions. One tube contained a shrimp (*Crangon crangon*), the preferred prey of cuttlefish, one tube contained a crab (*Hemigrapsus sanguineus*), a less preferred prey, and one tube was empty. The phase started by placing a netting ten centimetres away from one side of the tank (*i.e.* to make cuttlefish able to see the tubes but not to choose one of them). The three patterned tubes were placed behind the netting, next to each other. They were rotated one after the other, in a random order, so that their content was visible for the cuttlefish for 15 seconds before being hidden again. Tubes were removed all at once and a delay of 120 seconds began.

Next, the secondary event phase was conducted: one (non-misleading condition) or two (misleading conditions) tubes were presented, with their content not visible but their pattern clearly visible. 250 mL of blank sea water or sea water with shrimp odour was gradually poured behind the single tube or between the two adjacent tubes in front of the water inflow. For the non-misleading condition, a shrimp patterned tube (*i.e.* a tube with a shrimp during the original event) was presented with shrimp odour. For the olfactory and visual misleading condition, the shrimp and the empty patterned tubes (tubes with a shrimp or empty during the original event, respectively) were presented with shrimp odour. For the visual misleading condition, the shrimp and the empty patterned tubes were presented with blank sea water. The tubes and netting were removed after 60 seconds and a delay of one hour began.

Next, during the choice phase, the crab patterned tube and the empty patterned tube were simultaneously placed in the tank (without the netting partition). Cuttlefish could choose one of the tubes, and they were not rewarded whatever the choice made. If no choice was made within ten minutes, tubes were removed from the tank.

At last, the last motivational phase was conducted similarly to the first motivational session, to assess and maintain the motivation of cuttlefish to choose for a tube to obtain a reward. In this motivational phase, if the cuttlefish did not choose the opaque tube (which presented the same pattern as in the first motivational phase) within 120 seconds, it was still rewarded by placing a shrimp next to the tube.

#### *d. Complementary experiment procedure (Figure 34)*

The complementary experiment was conducted after the false memory experiment to explore the influence of an odour on the attentional processes of cuttlefish.

The experiment started by placing a netting ten centimetres away from one side of the tank. An opaque tube (*i.e.* without its content visible) was placed behind the netting and 250 mL of either blank sea water (blank water condition) or sea water with shrimp odour (shrimp odour condition) was poured next to the tube. After 30 seconds, a second tube, with two live shrimps visible inside, was placed ten centimetres away from the first tube, during 30 seconds. We noted whether the cuttlefish oriented their body or their eyes toward the tube with shrimps visible or not. The tube was then turned so its content was not visible anymore, and the netting was removed so the cuttlefish could choose. Cuttlefish were tested once per condition.

### ***3. Quantification and statistical analysis***

All choices in the false memory experiment were recorded using a video camera (Sony Handycam® FDR-AX53 4K). Choices as well as latency before choice were scored by one experimenter (L.P.). Latency (an indicator of decision time) was measured from the time tubes were put in the tank to the time the cuttlefish approached less than ten centimetres away from the chosen tube. The distance was estimated using reference points on top of the home tank.

Choices and latencies were analysed using R software (version 3.6.3, R Core Team, 2019). Choices made during the false memory experiment were analysed using binomial tests and a Generalised Linear Mixed Effect Model (GLMER, package `lmerTest`) with a binomial distribution. We included the choice cuttlefish made as the response variable, the condition as the fixed effect and the cuttlefish as the random intercept effect. Latencies were analysed using non-parametric Fligner tests and Linear Mixed Models (package `lmerTest`), with the duration of the choice as the response variable, the interaction between choice and condition as the fixed effect, and the cuttlefish as the random intercept effect.

Statistical analyses could not be performed in the complementary experiment because of the small sample size.

## Supplementary materials

### Training methods

Firstly, cuttlefish were trained to spontaneously approach a glass tube covered with paper with a pattern randomly chosen for each trial (among 13 different patterns). Three to five training trials were conducted each day. To do so, a tube was placed in their tank, and after a delay of 15 to 120 seconds (shorter at the beginning of the training, longer at the end), a shrimp on a fishing line was put next to the tube, so the cuttlefish could catch it. After the cuttlefish spontaneously approached the tube in less than 120s three times within the same day, the next step of the training was conducted.

Secondly, the cuttlefish learnt to choose between two tubes, one containing a shrimp and one containing a crab. To do so, a first tube was put and the cuttlefish could see the prey inside it (a shrimp or a crab) for 15 seconds before the tube was turned, hiding the prey. A second tube was presented in the same way, containing the other prey type. A netting, placed between the cuttlefish and the tubes, prevented the access to the tubes. It was removed after at least five seconds and the cuttlefish could choose between the two tubes. The cuttlefish was rewarded with the prey corresponding to the chosen tube, and it was considered a successful trial. If the cuttlefish did not choose after three minutes, a shrimp was put next to the tube containing the shrimp, and it was considered a failed trial. After at least 9 successful trials in less than 15 consecutive trials, a third tube was added, which did not contain any prey, for at least three consecutive successful trials.

Thirdly, a preference test was conducted: a crab and a shrimp at the end of a fishing line were presented in front of the cuttlefish at the same time, and the seized prey was noted. After twelve successive presentations, preference for one prey was assessed using binomial tests. The false memory experiment started the day after the completion of the preference test.

### Training results

All tested cuttlefish succeeded the training phase 1 (*i.e.* approaching a tube to get food). They learnt to spontaneously come next to the tube in  $119 \pm 57$  trials. They all learnt to choose a tube out of two in  $10.7 \pm 2.2$  trials (mean  $\pm$  SD; training phase 2). None choose the empty tube instead of the shrimp or the crab tube during the three trials of the training phase 3. All tested cuttlefish preferred shrimps over crabs: 10 to 11 choices of shrimps out of 12 successive trials (mean  $\pm$  SD:  $10.3 \pm 0.5$ ; binomial test,  $p < 0.039$ ; see Table 6).



Figure 35: Glass tube used during the experiment.

The tube was partially covered with patterned paper, so the prey inside could be visible through a window then became invisible when the tube was rotated.

Table 6: Summary table of the choices made by each cuttlefish in the false memories experiment.

Conditions are abbreviated as N: non-misleading, V: visual misleading, OV: olfactory and visual misleading. Numbers within parentheses in the food preference column correspond to the number of times a prey item was chosen during the food preference test. Position of the tubes is presented from left to right, with C: Crab tube E: Empty tube, S: Shrimp tube, with the chosen tube in bold.

Individual	Sex	Age at test (months)	Food preference	Condition N		Condition V		Condition OV	
				Choice	Tubes position	Choice	Tubes position	Choice	Tubes position
1	M	5	Shrimp (11/12)	Crab	<b>E C S</b>	Empty	<b>C S E</b>	Empty	<b>S E C</b>
2	F	5	Shrimp (10/12)	Crab	<b>C E S</b>	Crab	<b>E S C</b>	Crab	<b>E C S</b>
3	F	5	Shrimp (11/12)	Crab	<b>C E S</b>	Empty	<b>E C S</b>	Empty	<b>E S C</b>
4	M	5	Shrimp (10/12)	Empty	<b>C E S</b>	Empty	<b>E C S</b>	Crab	<b>S E C</b>
5	NA	5	Shrimp (10/12)	Crab	<b>C E S</b>	Empty	<b>C S E</b>	Empty	<b>E S C</b>
6	F	5	Shrimp (10/12)	Crab	<b>C E S</b>	Empty	<b>C S E</b>	Crab	<b>E C S</b>
7	M	5	Shrimp (10/12)	Crab	<b>C S E</b>	Crab	<b>S C E</b>	Crab	<b>C S E</b>
8	M	5.5	Shrimp (10/12)	Crab	<b>S C E</b>	Crab	<b>E C S</b>	None	<b>C S E</b>
9	F	5.5	Shrimp (10/12)	Empty	<b>E S C</b>	Empty	<b>C S E</b>	Crab	<b>C S E</b>
10	M	5.5	Shrimp (11/12)	Crab	<b>E S C</b>	Crab	<b>C S E</b>	Crab	<b>S C E</b>
11	F	6.5	Shrimp (10/12)	Empty	<b>S E C</b>	Crab	<b>E S C</b>	Crab	<b>S C E</b>
12	M	7	Shrimp (10/12)	Crab	<b>S E C</b>	Crab	<b>S C E</b>	Crab	<b>C E S</b>
13	M	7	Shrimp (11/12)	Crab	<b>S C E</b>	Empty	<b>C E S</b>	Crab	<b>S E C</b>
14	M	7.5	Shrimp (10/12)	Crab	<b>S E C</b>	None	<b>C E S</b>	Crab	<b>S E C</b>
15	F	8	Shrimp (10/12)	Crab	<b>E C S</b>	Crab	<b>S E C</b>	Empty	<b>C E S</b>

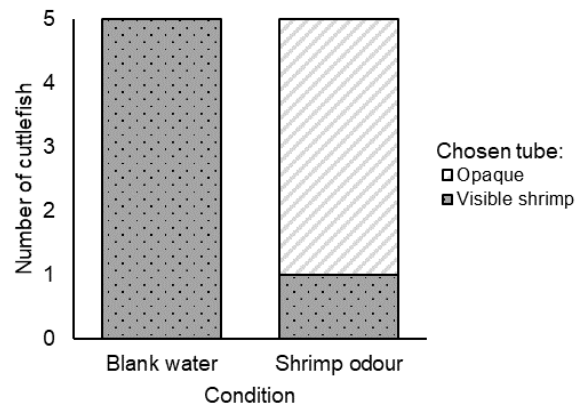


Figure 36: Tubes chosen by cuttlefish for each condition in the complementary experiment.

When exposed to blank water, all cuttlefish detected and oriented toward the tube containing the shrimps and subsequently chose it, while when exposed to shrimp odour, four individuals out of five did not seem to detect the tube containing the shrimp and subsequently chose the opaque tube. Due to the small sample size, statistical analyses were not performed.

## Acknowledgements

We would like to thank the staff of the marine station (CREC, Unicaen, France) for their help. This work was supported by a grant to C.J.A. from the ANR (French National Agency for Research; COMeTT project: ANR-18-CE02-0002)



## **Conclusion of chapter 2**

False memories are a valuable tool to explore reconstructive and source-monitoring processes in animals. Cuttlefish appear to form false memories, indicative of reconstructive processes in the episodic-like memory of this invertebrate.

Exploring false memories in other species presenting episodic-like memory abilities would allow to better understand what are the processes at the basis of episodic-like memory and how they evolved. Moreover, exploring the link between false memories and future planning would bring some light to the linkage between retrospective and prospective mental time travel: induced false memories could modify the behaviour of the subjects in planning tasks, preventing them to perform the adequate behaviour compared to control individuals. This would indicate how reconstruction is involved in imagining the future.

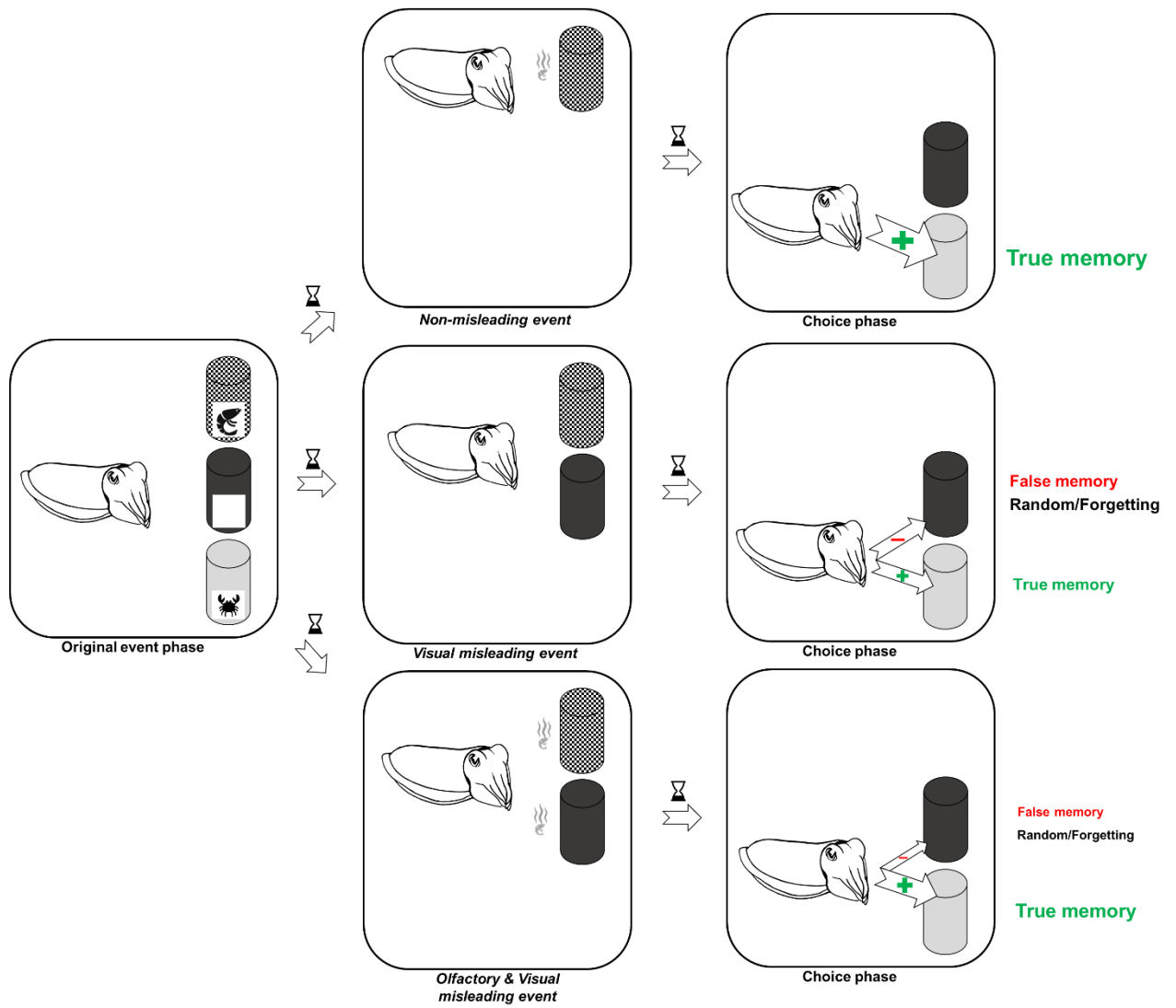


Figure 37: Summary of chapter 2 – False memories in cuttlefish

## Chapter 3:

# Future planning in coleoids

## **Chapter 3: Future planning in coleoids**

**Article 3: Poncet, L., Roig, A., Billard, P., Bellanger, C., and Jozet-Alves, C. (under revision). Different evolutionary pathways for episodic-like memory and future planning: insights from cephalopods.** Proceedings of the Royal Society B: Biological Sciences

**Preliminary study 2: Poncet, L., Bellanger, C., and Jozet-Alves, C. First indications of planning for future needs in adult common cuttlefish.**

### **Introduction of Chapter 3**

#### **Part I: Future planning in the cuttlefish and the octopus (Article 3)**

Mental Time Travels show both a retrospective side, through episodic memory, and a prospective side, through future planning. Both abilities are intimately linked, and episodic memory might have evolved to allow future planning. Since cephalopods show episodic-like memory abilities, we decided to investigate future planning abilities in cuttlefish and octopuses. Cuttlefish underwent an experiment where they could plan for a future need for food instead of following their current need for shelter, while octopuses could plan for both their future need for shelter and their future need for food. Neither cuttlefish or octopuses did plan for their future needs. Cephalopods might thus not possess future planning abilities, or our experiments could not bring to light such abilities.

#### **Part II: Future planning in adult cuttlefish (Preliminary study 2)**

To explore the influence of the age and the physiological status of cuttlefish, we reproduced the future-planning experiment initially conducted with juvenile cuttlefish with sexually mature cuttlefish. These cuttlefish underwent the same experiment where they could plan for a future need for food instead of following their current need for shelter. Some cuttlefish chose to secure a future need. These preliminary results which need to be confirmed might indicate that cuttlefish possess future planning abilities, but that the trade-off between food and shelter might be influenced by multiple parameters which conducted individuals to favour the shelter rather than planning for food.

## **I. Future planning in the cuttlefish and the octopus**

### **Different evolutionary pathways for episodic-like memory and future planning: insights from cephalopods**

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#### **Abstract**

Episodic memory and future thinking are generally considered as two parts of the same mental time travelling system. Common neurobiological and developmental features observed between these abilities in vertebrates might be the products of a closely intertwined evolution or of a shared phylogeny. Modern cephalopods, with their independent evolutionary lineage and their complex cognitive abilities, appear as promising species to determine whether these abilities have or not separate evolutionary histories. In our study, we tested future-planning abilities in two cephalopod species which have been shown - or not - to possess episodic-like memory abilities: cuttlefish and octopus, respectively. Common cuttlefish were tested on their ability to plan for a future need for food instead of following their current need to hide. To explore the flexibility in such future-planning behaviour, we varied the protective value of the shelter. Future-planning abilities of octopuses were examined by allowing them to displace food and shelter to locations in which they would later need them. We observed that neither cuttlefish nor octopuses showed future-planning abilities during our experiments. These results might be explained by experimental contingencies, but they might also reflect the simple absence of future-planning abilities in cephalopods. Since cuttlefish possess episodic-like memory abilities, such results suggest that episodic memory and future planning have separate evolutionary histories. Identifying both similarities and differences in complex cognition between vertebrate species and cephalopods, and within cephalopods, will be of importance to pinpoint which evolutionary pressures have led to the emergence of complex cognitive abilities.

#### **Key-words**

Cephalopods, Future-planning, Octopus, Cuttlefish, Mental Time Travels, Trade-off

## A. Introduction

Mental Time Travels (MTT) are the ability to travel mentally in one's personal past and future, in order to re-experience or pre-experience events (Suddendorf, 1994). The retrospective side of MTT, also known as episodic memory, has been extensively studied in humans (Michaelian, 2016). The prospective side of MTT, sometimes called episodic future thinking or foresight (Atance and O'Neill, 2001), has been the subject of a more recent interest (Schacter et al., 2017). Past and future MTT share common phenomenological (*i.e.* auto-noetic consciousness; Szpunar et al., 2007), developmental (Coughlin et al., 2014) and neurobiological features. Several neurobiological studies have shown that the default network is activated in the same way by episodic memory and future thinking (Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007). In a popular view, remembering and imagining events might be the expression of the same psychological ability allowing to simulate events located either in the past or in the future. These abilities might have 1) either separate evolutionary histories, the shared features described above resulting from the fact that they are subserved by the same simulating system; 2) or have a closely intertwined evolution (*e.g.* one being the by-product of the other). It has been hypothesised for example that episodic memory evolved to allow future anticipation (Addis et al., 2007; Schacter and Addis, 2007b; Schacter et al., 2012; Suddendorf and Busby, 2003; Tulving, 2005).

Prospective mental time travels are often considered as uniquely human (Suddendorf, 1994; Suddendorf and Corballis, 1997; Tulving, 2005). According to the Bischof-Köhler hypothesis, an animal is bound to its present motivational state and cannot anticipate its future needs independently of its current needs (Suddendorf, 1994; Suddendorf and Corballis, 1997). However, a growing number of studies over the past fifteen years has explored the ability of animals to plan for the future. Future planning has mostly been explored in great apes (Kabadayi and Osvath, 2017; Mulcahy and Call, 2006; Osvath, 2009; Osvath and Osvath, 2008) and corvids (Cheke and Clayton, 2012; Correia et al., 2007; Raby et al., 2007), but also in squirrel monkeys (McKenzie et al., 2004) and chickadees (Feeney et al., 2011b). Retrieving a past event (episodic-like memory) and imagining an upcoming event seem to depend on the same neural machinery in rodents. A study of the activation of hippocampal place cells in rats has shown that future trajectories are depicted in the brain before the individuals were actually moving (Pfeiffer and Foster, 2013). As most studied species share a common evolutionary history, it is difficult to disentangle whether the tight linkage observed between retrospective and prospective MTT is the consequence of the properties of the underlying neural networks, or whether episodic memory has evolved to allow individuals to mentally simulate future scenarios based on their own past experiences. In the second case, the

presence of episodic memory abilities in a species will then be indicative of future episodic cognitive abilities.

Modern cephalopods (*i.e.* cuttlefishes, octopods and squids), with their centralised brain, their high cognitive abilities and the diverse evolutionary pressures they are exposed to, recently became valuable candidates to better understand the evolution of these complex cognitive abilities. Cuttlefish have drawn attention over the recent years, when Jozet-Alves and colleagues demonstrated their episodic-like memory abilities (*i.e.* they remember which prey they ate, where and how long ago; Jozet-Alves et al., 2013), and their ability to retrieve specific features of an episodic memory (Billard et al., 2020b). It has also been shown that they display future-dependent foraging behaviour, as they do not consume a less preferred prey when they know they would get their preferred prey hours later (Billard et al., 2020a). These abilities associated with their flexible decision-making behaviour (Kuo and Chiao, 2020; Yang and Chiao, 2016) and their delayed gratification performance (Schnell et al., 2021b) suggest that cuttlefish might use previous experiences to optimise their current foraging behaviour according to future predictable scenarios. Thus far, no study has directly tested cuttlefish future planning abilities.

If episodic memory evolved to allow future thinking, then cuttlefish can be expected to present future planning abilities as they were already shown to possess episodic-like memory abilities (Jozet-Alves et al., 2013b; Schnell et al., 2021c). On contrary, it would be unlikely in octopuses as they do not show the same propensity to rely on this cognitive ability (Poncet et al., 2022). If we consider that remembering the past and planning for the future have separate evolutionary histories, each one would have its own selective advantages and could have been selected independently to the other. From an adaptive point of view, future planning might provide a higher selective advantage in octopuses than in cuttlefish. Indeed, octopuses modify their environment, arrange a den in response to predatory threat, or hoard food when resources run out of supply, while cuttlefish are not known for such behaviours (Hanlon and Messenger, 2018).

In order to explore the ability of cephalopods to plan for their future, we designed experiments fulfilling the criteria defined by Suddendorf and Corballis (2007, 2010): 1) species-typical and innate behaviours should be avoided; 2) new problems with single trials and long timescales should be favoured to avoid conditional learning and generalisation (Clayton et al., 2003b); 3) temporal and spatial separation between the action and its consequence should be employed to favour the use of long-term memory; 4) various needs in different contexts should be tested to observe flexibility; 5) and animals should be able to anticipate their future needs independently of their current ones. To do so, in our procedure, cuttlefish could choose to take actions to ensure either a future need

for food (*i.e.* cuttlefish were satiated at choice time) or a current need for a shelter (*i.e.* cuttlefish usually avoid lit areas when they cannot bury). Tested cuttlefish were placed in a Y-shaped apparatus where they were first fed to satiety and subsequently offered a choice between going into an arm with a shelter (*i.e.* current need) or into an arm with food (*i.e.* future need). They were then confined in the chosen arm until the following day. No food was provided at night in the shelter arm. The next day, cuttlefish were again fed to satiety and proposed the same choice as the day before (*i.e.* food arm *versus* shelter arm). On the first day, we hypothesise that cuttlefish will respond to their current need to hide and choose the shelter arm. However, on the second day, if cuttlefish can plan for their future desire to eat, we hypothesise that they might choose the food arm (to make them able to eat later at night) instead of the shelter arm. To test the flexibility of future-planning, the protective value of the shelter was modified between two cohorts of cuttlefish, with the shelter arm being either highly attractive (shade, sand and algae) or less attractive (shade only). The rationale of the procedure was that cuttlefish exposed to a trade-off decision (*i.e.* decision to ensure either a current or a future need) will prioritise a future need if its relative importance is higher than the current need.

To explore future-planning abilities in octopus, we adapted the procedure used in western scrub jays to assess whether they could spontaneously plan for the future (Raby et al., 2007). In this study, the authors ingeniously showed that jays are storing different food items depending on where these items will not be available the next day (*i.e.* storing food A where only food B will be available, and *vice versa*). In our experiment, we wanted to determine whether octopuses would spontaneously displace food in a place in which only a shelter will be available, and displace a shelter in a place where only food will be available. To do so, octopuses were pseudo-randomly confined in either a compartment containing food but no shelter, or a compartment containing a shelter but no food. After experiencing three days each compartment, octopuses were placed in the centre of the apparatus with movable food and a shelter and given the opportunity to access to both compartments. If octopuses could plan for their future need for food and shelter, we hypothesise that they would relocate the food on the shelter side and the shelter on the food side.



## B. Material and methods

### 1. Ethical statement

All experiments were conducted following the directive 2010/63/EU of the European parliament and the French regulation for the protection and use of animals in research. Procedures were approved (#22429 2019101417389263 v2) by the regional ethical committee of Normandy region (Comité d'Éthique de NORmandie en Matière d'EXpérimentation Animale, CENOMEXA; agreement number 54).

### 2. Subjects

40 cuttlefish (*Sepia officinalis*) from two to five months old were tested between August and November 2021. They were either raised from eggs at the CREC (n=8; Centre de Recherches en Environnement Côtier, Luc-sur-Mer, France) or at the SMEL (n=32, Synergie Mer et Littoral, Blainville-sur-Mer, France) during two months before being transported to the CREC (several weeks before starting the experiments). In each cohort (*i.e.* high shelter value *versus* low shelter value), cuttlefish were divided in two groups of ten individuals: a test group (future need to find food) and a control group (no future need for find food). Cuttlefish were reared in groups in white squared plastic tanks (78 x 78 cm; enriched with plastic plants, rocks, shells, shelters...) with natural circulating seawater at  $17 \pm 2^\circ\text{C}$ , under natural light conditions. They were fed daily with live shrimps (*Crangon crangon*) or live crabs (*Hemigrapsus sanguineus*) of suitable size.

Four sub-adult common octopuses (*Octopus vulgaris* Cuvier, undetermined sex, dorsal mantle length ranging from 6.5 to 10 centimetres) were tested in our experiment. They were collected in the Mediterranean Sea by specialised fishermen (Carrodano, Poissons vivants, La Ciotat, France) in June 2022. They arrived two and a half months prior to the experiment at the CREC. Octopuses were individually housed in glass tanks of 100x50x50cm or 120x40x50cm, enriched with a sand bed, pebbles, seashells and a shelter in the form of a terracotta pot or a PVC tube. Octopuses were maintained in circulating natural seawater in a semi-closed system at  $16 \pm 1^\circ\text{C}$  with artificial lighting following the natural light cycle. Octopuses interacted daily with their handlers and were fed during these interactions with live crabs (*Hemigrapsus sanguineus* and *Carcinus maenas*) and thawed shrimps (*Litopenaeus vannamei*).

### 3. Cuttlefish experiment

#### a. Testing apparatus

During the experiment, each cuttlefish was placed in a white Y-shaped apparatus with circulating natural seawater at  $17 \pm 3^\circ\text{C}$  under natural light conditions. Each arm of the apparatus was 9 cm wide and 30 cm long. At the end of each arm, a compartment (20 x 20 cm) could be closed by an opaque plastic sliding door. The compartment at the end of the shelter arm was shadowed with an opaque PVC top for the low value shelter cohort (Figure 38d), and enriched with a layer of sand and two plastic seaweed plants for the high value shelter cohort (Figure 38b). In the food arm, seven shrimps (*Crangon crangon*) were placed in a glass tube in the middle of the arm. The right-left position of each arm was randomised between cuttlefish.

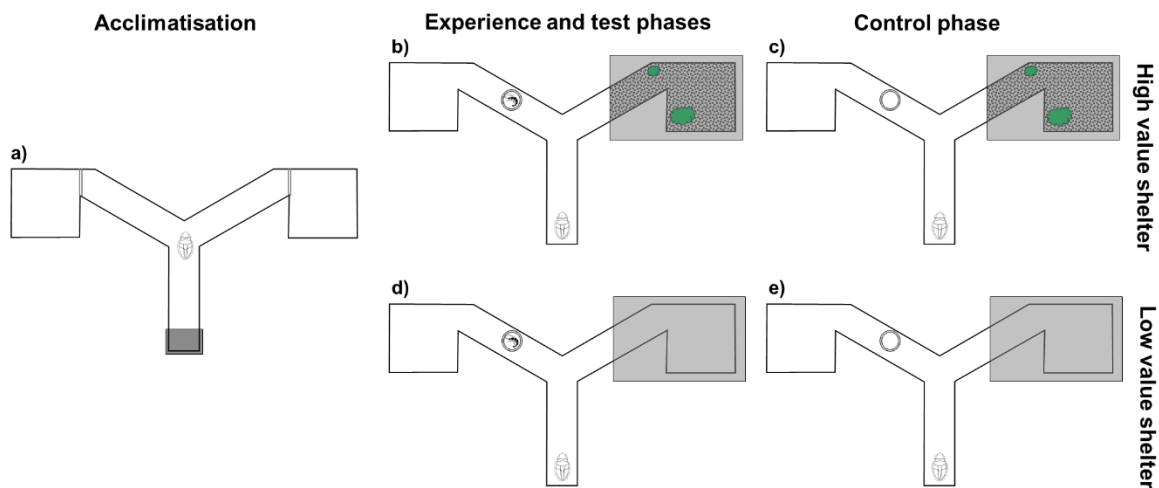


Figure 38: Schematic representation of the Y-shaped apparatus used during the cuttlefish experiment.

a) Apparatus during the acclimatisation. b) and d) Apparatus organisation when cuttlefish were offered a choice between a food arm (shrimps in a glass tube) and a shelter arm (b: high value shelter with shadow, sand and plastic plants; d: low value shelter, only shadow) during the experience and the test phases. c) and e) Apparatus organisation when cuttlefish are offered a choice between an empty arm and a shelter arm during the Control phase.

#### b. Procedure

The acclimation started in the morning and lasted a minimum of 24 hours and up to three days until cuttlefish accepted to eat at least one shrimp in front of the experimenter. The animals could move freely in the Y-shaped apparatus during the acclimation (Figure 38a), and were fed with one shrimp a day. No shelter was provided. The experiment was then organised in three consecutive phases: the **experience phase** (day 1), the **test phase** (day 2), the **control phase** (day 3).

On the first day, at the beginning of the ***experience phase***, the cuttlefish was fed to satiety with live shrimps. At first, four shrimps were put in the apparatus. When they were all captured and eaten, new preys were added one by one each time the previously introduced shrimp was caught and eaten. The last prey was left with the cuttlefish for half an hour before being removed, to ensure that the cuttlefish had been fed to satiety. Then, the cuttlefish was gently chased in the start arm of the apparatus using a small net. This arm was then closed for 30 minutes, while a ring light (FotoQuantum LED FQVL-800) placed one metre above the centre of the apparatus was turned on. During this delay, the shelter and the food arm were set up according to the description above (see Testing apparatus and Figures 38b,d). After this delay, the sliding door was opened and the cuttlefish could choose to enter either the shelter or the food arm. If the cuttlefish did not move within ten minutes, it was gently pushed until its head reached the centre of the apparatus, from which both the shelter and the food arms were visible. After the animal went into an arm, the entrance was blocked off and the cuttlefish stayed in the chosen arm until the following day. If the shelter arm was chosen, no food was provided until the following day for the test group, while one to three shrimps (depending on their size) were provided ten minutes after the choice for the control group. If the food arm was chosen, four of the seven shrimps visible in the glass tube were released to allow the cuttlefish to eat at the end of day (the three other shrimps were removed from the apparatus).

On the second day, at the beginning of the ***test phase***, the cuttlefish was gently chased outside the compartment chosen the previous day until it reached the start arm of the apparatus. The sliding door was then closed. The shelter and the food arm were completely cleared out before releasing the cuttlefish in the empty apparatus (all sliding doors open, shelter and food arms empty). Then the procedure was conducted exactly the same way as during the first day, with the cuttlefish being fed to satiety and then offered to choose between a shelter arm and a food arm. Food was provided or not depending on the arm chosen and the group as for the experience phase.

On the third day, a ***control phase*** was conducted: the procedure was done exactly the same way, except that the cuttlefish was offered a choice between a shelter arm and an empty arm, where there was only an empty glass tube without food or shelter (Figure 38c,e). This control aimed to determine whether cuttlefish choosing the food arm on the second day (*i.e. test phase*) were avoiding the shelter arm (*i.e. potentially associated with a negative reinforcement*) or actually choosing the food arm (*i.e. planning for the future*).

## 4. Octopus experiment

### a. Testing apparatus

The experiment was conducted inside the home tank of each octopus. Using five centimetres thick filtering foam panels, the tanks were divided in three adjacent compartments: a shelter compartment, containing a grey PVC tube, a black PVC half-pipe, a scallop shell and 15 pebbles; a food compartment, containing two crabs and half a dozen of mussels; and a central zone, containing a terracotta pot and a piece of thawed shrimp (Figure 39a).

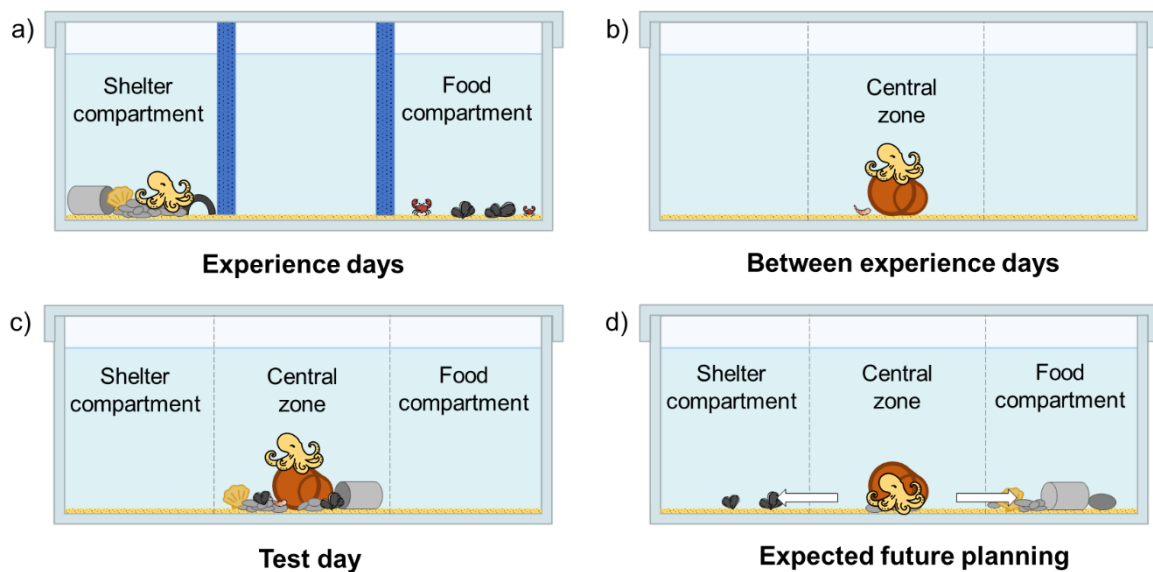


Figure 39: Schematic representation of the tank during the octopus experiment.

a) Compartmental layout during the six experience days. Each day, the octopus was pseudo-randomly assigned either to the shelter compartment (containing a grey PVC tube, a black PVC half pipe, a scallop shell and 15 pebbles) or to the food compartment (containing two crabs and half a dozen of mussels). b) Between two experience days, elements in the shelter and the food compartments and all the partitions were removed, and the octopus was allowed to freely access to the whole tank during two hours. c) Tank organisation on test day. Along with the terracotta pot and the piece of shrimp usually present in the central zone, movable items (a plastic tube, ten pebbles, a scallop shell and five mussels) were provided in the central zone, and the octopus was allowed to freely access to the whole tank and displace items. d) In the case the octopus showed future-planning, it was expected to displace food items in the shelter compartment and shelter items in the food compartment.

### b. Procedure

One day before the start of the experiment, the octopus was removed from its tank and placed in a temporary plastic tank (60x40x40cm) for about ten minutes. During this time, all enrichments were withdrawn, excepting the thin layer of sand and the terracotta pot placed in the middle of the tank. The octopus was then acclimatised to its newly arranged tank for 24 hours before the

experiment began. The experiment was conducted over six successive *experience days* (day 1 to day 6) and one *test day* (day 7).

During the *experience days*, octopuses were pseudo-randomly assigned the food or the shelter compartment so they experienced each compartment three times each, and never more than two times in a row. At around 14:00, the octopus was attracted to the assigned compartment using a fishing net. The octopus was then enclosed in the compartment (with a foam panel), and the corresponding elements were added inside (food or shelters and pebbles; see Testing apparatus and Figure 39a). The octopus remained inside the compartment for the next 22 hours. At around 12:00 pm, the elements of the compartment and the foam panel were removed. The octopus then had access to the entire tank (*i.e.* to the three compartments) for about an hour and a half. During this time, the food and the shelter compartments were empty, while the central zone of the apparatus contained the terracotta pot and a piece of thawed shrimp (Figure 39b). The organisation of the six experience days followed exactly the same schedule.

On the *test day*, at 12:00 pm, the octopus was given access to its whole tank with the shelter and the food compartments empty as previously. However, this time, movable elements (*i.e.* a plastic tube, ten pebbles, a scallop shell and five mussels) were placed in the central zone along with the piece of shrimp and the terracotta pot (Figure 39c). The tank was video recorded for two hours (from 12:00 pm to 14:00 pm) with a camera Sony Handycam® FDR-AX53 4K in absence of the experimenter. At the end of the experiment (*i.e.* at 14:00), the number, the nature and the position of items displaced were noted.

## ***5. Statistical analyses***

All statistical analyses were conducted on R (version 3.6.1, R Core Team, 2019). For the cuttlefish experiment, we conducted Fisher exact tests and Cochran tests (package RVAideMemoire) to compare the choices between phases within a group and to compare groups within the same phase, respectively. Binomial tests were used to determine whether cuttlefish made non-random choices (*i.e.* preference for the shelter or for the other arm) within each group and each phase.

## C. Results

### 1. Cuttlefish experiment

Whatever the phase of the experiment (*i.e.* experience, test and control phases), the group (test and control groups), the cohort (high value shelter and low value shelter cohorts), most cuttlefish preferentially choose the shelter arm over the other arm (*i.e.* food arm or empty arm; Binomial tests, 10 out of 10 cuttlefish:  $p=0.002$ ; or 9 out of 10 cuttlefish:  $p=0.021$ ; Figures 40a,b).

There were no significant differences in the choices made between the three phases of the experiment whatever the group and the cohort considered (Cochran test,  $Q = 2$ ,  $df = 2$ ,  $p\text{-value} = 0.368$ ). No difference was found between the two groups whatever the phase and the cohort considered (Fisher exact tests,  $p=1$ ).

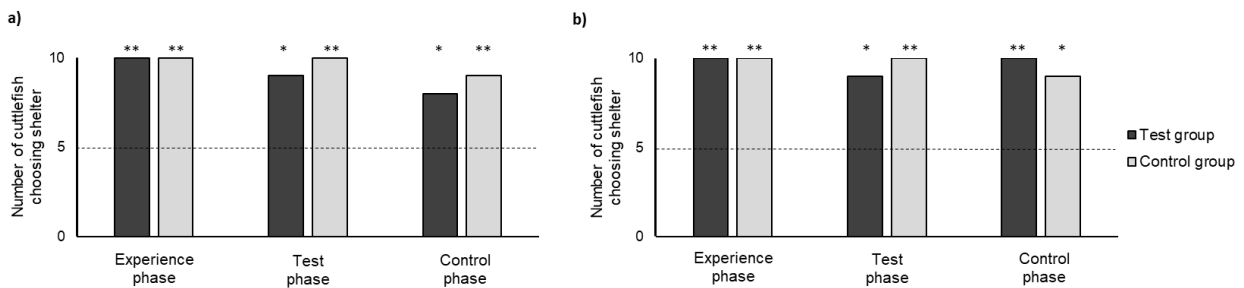


Figure 40: Number of cuttlefish choosing the shelter arm during the three phases of the experiment.

a) High value shelter cohort; b) Low value shelter cohort. Cuttlefish significantly preferred the shelter arm whatever the group (*i.e.* test and control groups) and the phase of the experiment (binomial test, \*\*  $p < 0.01$ , \*  $p < 0.05$ ). No difference was found between phases within the same group (Cochran tests) or between groups within the same phase (Fisher exact tests).

### 2. Octopus experiment

During the two hours after the introduction of the movable food and shelter items, none of the octopuses transported these elements either in the food or the shelter compartment. Two individuals displaced a few shelter elements to arrange the terracotta den and three individuals moved mussels toward the terracotta den, with one consuming a mussel within the two hours. They spent most of their time in the central zone of the tank (median = 106.5 min), mainly hidden in the terracotta den (Table 7).

Table 7: Objects displaced by octopuses and time spent in each compartment during the test day.

Octopuses moved objects but only within the central zone, and they spent most of their time in the central zone and the terracotta den.

Octopus	1	2	3	4
Objects displaced to the empty shelter compartment	None	None	None	None
Objects displaced to the empty food compartment	None	None	None	None
Objects displaced into the terracotta den	2 mussels 1 pebble + 1 shell	3 pebbles 1 tube + 1 shell	2 mussels	1 mussel
Time spent in the empty shelter compartment (in min)	5	0	30	4
Time spent in the empty food compartment (in min)	8	0	7	10
Time spent in the central zone [Time in the terracotta den] (in min)	107 [70]	120 [110]	83 [53]	106 [67]

## D. Discussion

When cuttlefish were offered a choice between ensuring a future need for food or responding to a current need for a shelter, they favoured the shelter, whether it was of high or low quality. When octopuses were allowed to displace food and shelter items to locations in which they would later need them, they did not displace any items. Our experiments do not demonstrate future-planning abilities in cuttlefish and octopuses.

The results obtained with cuttlefish might be explained by the fact that the shelter could be considered as too attractive in an environment perceived as too aversive. Indeed, the apparatus was a novel, white and illuminated environment, which was quite different from their regular home tank (*i.e.* grey walls, environmental enrichment, natural light). The features of such a testing apparatus might be intrinsically aversive for neophobic animals relying on camouflage on complex substrates for safety such as cuttlefish (Hanlon and Messenger, 2018). The cuttlefish behaviour would also be consistent with the fact that under predatory pressure, animals often minimise their foraging time, especially in areas which do not offer protection (Verdolin, 2006), and favour hiding in sheltered areas (Cooper, 2000; Uiblein et al., 1996). Moreover, food might have been perceived as of low value. Indeed, cuttlefish may have not considered the delay without food as negative since they were accustomed to be fed once a day in their home tank and they were completely satiated at the beginning of the test phase. Furthermore, when taking the future aspects of the study into account, a delayed reward discounting might have occurred. This is defined as a process by which rewards lose their subjective value as the delay to their obtention increases (Vanderveldt et al.,

2016). If we apply this effect to our experiment, we can suppose that satisfying an immediate need might present a higher subjective value than satisfying a future need.

The results obtained with octopuses could be explained by the fact that future needs for food and shelter were low. Indeed, the amount of food used between experience days corresponded to the usual amount fed to octopuses outside of the experiment. Secondly, octopuses' need for shelter was low as they were in their home tank in the absence of the experimenter, thus without predation risk. Nevertheless, these considerations should be pondered by the observation that octopuses readily consumed more food than the usual amount and always preferred to hide even in their home tank, indicating their desire to eat and hide at all times. Relocation of objects and food might not be a behaviour as flexible as we expected. Octopuses are known to carry food toward their den (Mather, 1991a) and to arrange it with nearby elements (Mather, 1994), but these behaviours seem to be den-centred. *Amphioctopus marginatus* are known to carry coconut shells as a portable shelter (Finn et al., 2009), but this behaviour was only never observed in *Octopus vulgaris*. Moreover, we explored the abilities of only four individuals and this species is reputed for its inter-individual variability during cognitive tasks (Bublitz et al., 2017; Bublitz et al., 2021; Poncet et al., 2022; Richter et al., 2016), we might have thus not tested enough individuals to observe a future-planning behaviour.

We can also consider the possibility that cuttlefish and octopuses might not be able to plan for a future need. In humans (Addis et al., 2007) as well as in other vertebrate species such as great apes (Martin-Ordas et al., 2010; Mulcahy and Call, 2006; Osvath and Osvath, 2008), western scrub jays (Clayton and Dickinson, 1998b; Correia et al., 2007; Raby et al., 2007) and rats (Eacott and Norman, 2004; Pfeiffer and Foster, 2013), future planning abilities are always paired with episodic-like memory abilities. This co-existence, associated to common phenomenological, developmental and neurobiological features have led researchers theorise about the mechanistic and evolutionary links between these cognitive abilities (Addis et al., 2007; Schacter and Addis, 2007b; Schacter et al., 2012; Suddendorf and Busby, 2003; Tulving, 2005). Our experiment raises an interesting case of a species known to possess episodic-like memory abilities (Jozet-Alves et al., 2013b; Schnell et al., 2021c) which does not appear able to plan for the future. This result might indicate that episodic memory and future planning are distinct cognitive traits with their own evolutionary histories. As remembering the past and imagining the future both rely on the ability to mentalise about personal events, that would explain why there is a neural substrate overlap and a late maturation of these abilities in vertebrates.



Episodic-like memory might have an intrinsic adaptive value in cuttlefish, while it might not be the case for future planning. As in primates and corvids (Seed et al., 2009), relying on episodic-like memory in cuttlefish could be explained by the ecological challenge of searching for spatiotemporally dispersed food. Concerning future-planning, we can wonder how this specific cognitive ability would provide a fitness benefit in cuttlefish as they do not modify their environment by rearranging a shelter, or by transporting and storing food. Cuttlefish might thus not need to plan for the future as they cannot typically act in the present to secure a future need. From an adaptive point of view, octopuses are known to modify their environment (Mather, 1994) and veined octopus have even been shown carrying coconut shells (Finn et al., 2009). While we could then have expected them to plan for the future, it has not been evidenced in our study. The transport of coconut shells for protection might be more parsimoniously explained by a simple association between the shell and a positive reinforcement (*i.e.* protection against a threat) rather than planning for a future den use (Amodio et al., 2019). Their ability to camouflage quickly or crawl into any crevice to hide from predators, to hunt multiple types of prey and to rely on multiple and variable cognitive strategies (Poncet et al., 2022; Richter et al., 2016) might be sufficient abilities to thrive without the need to plan for the future. The main difference between the cephalopod species studied here and the vertebrate species in which future planning abilities have been demonstrated is that they are not exposed to comparable socioecological challenges (*i.e.* great apes, corvids, rats; Emery and Clayton, 2004). Cuttlefishes are considered solitary most of their lives, excepting during reproductive periods when they can form large aggregations (Hall and Hanlon, 2002) and possibly during migration (Drerup and Cooke, 2021). Octopuses are generally solitary (Boal, 2006) with rare observations of social aggregations which are more likely attributed to food availability and low predation pressures than to social attraction (O'Brien et al., 2021). The evolution of future planning in vertebrate species might be explained by the conjunction of ecological and social selective pressures, as animals need to cope with the challenges linked to their physical environment (*e.g.* perishability of food) and to group living (*e.g.* pilfering).

To sum up, our experiments did not demonstrate future-planning abilities in cuttlefish and octopuses. This can be explained by experimental parameters, such as an adverse environment, a low drive for food or an inability to carry objects away from a den. Alternatively, it could be explained by the fact that these species do not possess future planning abilities. This would indicate that episodic-like memory and future planning are not intertwined abilities, but evolutionary independent capacities with different evolutionary histories. Identifying both similarities and differences in complex cognition between vertebrate species and cephalopods (*i.e.* which possess or not future planning abilities), and within cephalopods (*i.e.* cuttlefish rely on episodic-like memory

for foraging unlike octopuses) is of importance. That will make researchers able to pinpoint which evolutionary pressures (ecological and/or social) have led to the emergence of complex cognitive abilities.

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## II. Future planning in the adult cuttlefish

### First indications of planning for future needs in adult common cuttlefish

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### **Abstract**

Future-planning abilities are often considered as a specificity of humans, as stated by the Bischof-Köhler hypothesis. Even though this hypothesis has been challenged with studies on mammals and birds, a previous experiment on cephalopods could not bring to light future planning abilities in cuttlefish and octopuses. However, the age and the individual experience (captive-reared individuals) might have influenced their cognitive abilities and their physiological status, which might have prevented them to express future-planning abilities. To explore this hypothesis, we reproduced the future-planning experiment initially conducted with captive-reared juvenile cuttlefish with wild-caught sexually mature cuttlefish. These cuttlefish underwent an experiment where they could plan for a future need for food instead of following their current need for shelter. Contrary to our previous experiment undertaken in younger individuals, some adult cuttlefish prioritised a future need instead of a current need. Most individuals still favoured the immediate need for a shelter, indicating that planning for the future is the result of a trade-off between a current need for shelter and a future need for food. It might be influenced by multiple parameters (*e.g.* motivational state, physiological status) which make future-planning abilities difficult to highlight. As major changes were undertaken throughout this preliminary experiment (*i.e.* changes in apparatus design, procedure), it needs to be replicated to confirm the results obtained and conclude on the future planning abilities in cuttlefish.

### **Key-words**

Future-planning, Cuttlefish, Mental Time Travels, Trade-off, Age-related differences

## A. Introduction

Future-planning is defined as the ability to plan for a future need independently of its current needs (Suddendorf, 1994; Suddendorf and Corballis, 1997). The Bischof-Köhler hypothesis states that an animal is bound to its present state and thus cannot plan for its future needs (Suddendorf, 1994; Suddendorf and Corballis, 1997), but a growing number of studies on vertebrates tend to show the contrary (Cheke and Clayton, 2012; Correia et al., 2007; Feeney et al., 2011b; Kabadayi and Osvath, 2017; McKenzie et al., 2004; Mulcahy and Call, 2006; Osvath, 2009; Osvath and Osvath, 2008; Pfeiffer and Foster, 2013; Raby et al., 2007). Several vertebrates thus seem to be able to plan for the future, but also to remember in an episodic-like manner (Crystal, 2018). However, as these species share a common evolutionary history, detangling the link between future-planning and episodic memory is difficult, since this link might equally originate from similar neural networks or from the requirement of episodic memory to simulate the future.

Cuttlefish, known to possess complex cognitive abilities, have a centralised brain which presents an independent evolutionary history from vertebrates' brain, making them valuable candidates to explore the evolution of complex cognitive abilities. Moreover, cuttlefish were shown to possess episodic-like memory abilities (*i.e.* they remember which prey they ate, where and how long ago; Jozet-Alves et al., 2013b; Schnell et al., 2021c), paired with future-dependent foraging behaviour (Billard et al., 2020a), flexible decision-making behaviour (Kuo and Chiao, 2020; Yang and Chiao, 2016) and an ability to delay gratification (Schnell et al., 2021b). They thus seemed to be an ideal candidate to study future planning abilities, however, a previous study (Poncet et al., article 3, Chapter 3. I.) showed that juvenile cuttlefish did not plan for the future when they were presented a choice between acting for a current need to hide *versus* acting for a future need to eat.

This behaviour (*i.e.* acting to secure the current need) could be interpreted as an inability of cuttlefish to plan for the future or as the consequence of several experimental parameters. Firstly, in our previous study, we tested juvenile cuttlefish, and it is possible that young individuals do not possess future planning abilities while older individuals would. Indeed, in humans, future thinking develops late (Friedman, 2007; Suddendorf and Busby, 2005), this could also be the case in cuttlefish. Indeed, some parts of the brain, such as the vertical complex (commonly considered as the analogue of the limbic system of mammals; Shigeno et al., 2018), are still maturing several months after hatching as it has been shown by Dickel and colleagues (2001). Secondly, juvenile individuals might present a lower food drive than sexually mature adults, because the later might have a higher energy expenditure due to reproductive activities. Indeed, reproduction requires a significant amount of energy when searching for a mate, fighting competitors or laying eggs

(Hanlon and Messenger, 2018). Finally, captive-reared cuttlefish might favour a current need to hide as they know that food is provided every day in the facilities without requiring them to forage for food.

We here reproduced the previously described study with sexually mature wild-caught cuttlefish. During the experiment, cuttlefish could ensure either a future need for food or a current need for a shelter. To do so, cuttlefish were first fed to satiety, then they were offered a choice between a shelter compartment (with no food) and a food compartment (with no shelter). They were then confined in the chosen compartment until the following day. The next day, they were again fed to satiety and proposed the same choice as the day before (*i.e.* food compartment *versus* shelter compartment). We hypothesise that on the first day, cuttlefish will favour their current need to hide and choose the shelter compartment. On the second day, we hypothesise that cuttlefish will plan for their future need for food and thus choose the food compartment.

## **B. Material and methods**

### ***1. Ethical statement***

Experiments were carried out in accordance with directive 2010/63/EU of the European parliament and the French regulation relative to the protection and use of animals in research. Procedures were approved (#22429 2019101417389263 v2) by the regional ethical committee (CENOMEXA; agreement number 54).

### ***2. Subjects***

28 adult cuttlefish (*Sepia officinalis*, around two years of age) were tested in spring 2019 (n=6), 2020 (n=11) and 2022 (n=11). They were caught in the vicinity of Luc-sur-Mer (English Channel, France) using basket traps, and housed in the Centre de Recherche en Environnement Côtier (CREC, Luc-sur-Mer, France), excepting three individuals reared from hatching at the CREC and tested in 2019. Due to methodological differences, two cohorts of cuttlefish were considered: a first cohort (2019-2020: n=17) and a second cohort (2022: n=11). Each cohort was divided between a test group and a control group (cohort 1: n=10 and n=6, respectively; cohort 2: n=5 and n=6, respectively).

### 3. Material

Cuttlefish were reared either in group segregated by sex in round plastic tanks (Ø155xh55cm) with circulating natural seawater at  $15 \pm 1^\circ\text{C}$ , or individually in rectangular plastic tanks (56x77x30cm) at  $15 \pm 3^\circ\text{C}$ , under artificial light conditions following the natural cycle. They were fed daily with live crabs (*Carcinus maenas* and *Hemigrapsus sanguineus*) of suitable size.

During the experiment, each cuttlefish was placed in an apparatus with circulating natural seawater at  $15 \pm 3^\circ\text{C}$  under natural light conditions (Figure 41). The apparatus consisted in three connected compartments: an empty starting compartment and two choice compartments containing either a shelter or food. Three PVC apparatuses of different dimensions were used: a white Y-shaped apparatus (compartments dimensions of 50x30 cm, water level of 20cm) and a white Plus-shaped apparatus (dimensions 200x110cm, with compartments of 80x80cm, water level of 20 cm) for the cohort 1, and a grey rectangle apparatus (dimensions 180x77 cm, starting compartment of 39x77cm and choice compartments of 147x33 cm, water level of 15 cm) for the cohort 2. While the apparatus used for the cohort 2 allowed cuttlefish to see inside the choice compartments from the starting compartment, the apparatuses used for the cohort 1 did not provide a direct visual access to the choice compartments. Each compartment of each apparatus could be closed by opaque plastic sliding doors. The end of the shelter compartment was covered by an opaque plate to provide shadow and a layer of sand was also provided on the bottom. In the cohort 1 but not in the cohort 2, several rocks, shells and plastic algae were added in the apparatus). Shrimps (*Crangon crangon*) and a crab (*Hemigrapsus sanguineus* or *Carcinus maenas*) were either attached to a wire at the end of the food compartment (cohort 1) or put in a glass tube (cohort 2). The position of each compartment was randomised between days.

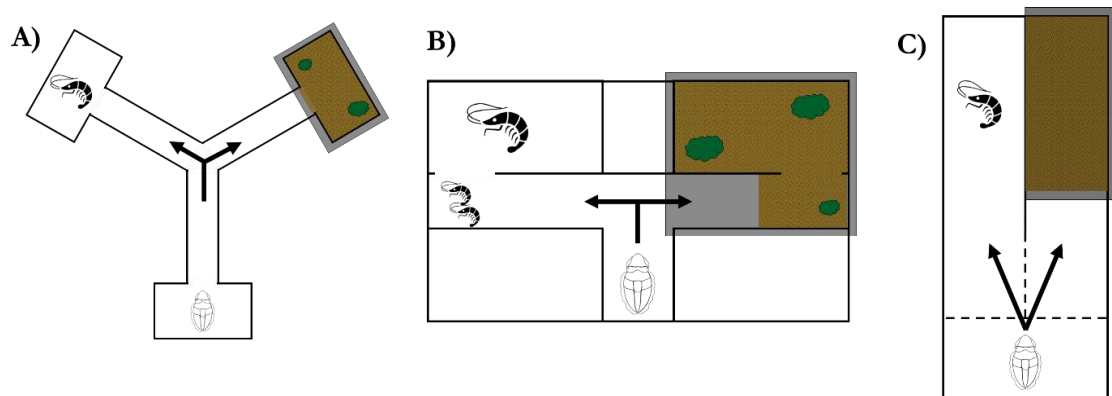


Figure 41: The three apparatuses used during the experiment.

A) Y-shaped apparatus for the cohort 1; B) Plus-shaped apparatus for the cohort 1; C) Rectangle apparatus for the cohort 2. Cuttlefish were placed in a starting compartment then could choose between a food compartment with shrimps and crabs (shrimp symbol) and a shelter compartment with sand.

#### ***4. Course of the experiment***

An acclimation phase to the apparatus started in the morning and lasted a minimum of 24 hours and up to three days if the cuttlefish did not eat at least one crab during the night. The animals could move freely in the apparatus during the acclimation, and were fed *ad libitum* with live crabs. The compartments of the apparatus were partially covered to reduce the amount of light in the apparatus and thus attenuate the level of stress of the animals. No shelter was provided.

The future planning experiment was subdivided into three phases on three consecutive days, with one phase per day: experience phase (shelter *versus* food); test phase (shelter *versus* food), to determine whether cuttlefish plan for their future needs; control phase (shelter *versus* nothing), to determine whether cuttlefish which chose the food compartment during the test phase were avoiding the shelter compartment or actually choosing the food compartment.

On the first day, at the beginning of the experience phase, the compartment of the apparatus where the cuttlefish was resting (*i.e.* the starting compartment) was closed, and the cuttlefish was fed to satiety with live preys. A new prey was added each time one was eaten, until the cuttlefish stop eating. The last prey was left with the cuttlefish for half an hour before being removed, to insure satiety. Then, the door was opened and the cuttlefish was allowed to move and choose between the food and the shelter compartments. After the animal went into one of the two compartments, the chosen compartment was closed and the cuttlefish stayed inside until the following day. If the cuttlefish chose the shelter compartment, no food was provided until the following day. If the cuttlefish chose the food compartment, crabs and shrimps were released from the wire or the glass tube.

On the second day, at the beginning of the test phase, elements of the shelter and/or the remaining preys were removed from the compartment where was the cuttlefish. For the cohort 1, this compartment became the new starting compartment, while for the cohort 2, the cuttlefish was gently pushed back to the starting compartment. Then the procedure was conducted exactly the same way as the previous day, with the cuttlefish being fed to satiety and then offered to choose between a shelter compartment and a food compartment.

On the third day, a control phase was conducted: the procedure was done exactly the same way as the previous day, except the cuttlefish was offered to choose between a shelter compartment and an empty compartment (*i.e.* without shelter or food).

The control group underwent the same procedure than the test group, except that when cuttlefish chose the shelter compartment, food (crabs and shrimps) were provided in the chosen compartment half an hour after the choice.

## 5. Statistical analyses

Statistical analyses were conducted on R (version 4.2.2). We conducted binomial tests to compare the choice between compartment of the apparatus within each phase, Fisher exact tests to compare the choices of cuttlefish between groups and McNemar exact tests (package `exact2x2`) to compare the choices between phases (*i.e.* experience, test and control phases). Differences between the two apparatuses used for cohort 1 could not be analysed due to missing data (*i.e.* the type of apparatus used – Y *versus* Plus-shaped – to test each cuttlefish had not been systematically reported), thus data from both apparatuses were indiscriminately pooled.

## C. Results

### 1. Cohort 1

Two individuals (one in the test group and one in the control group) were removed from the experiment in the morning of the third day (*i.e.* before starting the control phase) as they showed clear signs of senescence (*i.e.* buoyancy failure).

All cuttlefish from the test group chose the shelter during the experience phase and the control phase. During the test phase, four out of 10 tested cuttlefish chose the food compartment (Figure 42). Test cuttlefish chose the shelter during the experience and the control phase significantly more than chance (binomial test,  $p_{\text{exp}}=0.002$ ,  $p_{\text{control}}=0.004$ ), but they did not during test phase (binomial test,  $p_{\text{test}}=0.754$ ). However, due to the small number of tested individuals, there was no significant difference in the choices realised between the experience and the test phases (McNemar exact test,  $p=0.125$ ).

All cuttlefish from the control group chose the shelter during the three phases of the experiment (*i.e.* experience, test and control phases). Control cuttlefish chose the shelter significantly more than chance during the three phases of the experiment (binomial test,  $p_{\text{exp}}=p_{\text{test}}=0.016$ ,  $p_{\text{control}}=0.031$ ). Choices during experience and control phases were not significantly different between the test group and the control group (Fisher exact test,  $p=1$ ) Repartition of choices during the test phase was not significantly different between the test and the control groups (Fisher exact test,  $p=0.103$ ).



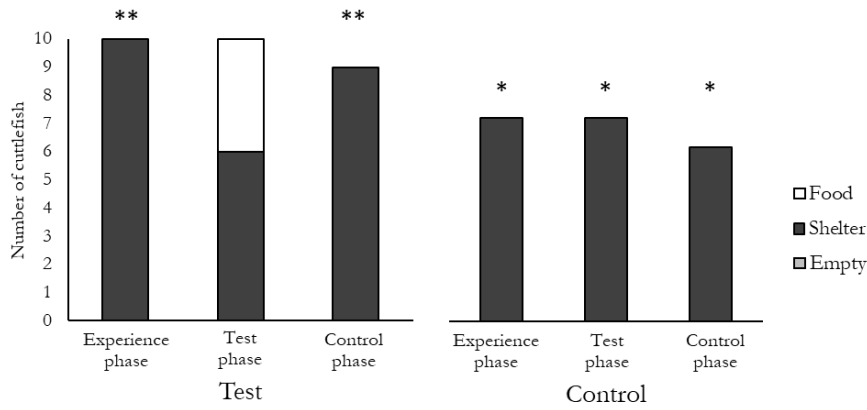


Figure 42: Number of cuttlefish choosing the shelter, the food or the empty compartment during the three phases of the experiment in the test (on the left) and the control (on the right) groups for the cohort 1.

Cuttlefish significantly favoured the shelter arm during experience and control phases for both test and control group, but test cuttlefish choices did not differ from chance during test phase (i.e. dotted line; binomial test, \*\*  $p < 0.01$ , \*  $p < 0.05$ ).

## 2. Cohort 2

Overall, cuttlefish from the test and the control groups chose the shelter during the three phases, except for one control cuttlefish and one test cuttlefish which chose the empty compartment during the control phase (Figure 43). Control cuttlefish chose the shelter during experience and test day significantly more than chance (binomial test,  $p_{\text{exp}} = p_{\text{test}} = 0.0313$ ) but not during control phase (binomial test,  $p_{\text{control}} = 0.219$ ). Due to the small number of individual, test cuttlefish did not show a significant preference for shelter during any phase (binomial test,  $p_{\text{exp}} = p_{\text{test}} = 0.0625$ ,  $p_{\text{control}} = 0.375$ ). There were no significant differences in the choices realised during the experience and the test phases for both groups (McNemar exact test,  $p = 1$ ). Choices during all three phases were not significantly different between the test group and the control group (Fisher exact test,  $p = 1$ ).

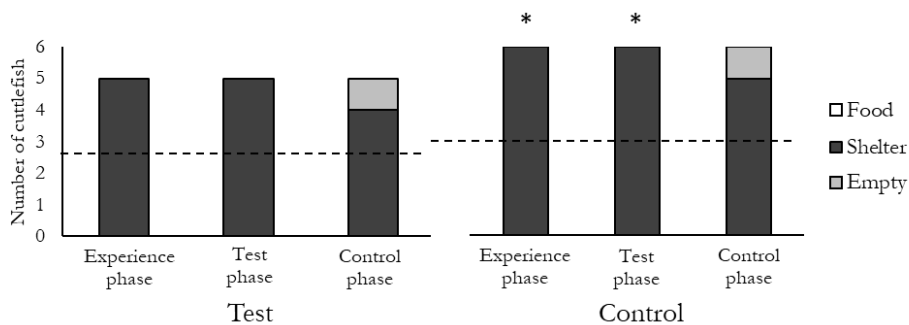


Figure 43: Number of cuttlefish choosing the shelter, the food or the empty compartment during the three phases of the experiment in the test (on the left) and control (on the right) groups for the cohort 2

Control cuttlefish significantly favoured the shelter arm during experience and test phases, but preference was not significantly different from chance (i.e. dotted line) for test cuttlefish due to the small number of individuals (binomial test, \*  $p < 0.05$ ).

## D. Discussion

This preliminary experiment provides indications that satiated cuttlefish can choose a compartment containing food after experiencing a lack of food in one single exposure in the shelter. Unlike the previous experiment we ran in juvenile cuttlefish (Poncet et al., article 3, Chapter 3. I.), these results suggest that cuttlefish might be able to plan for their future by acting in the present to secure a future need for food over a current need to hide. However, this ability was observed only in few individuals and the interindividual variability can be attributed to several factors.

On the first day of the experiment, during the experience phase, cuttlefish fed to satiety experienced for the first time a choice between a compartment with food and a compartment with a shelter. All cuttlefish went to the shelter, indicating that, as expected for a first choice, they all prioritise an immediate need to hide. This was similarly observed in the experiment with juvenile cuttlefish (see Chapter 3.I.), but also in experiments on anticipation with squirrel monkeys (McKenzie et al., 2004) or black-capped chickadees (Feeney et al., 2011b). Consequently, all the cuttlefish were confined in the shelter compartment until the next day, without food for the test group, and with food for the control group.

On the second day, during the test phase, cuttlefish were again fed to satiety before being allowed to choose a compartment. Our hypothesis was that cuttlefish planning for their future needs would go to the food compartment, while cuttlefish favouring their current needs would go to the shelter compartment. We observed that half of the cuttlefish from the test group in the cohort 1 chose the food compartment over the shelter compartment, while all the cuttlefish from the control group chose the shelter. Two hypotheses can explain these results: 1) either cuttlefish anticipated the lack of food in the shelter, or 2) they avoided the shelter because of their negative experience. Such results were not observed in cohort 2, as all cuttlefish chose the shelter compartment over the food compartment.

On the third day, during the control phase, cuttlefish were fed to satiety then could choose between the shelter compartment and an empty compartment. If cuttlefish were avoiding the shelter after a negative experience as hypothesised, they should choose the empty compartment. We observed that none of the cuttlefish chose the empty compartment, indicating that the shelter compartment was not negatively valued, thus invalidating the second hypothesis. The behaviour of half of the cuttlefish in test group of the cohort 1 thus corresponds to a future-planning behaviour, where cuttlefish planned for a future need for food instead of following their current need for a shelter, based on a single experience of a lack of food in the shelter.

However, our results show a discrepancy of results between the tested cohorts with only half of the cuttlefish in the cohort 1 and all cuttlefish in the cohort 2 favouring the shelter on test phase. This might reflect the difficulty cuttlefish had between choosing to answer their immediate need for a shelter or their future need for food. Planning in animals is often complex to observe as the cost associated with delayed rewards is largely underestimated (Zentall, 2010). Differences in apparatus, and individual parameters such as hunger, physiological needs, previous exposition to predators, sex and personality may have accounted for the differences observed.

Our experiment indicates that contrary to juvenile cuttlefish, some sexually mature adult cuttlefish might be able to plan for the future. Even if further studies with more individuals are required to confirm the tendencies observed here, this experiment indicates that future planning abilities might emerge late in cuttlefish, as observed in humans (Friedman, 2007; Suddendorf and Busby, 2005). Adult cuttlefish might require future-planning abilities during reproductive period, where they undergo complex social situations with mating competitors. This period might also coincide with an increased need for food as individuals might require energy to compete with others and to store the energy needed to produce and fertilise eggs (Hanlon and Messenger, 2018). It might explain why some adult cuttlefish seem to plan for their future need for food while juvenile cuttlefish did not. This shows how complex it can be to explore future planning abilities, as multiple parameters should be considered when conceiving and analysing a future-planning task.

Our experiment is still preliminary, with lots of changes in experimental contingencies and a low number of tested individuals. This prevents reliable statistical analyses, especially since differences in methodology lead to a lack of reproducibility between years, preventing us to pool the results from the two cohorts. Considering the exciting results obtained, we thus decided to construct several copies of one of the apparatus used to be able to test in parallel several individuals. Indeed, the seasonality of the cuttlefish make the experiment possible only few weeks each year: senescence can occur quickly after they are caught next to the coast of Normandy.

### **Conclusion of chapter 3**

Juvenile cuttlefish and subadult octopuses have not been shown to possess future planning abilities, while some adult cuttlefish did plan for a future need for food.

Future planning might thus exist in cephalopods, but this ability is complex to explore as multiple parameters have to be considered: the valence of the current and future needs, the delay discounting, the developmental stage of the individual, or the metabolic requirements or the life history of the animal.

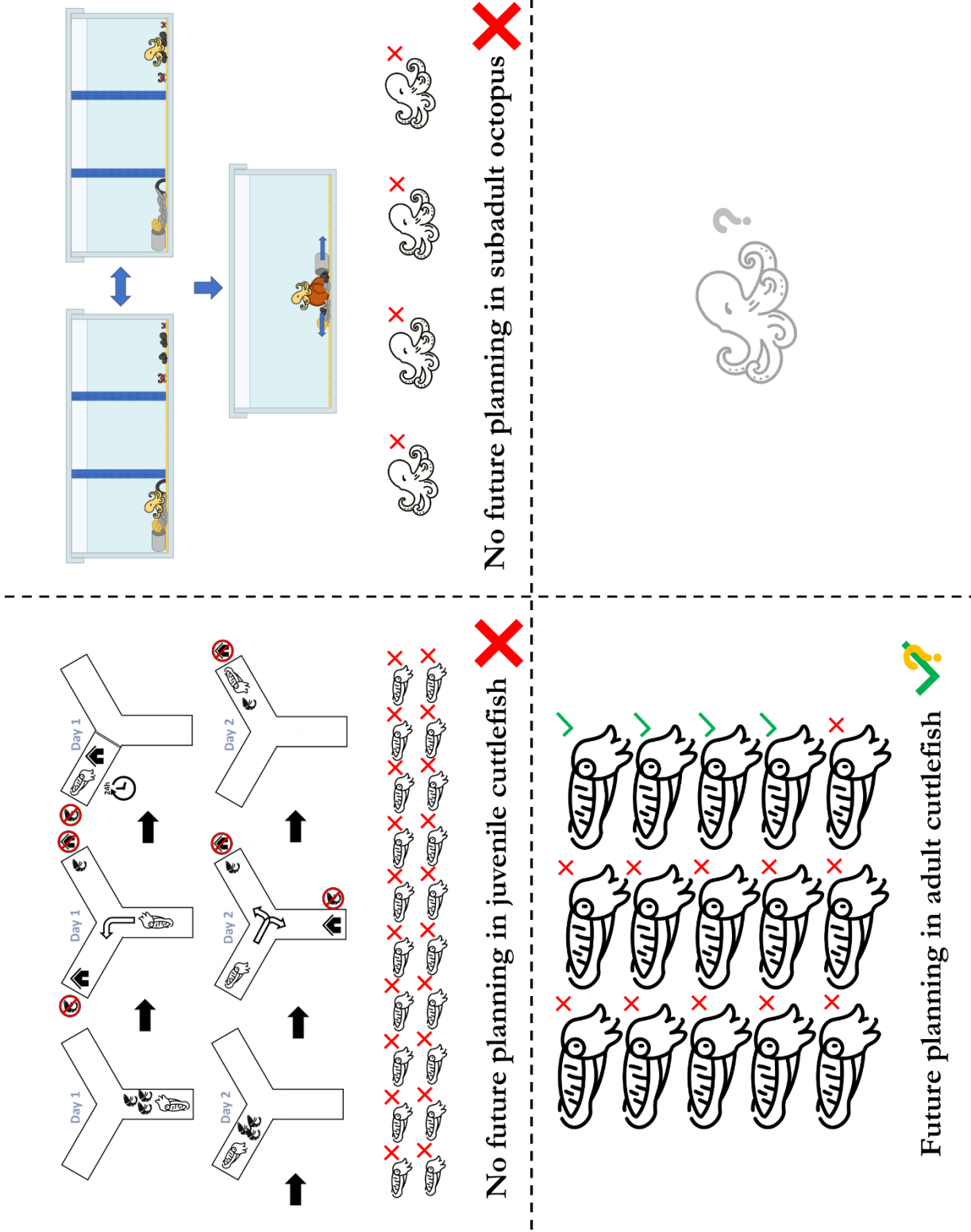


Figure 44: Summary of chapter 3 – Future planning in coleoids

# **General discussion**

# General discussion

This thesis explores the Mental Time Travels abilities of common cuttlefish (*Sepia officinalis*) and common octopuses (*Octopus vulgaris*). In a first chapter, an exploration of the retrospective side of Mental Time Travels known as episodic-like memory, was conducted with octopuses. The inability of octopuses to learn replenishing rates (a pre-requisite to run the episodic-like memory task adapted from the protocol used in cuttlefish) led us to test whether octopus could use another type of temporal encoding than the temporal distance. Octopuses were tested on their ability to encode the relative times of occurrence (sequence of images) and succeeded in the task. In a second chapter, false memories were defined and presented as a tool to study reconstructive processes of memory. They were then explored in cuttlefish, which were shown to create false memories, indicative of reconstructive processes in their episodic-like memory. In a third chapter, the prospective side of Mental Time travels, known as future planning, was explored in both cuttlefish and octopuses. Young individuals of both species did not show any future planning behaviour but a preliminary study suggests that some adult cuttlefish might be able to plan for their future. I will here address the limitation of each of the studies conducted in this PhD and rise a few perspectives.

## A. Spatiotemporal memory in octopuses

### *1. Exploration of episodic-like memory in octopuses*

In order to understand the evolutionary pressures shaping episodic-like memory abilities in invertebrates, we adapted with octopuses a previous experiment conducted with cuttlefish and explored whether octopuses could remember what prey they ate, where and how long ago. Out of the seven octopuses tested, only one succeeded in the task in twice as much trials than the number of trials necessary for cuttlefish. The other octopuses relied on various foraging strategies such as familiarity avoidance, risk-sensitivity, constancy or win-stay strategy. These results made us hypothesise that the need to rely on episodic-like memory abilities to forage might bring a higher selective advantage in cuttlefish than in octopus.

#### *Limitations of our experiment*

We can also consider that octopuses do possess episodic-like memory abilities, but we could not bring to light such abilities. Firstly, the number of trials might have been too limited for the animals to understand the rule. However, it seems unlikely as we doubled (for three individuals) or

quadrupled (for three other individuals) the maximum number of trials needed for cuttlefish to understand the rule and it was still not enough for octopuses. Maybe more trials would have allowed this ability to emerge, but it might have not been pertinent to conduct so many trials, as it would promote the use of semantic rules rather than episodic memory (Zentall et al., 2001; Zentall, 2006; Zentall et al., 2008).

Another point to draw is that we did not use any negative reinforcement. With cuttlefish, the mere absence of the preferred reward after an hour made them rapidly shift toward the less preferred reward, but it did not seem to work with octopuses. Maybe the use of a negative stimulus, like the decayed worm in western scrub jays experiments (Clayton and Dickinson, 1998), might be necessary to motivate octopuses to learn the task. Moreover, before the 2000s, octopuses' learning abilities (discriminative or associative learning tasks) were generally studied using a negative reinforcement in the form of an electric shock following an incorrect choice, which allowed to obtain significant results within a limited number of training trials (see for example Fiorito and Scotto, 1992; Sutherland, 1957; Wells and Young, 1970). On the opposite, the food rewards could have not been motivating enough. Mussels were available at all times during the experiment, which might have reduced the food motivation of octopuses. However, octopuses rarely consumed mussels, and appeared to be quite motivated by crabs. The combination of the absence of negative reinforcement and a positive reinforcement of low value might have not been sufficiently motivating for octopuses to succeed the task.

Another possibility is that octopuses might have difficulty in perceiving the differences between the delays used, and it might have been necessary to use delays of a different magnitude, such as Martin-Ordas and colleagues (2010) who used delays of five minutes and one hour in their episodic-like memory experiment. Moreover, octopuses might have difficulties in encoding time using temporal distance (*i.e.* "How long ago"), and might rather rely on temporal location (*i.e.* "When") or the relative times of occurrence (*i.e.* the order in a sequence). This idea is intriguing, and we thus subsequently explored the perception of the relative times of occurrence in octopuses.

## ***2. Exploration of the memory for time in octopus***

Our experiment explored for the first time a cephalopod understanding of relative times of occurrences. The four tested octopuses learnt to select an image which appeared the earliest in a sequence observed 10 to 20 minutes earlier, and octopuses seemed to be able to spontaneously transfer this learning to novel symbolic images. Indeed, three out of four octopuses spontaneously



obtained at least two third of correct choices out of the 15 choice trials (10/15 for two individuals and 12/15 for another one).

### *Limitations of our experiment*

This learning took about 200 trials with the use of a negative reinforcer for incorrect responses. It is thus not an indicator that octopuses might be better at encoding time in terms of relative times of occurrence rather than temporal distances. Interestingly, all octopuses reached the learning criterion in about the same number of trials, showing surprisingly little inter-individual variability, contrary to the episodic-like memory experiment (it is to be noted that different individuals were tested in the two experiments). It might be an indication that a rule based on the relative times of occurrence might be more spontaneously acquired by octopuses.

One point we did not control in our experiment is the use of decaying memory trace to choose which image appeared the earliest. The use of a simple rule such as how much the memory has faded can be difficult to rule out, but we observed that octopuses succeeded in the task whether the two images were consecutive (*e.g.* second and third images) or spaced in the sequence (*e.g.* first and fourth images). Moreover, the use of a 10- and a 20-minutes delay between the presentation of the sequence and the test might attenuate the differences in decaying memory traces between the images within a sequence.

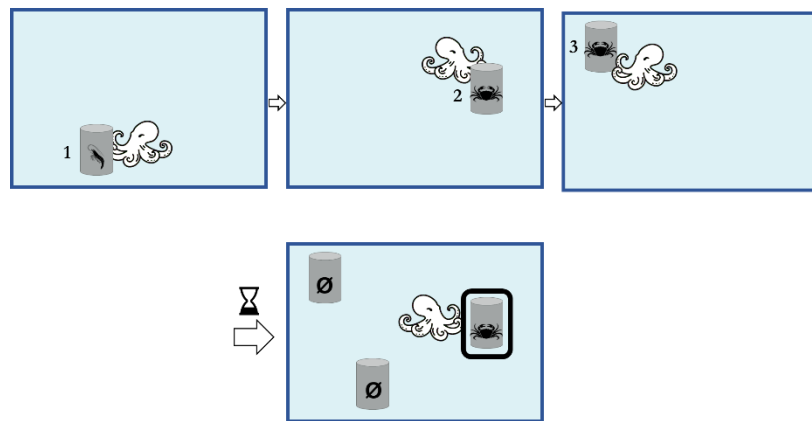
This experiment would be strengthened with more individuals, and with the use of a negative reinforcer from the beginning of the experiment instead of starting after 100 trials. Replicating this experiment would allow us to see the effect of the negative reinforcer and whether all octopuses require 200 trials to understand the task.

### *Perspectives*

First of all, it would be worthwhile to reproduce the experiment on the temporal order of a sequence with cuttlefish, to see whether cuttlefish thrive in both temporal distances and relative times of occurrence. It would be valuable to compare the results between octopuses and cuttlefish to understand what drives the use of one type of temporal encoding over the other.

As octopuses show an ability to encode time in terms of relative times of occurrence, it would be useful to explore whether they can use this type of encoding in an episodic-like memory task. It would more clearly indicate whether octopuses do possess episodic-like memory abilities or not,

and whether this ability is observable using only a certain type of temporal encoding. Such experiment could be conducted as the following: octopuses would be presented with opaque pots containing either crab (their preferred prey) or shrimps (a less preferred prey; Figure 45). One pot would contain shrimp, and two pots would contain crab. The pots would be presented one after the other in a distinct location in a random order. After a delay, the three pots would be presented at the same time at their previous locations. Only the crab seen the earliest in the sequence would be replenished. In order to be rewarded, octopuses would thus need to learn what prey was where and in which order in the sequence, in order to successfully retrieve where was the first crab.



*Figure 45: Proposition of an episodic-like memory experiment using relative times of occurrence.*

*The octopus is presented successively with three pots containing crab or shrimp, then it has to retrieve where was the first crab.*

Another experiment that would bring valuable insights to both cuttlefish's and octopuses' abilities would be an episodic-like memory experiment with contextual information instead of temporal information, such as the one conducted with rats by Eacott and colleagues (2005). It would indicate whether cephalopods can use episodic-like memory with only contextual cues and not temporal cues. For example, an experiment could use octopuses' natural tendency to explore novel objects. Octopuses would be placed in a first E-shaped maze with distinctive contextual cues (hue, texture of the walls), and they would be able to explore two different objects located in two arms not visible from the starting point (Figure 46). Then octopuses would be placed in a second maze with different contextual cues and would explore the same objects, but this time in reversed locations. Then, they would be placed back into their home tank and would be able to explore one of the objects, before being placed back into one of the mazes. If they remember what object was where and in which context, they should go to the object they did not spent time with in their home tank.

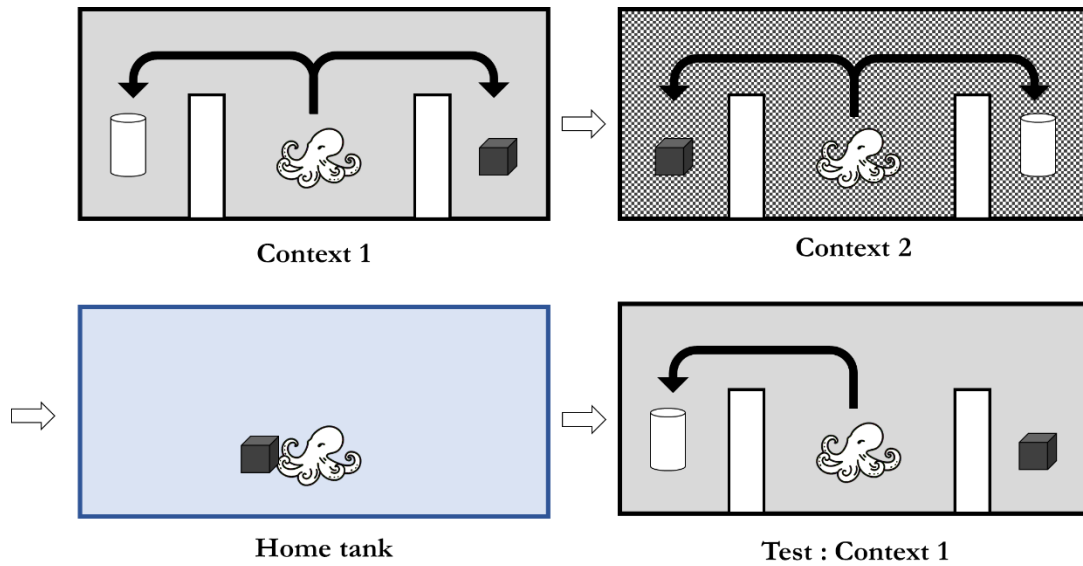


Figure 46: Proposition of a “What-Where-Which” episodic-like memory experiment using contextual information. The octopus is presented two objects in two different contexts, then it can interact with one of the objects in its home tank. It is then placed in one of the contexts and has to find the object it did not interact with.

## B. False memories in cuttlefish

### 1. False memories

We set up criteria that should be used to explore false memories in animals. In a misinformation effect paradigm, the original event should contain at least three different features to be encoded in memory; the misleading event should contain a modified feature from the original event; a delay of several minutes should be respected before the test; single trials should be favoured; the test group should be uniform in age and experimental modalities; and a control group should be constituted. We applied those criteria to generate false memories in the cuttlefish.

### 2. False memories in the cuttlefish

By creating an experiment promoting false memories, we aimed to explore the reconstructive processes in the memory of cuttlefish. To do so, cuttlefish were presented a misinformation effect paradigm with an original event constituted of three different tubes containing either a crab, a shrimp or nothing. It was followed by either a visual misleading event (*i.e.* the shrimp and the empty tube, without preys visible, with blank water), an olfactory and visual misleading event (*i.e.* the shrimp and the empty tube, with shrimp odour) or a non-misleading event (*i.e.* the shrimp tube with shrimp odour). A delay of one hour was conducted before the test, which was constituted of

a choice between the empty tube (*i.e.* the “false-memory” tube) and the crab tube (*i.e.* the “true-memory” tube). Each individual was its own control by being tested in the non-misleading condition, using the same procedure than in the misleading conditions. Cuttlefish performed at chance level in the visual misleading condition, above chance level in the olfactory and visual misleading condition, tending to choose the crab tube more than the empty tube, and significantly above chance level in the non-misleading condition, significantly favouring the crab tube. Cuttlefish thus seem to have created false memories in the visual misleading condition, while being able to correctly remember in the non-misleading condition. This study is the first to indicate the potential presence of false memories in cuttlefish, which are indicative of source monitoring failure and reconstructive processes. This result argues in favour of the existence of and reconstructive processes in episodic-like memory in cuttlefish.

#### *Limitations of the experiment*

The main limitation of our experiment is that it is difficult to disentangle whether we are witnessing false memories or simple forgetting. Our non-misleading condition controls for forgetting and indicates that cuttlefish could retrieve the correct information when not misled; but maybe the presence of the empty tube during the misleading event was enough to impair memory of cuttlefish and lead to forget what was where. It is the main difficulty of false memories studies in animals: in the absence of language, it is difficult to know whether the animals forgot and chose randomly, or whether some individuals remembered the right answer while other remembered the false answer. Moreover, it is difficult to know whether we are in the presence of false memories, where the subject remembers wrongly, in an episodic way, or in the presence of false knowledge, where the subject makes a mistake in their knowledge, in a semantic way. Since we used unique events and did not train animals to answer the question, we can suppose that episodic memory was at work instead of semantic memory. However, animals could have relied on familiarity for their choices, and thus made mistakes due to familiarity rather than false memory.

Our study could have had more control conditions to explore into more details the processes at work in the formation of false memories. First, a non-misleading condition with no odour of shrimp would be interesting to see whether in the absence of odour, the cuttlefish are still not misled, or whether odours play a role in the memory of the tubes. Moreover, another useful control would be the presentation of the empty tube only, without the shrimp tube or the shrimp odour. In this situation, the empty tube should not mislead animals, thus animals should choose the crab tube if they remember the events correctly. Moreover, this control would allow an exploration of

the familiarity process, and thus if animals relied on familiarity, they should favour the empty tube at test. Another condition could explore the role of crab odour instead of the shrimp odour in the olfactory and visual misleading condition, which would allow to explore whether this odour allow cuttlefish to significantly favour the crab at test.

### *Perspectives*

Reconstructive processes are at the base of episodic memory in humans, as stated by the constructive memory framework (Schacter and Addis, 2007b; Schacter et al., 1998; Schacter et al., 2012). It is thus an impressive evolutionary convergence that we could find similar processes in such an evolutionary distant animal. It is an indication that episodic memory requires a reconstructive system, maybe to compress information to economise storage (Schacter and Addis, 2007b). Another possibility is that the role of episodic memory constraints its form: if this memory exists to combine events to imagine future potential events, elaborate alternative scenarios from past events and simulate future ones (Schacter and Addis, 2007b; Schacter et al., 2012; Suddendorf and Corballis, 2007), consequently its form is reconstructive. Since reconstructive processes are thought to exist to recombine past events to simulate future ones, thus to allow future planning (Schacter and Addis, 2007b; Schacter et al., 2012; Suddendorf and Corballis, 2007), the presence of reconstructive processes is a potential indicator of such ability in cuttlefish. If future planning abilities were not to be found in cuttlefish, it would require a reconsideration of the role of reconstructive processes, thus future planning abilities need to be explored in cuttlefish.

Another interesting element of our experiment is how cuttlefish were less misled when they were exposed to olfactory information. This experiment highlights how important olfaction is for cuttlefish, and how overlooked this sense might be. Further studies exploring how cuttlefish perceive the world through olfaction would bring valuable information about this sense. We could for example conduct an experiment combining episodic-like memory and odours, and explore whether cuttlefish can remember what prey they smelt where and how long ago. To do so, the episodic-like memory experiment would be reproduced, but in the first phase, they would only smell the crab at one location and smell the shrimp (preferred prey) at another location. Then, after a delay of one hour, cuttlefish could retrieve a crab at the location of the crab odour, but shrimp would not be present, while both preys would be present after a delay of three hours (Figure 47).

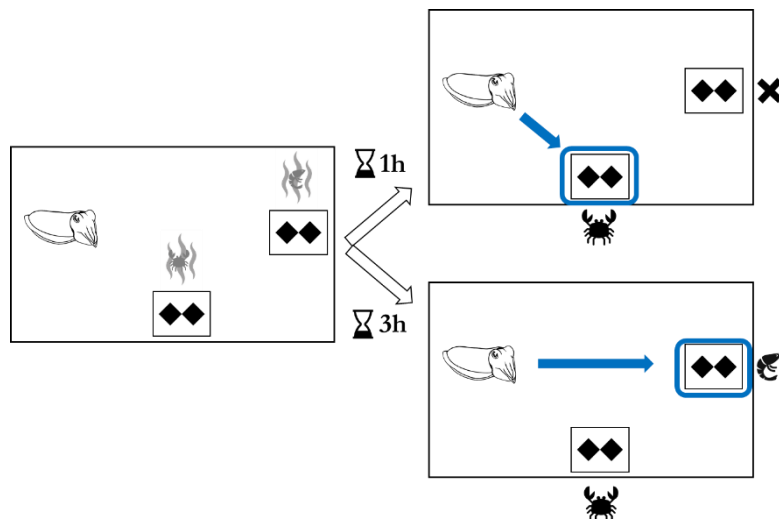


Figure 47: Proposition of a *What-Where-How-long-ago* experiment using olfactory information.

*Cuttlefish would be presented with the odour of a crab in one location, and the odour of shrimp (preferred prey) in another location. After a delay of one hour, the cuttlefish could retrieve the crab at the location of its odour, while after a delay of three hours, both preys would be available at their respective locations.*

Moreover, the false memories study underlines how focused cuttlefish can be. It is of common knowledge when we work with cuttlefish that when they see a prey, they forget the world around them while they focus on it. It is the reason why in our experiment we presented the tubes containing the preys one after the other, because the cuttlefish would be so focused on the first tube they saw that they would not look at the other tubes. An interesting conclusion of our study is that this focus seems to be not restricted to vision, but also olfaction. This information should thus be integrated in experiments working on prey detection and attentional processes in cuttlefish.

### C. Future planning in coleoids

To study future planning in the octopus and the cuttlefish, we elaborated protocols in order to refute the Bischof-Köhler hypothesis, which states that animals cannot escape their present state to plan for their future states (Osvath and Osvath, 2008; Suddendorf and Corballis, 2010; Suddendorf, 1994; Suddendorf and Corballis, 2007; Tulving, 2005). To do so, animals were tested on their ability to plan for a future need independently of their current needs. Two different set-ups were used: cuttlefish were tested on their ability to plan for a future need for food independently of their current need for shelter and their current satiety, while octopuses were tested on their ability to plan both for a future need for food and a future need for shelter while having access to both food and shelter. The consequence of the planning action took place an hour later or more at a different location than the current one, thus a clear spatiotemporal separation was

used. Behaviours were not cued by the environment, not conditioned and not innate, as single trials in a novel experimental set-up were used. As a result, juvenile cuttlefish as well as subadult octopuses did not plan for their future needs, while some adult cuttlefish planned for their future need for food.

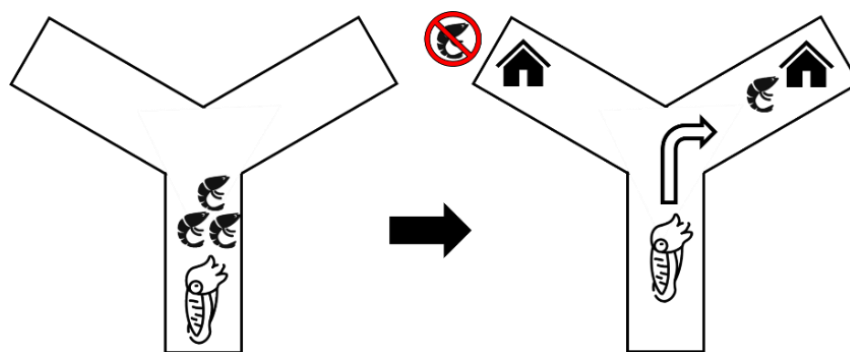
### *Limitations of the experiments*

This experiment with cuttlefish is impaired by a complex trade-off between the current need for shelter and the future need for food. It is thus complex to know why juvenile cuttlefish did not plan for their future. They might not possess future planning abilities, but they also might possess them but still favour their current need for shelter as it could be above their future need for food. The last hypothesis might be right, especially when we observe the behaviour of adult cuttlefish. Some individuals did plan for their future need for food, but most of the tested individuals did not. However, it was observed at the group level that tested cuttlefish spent more time choosing where to go on the second day compared to the first day and the control group (this was not described in the article). This increased latency might be an indicator that animals may have had to balance risks and benefits between choosing between their future need for food and their current need for shelter. The costs associated with future rewards are high and often underestimated (Zentall, 2010), thus securing a current need might be more valuable for survival than planning for a future need. Indeed, the current need to hide might be essential to avoid predation, especially if human experimenters were perceived as a threat, as it was observed in other studies on foraging and predatory risk trade-offs (Cooper, 2000). Under such a threat, animals favour hiding and minimise foraging (Cooper, 2000; Uiblein et al., 1996; Verdolin, 2006), and cuttlefish may have used such strategy. Moreover, the future need for food might be substantially decreased by delayed reward discounting, a process by which an increased delay to obtain a reward decreases the subjective value of the reward (Vanderveldt et al., 2016).

Our experiments might have been strongly influenced by the physiological needs of the individuals tested. The delays without food might have not been perceived as aversive or even as unusual, since both cuttlefish and octopuses were fed once a day during the rearing in captivity. Adult cuttlefish were caught in the wild and sexually mature, they might have been accustomed to eat more often and might have had higher food needs due to the energy allocated for reproduction, to eggs' production and fight for mates (Hanlon and Messenger, 2018).

## Perspectives

It would be valuable to explore future planning without any trade-off in cuttlefish. First, it would be interesting to explore whether in a similar set-up, cuttlefish show temporal myopia. Temporal myopia is commonly observed when an individual does not show any preference for the larger quantity of food when a lot of food is proposed (McKenzie et al., 2004). It is thought to indicate that animals do not think about their future need for food when choosing, but some authors such as Zentall (2005) rather linked it with the fact that hoarding food in a social group might be useless because of pilfering. Temporal myopia – or its absence – could be observed with the following experiment. Cuttlefish would be placed in a Y-maze, and fed to satiety (Figure 48). Then, they would be offered a choice between an arm with a shelter and no food, and an arm with a shelter and food. If individuals significantly favour the arm with the food, then they might take into account their future need for food. However, this experiment does not rule out the simple fact that food might enhance the subjective value of the shelter without any future thinking required.



*Figure 48: Proposition of an experiment exploring temporal myopia in cuttlefish*

*Cuttlefish are fed to satiety, then offered a choice between a shelter without food, and a shelter with food. Temporal myopic individuals would choose randomly, while animals with a sense of the future would choose the shelter with food.*

As future planning was observed only in adult cuttlefish, but not in juvenile conspecifics or in subadult octopuses, we can also make the hypothesis that future planning might emerge late in cephalopods. In humans, future planning as well as episodic memory emerge between the age of 3 to 5 years (Friedman, 2007; Suddendorf and Busby, 2005). Future planning in cephalopods may emerge when animals reach sexual maturity. However, episodic-like memory was shown to emerge earlier, as subadult cuttlefish (Jozet-Alves et al., 2013a; Schnell et al., 2021c) and some subadult octopuses (Poncet et al., 2022) possess it (no studies were conducted on younger individuals). The need of future planning in a late life stage might be linked to the terminal reproduction of both species, which might require complex abilities to find a mate and compete with other conspecifics, especially in cuttlefish (Hanlon and Messenger, 2018). To explore this hypothesis, the future-



planning experiment should be conducted with wild juvenile and wild subadult cuttlefish, which will bring a better understanding on the ontogenesis of the future planning abilities in the species. Moreover, testing wild adult octopuses on their future planning abilities would allow to disentangle whether their absence of future planning abilities came from the young age of the subjects, or whether octopuses really do not possess such abilities.

## **D. Mental time travels in coleoids**

This thesis explored Mental Time Travels abilities in two coleoids: the common cuttlefish and the common octopus. While several results indicate the potential presence of Mental Time Travels in the common cuttlefish, they tend to show the contrary in octopuses.

When studying the retrospective side of MTT, cuttlefish were shown to present the three criteria for episodic-like memory: content, structure and flexibility (Clayton et al., 2003b). Content was explored when cuttlefish remembered what prey they ate, where and how long ago (Jozet-Alves et al., 2013a; Schnell et al., 2021c). Structure was observed when cuttlefish were shown to form false memories, indicative of reconstructive and source monitoring processes linked with integrated and bound memories. Flexibility was observed when cuttlefish adopted flexible foraging behaviours, by reversing from opportunistic to selective foraging strategies in response to future conditions (Billard et al., 2020a). Prospective MTT was also explored in the cuttlefish, and while juvenile individuals did not seem to plan for a future need for food, some adult individuals did. Moreover, some phenomenological aspects of MTT, such as auto-noesis, were explored through Theory of Mind, and cuttlefish show a noteworthy potential in such task (see Annex 1). These multiple elements indicate that cuttlefish might be able to mentally travel through time, and that this capacity is not restricted to vertebrates such as great apes or corvids.

Mental Time Travels is more dubious in octopus. Indeed, we have shown in this thesis that octopuses hardly display retrospective MTT, in other words episodic-like memory, since only one out of seven octopuses learnt to remember what it ate, where and how long ago (Poncet et al., 2022). However, this absence of episodic-like memory abilities might be due to the use of temporal distance as a temporal cue, which might not be easily used by octopuses. Conducting an episodic-like memory task with relative times of occurrence as a time cue, as they seem to rely more readily on this cue, will bring a clearer view on their episodic-like memory abilities. Furthermore, octopuses did not show prospective MTT, as they did not plan for their future needs for food and shelter.

Differences in methodology cannot account for the differences we observed between these species. Concerning the episodic-like memory experiment, all parameters were identical except for the fact cuttlefish had to go near a target to obtain a prey while octopuses had to open a pot. Octopuses opened pots very easily, thus it cannot be considered that opening pots could have impaired octopuses' ability to solve the task. Concerning the future-planning experiment, the task used with octopuses did not contain any trade-off between needs that might have had impaired cuttlefish ability to plan for the future. The experiment with octopuses should have thus favoured the demonstration of future planning but it still did not. Another difference was the age of the subjects: cuttlefish were either juvenile of 2 to 5 months old or adults of 21 to 23 months old, while octopuses were subadults with an estimated age of 6 to 8 months. They thus might have been too young to express future planning abilities, but since they were reaching sexual maturity, they should have started to display such abilities if they had to be useful for reproduction.

Consequently, the observed differences between cuttlefish and octopuses might come from anatomical and ecological differences which lead to differences in cognitive abilities. The prehensile arms and the body without gladius of octopuses might allow them more means to find preys and avoid predators compared to cuttlefish. The increased environmental pressures might have favoured the development of cognitive tools in the cuttlefish that did not emerge in the octopus. Three main hypotheses are thought to drive the evolution of cognitive abilities: 1) the social intelligence hypothesis, 2) the ecological intelligence hypothesis and 3) the predator-prey interaction hypothesis. 1) The social intelligence hypothesis states that complex cognitive abilities have emerged from social complexity, which is visible in various strategies used in fights for dominance (Barton and Dunbar, 1997; van der Bijl and Kolm, 2016) but which is also visible with group size, linked with cooperative behaviour, social bonding and social learning (Dunbar, 1998; van der Bijl and Kolm, 2016). 2) The ecological intelligence hypothesis states that complex cognition emerged from the need to find and extract food in a patchy and unpredictable environment, to form mental maps and remember the spatiotemporal location of resources (Barton and Dunbar, 1997; Dunbar, 1998). At last, 3) the predator-prey interaction hypothesis states that the complex cognitive abilities emerged from the arm race between preys and predators (Byrne and Bates, 2007), which could be comparable to group members dynamics in dominance competition (Amodio et al., 2019). Each of these hypotheses could explain the results we obtained with the studied cephalopods. 1) The social intelligence hypothesis could partially explain why the more social cuttlefish developed more complex cognitive abilities than the solitary octopuses. Cuttlefish are generally considered in between solitary and gregarious. Recent studies indicate that juvenile cuttlefish might be found in group in the wild (Drerup and Cooke, 2021) and adults can be found

in group during the reproductive period (Hanlon and Messenger, 2018). Moreover, hatchlings (Sampaio et al., 2021) and maybe older individuals (Huang and Chiao, 2013) can learn by observing others. Octopuses, on the contrary, are considered as solitary and aggressive toward conspecifics in captivity, and reproduction does not happen in groups (Hanlon and Messenger, 2018). Nevertheless, it is to note that octopuses show observational learning (Fiorito and Scotto, 1992). Complex cognitive abilities might thus have emerged in cuttlefish because of the need to understand and learn from others, and maybe especially for reproduction, as it happens in group, which increase the competition between individuals of the same sex, which in turn rely on deception and other tactics to maximise reproductive chances, as seen in the Australian giant cuttlefish (*Sepia apama*; Hall and Hanlon, 2002).

2) Regarding the ecological intelligence hypothesis, it might explain why complex cognition emerged in coleoids, but it does not explain the differences between cuttlefish and octopuses. Indeed, both species need to find quite unpredictable preys in a patchy environment, and both need to adapt their hunting technics to the various preys they consume. Moreover, octopuses need to extract complex food from various shells, which is not the case of cuttlefish. However, sessile prey consumed by octopuses are more predictable and can form persistent patches which are thus easy to return to, while mobile preys favoured by the cuttlefish are more complex to find.

3) The predator-prey interaction hypothesis might be the hypothesis which explain best the results obtained in this thesis. Cuttlefish seem to possess less means to avoid predators, as they do not build den, hardly hide in crevices because of the lack of flexibility due to their cuttlebone, and cannot use their arms to defend themselves (octopuses were seen wrapping themselves in shells and pebbles and stick on the back of their predators to avoid being bitten). Cuttlefish mostly rely on sand burying and camouflage, abilities that are also used by octopuses. Cuttlefish would thus rely more heavily on their cognitive abilities, to remember where predators can be found and to plan for the strategies they will use to avoid predation. Moreover, cuttlefish do not predate upon sessile preys as octopuses do. While sessile preys can be found in persistent patches which can be easily found, mobile preys can be harder to find, can hide and use tactics to escape predation. Cuttlefish could thus have evolved complex cognitive abilities to remember where and when to find preys, but also to plan for their attack to maximise chance of eating. As cuttlefish spent most of their time resting hidden (Hanlon and Messenger, 2018), complex cognitive abilities might allow them to hunt efficiently in short bouts while avoiding predators, thus maximising their survival. Octopuses, with their various means of defence and their multiple types of prey, can rely on more lenient tactics which might not impair their survival as much as cuttlefish.

## General conclusion

To conclude, this thesis brings new data on Mental Time Travels abilities in cuttlefish and octopuses. On one hand, cuttlefish appear to possess reconstructive episodic-like memory abilities and potential future planning abilities, showing that this species might be able to mentally travel through time. Octopuses, on the other hand, hardly show episodic-like memory abilities and do not plan for their future needs. Their lack of episodic-like memory abilities might be because they encode time in terms of relative times of occurrence rather than temporal distance. Different environmental pressures might have shaped the cognitive abilities of these two species. Remembering the past and planning for the future must likely be necessary for cuttlefish to handle social, ecological, foraging and predatory constraints, while octopuses might rely on less cognitively demanding strategies for survival.

***“Of molluscs the sepia is the most cunning, [while] the octopus is a stupid creature.”***

Aristotle (350 B.C.). The History of Animals, Book IX, part 37.



			
<b>Episodic-like memory</b>	Content	✓ What-Where-How long ago (Jozet-Alves et al., 2013; Schnell et al. 2021)	✗ What-Where-How long ago (Poncet et al., 2022, this thesis)
	Structure	✓ Reconstructive processes in false memories (Poncet et al, this thesis)	■ Not explored
	Flexibility	✓ Flexible foraging (Billard et al., 2020)	■ Not explored
<b>Memory for time</b>	Temporal distance	✓ What-Where-How long ago (Jozet-Alves et al., 2013; Schnell et al. 2021)	✗ What-Where-How long ago (Poncet et al., 2022, this thesis)
	Temporal location	■ Not explored	■ Not explored
	Relative times of occurrence	■ Not explored	✓ What-Which order (Poncet et al., 2022, this thesis)
<b>Future planning abilities</b>		✗ No planning for a future need for food in juveniles (Poncet et al, this thesis)	✗ No planning for a future need for food or shelter in subadults (Poncet et al, this thesis)
		✓? Planning for a future need for food in some adults (Poncet et al, this thesis)	

Figure 49: Summary of Mental Time Travels abilities in the common cuttlefish and the common octopus

# Résumé en français

## **Introduction : Etat de l'art et présentation des modèles**

Cette introduction présente une revue de l'état de l'art de cette thèse de doctorat. Premièrement, je ferai une présentation générale des capacités de voyages mentaux dans le temps, à savoir la mémoire épisodique, et son équivalent chez les animaux connu sous le terme de mémoire de type épisodique, et la planification du futur. Ensuite, je présenterai un aperçu du domaine de la cognition comparée, et les hypothèses qui essaient d'expliquer l'émergence de la cognition complexe, ce qui me mènera à présenter les deux céphalopodes étudiés dans cette thèse.

### ***Partie A : Voyages mentaux dans le temps***

1. Mémoire épisodique chez l'humain : Dans cette section sont présentés les systèmes de mémoire, la mémoire épisodique est définie avec ses spécificités, ses propriétés reconstructives et ses rôles.
2. Mémoire de type épisodique chez l'animal : Dans cette section sont présentés les critères d'étude de la mémoire épisodique chez les animaux, et des expériences variées conduites chez les animaux sont détaillées
3. Planification du futur : Dans cette section est définie la planification du futur et des expériences variées conduites chez l'animal sont détaillées.

### ***Partie B : Etude comparative des voyages mentaux dans le temps***

1. Cognition comparée : Dans cette section est définie la cognition comparée, et les hypothèses émises à propos de l'émergence de la cognition complexe sont détaillées
2. Animaux étudiés : Dans cette section sont présentés les espèces de céphalopodes étudiées dans cette thèse, pour appréhender comment les spécificités anatomiques, écologiques et comportementales de ces deux espèces influencent leurs capacités cognitives.

## **A. Voyages mentaux dans le temps**

Les voyages mentaux dans le temps sont la capacité à voyager mentalement dans son propre passé et son propre futur, afin de revivre ou de pré-vivre des événements (Suddendorf, 1994). Le côté rétrospectif des voyages mentaux dans le temps est connu en tant que mémoire épisodique, tandis que le côté prospectif est généralement appelé planification épisodique du futur.

### ***1. Mémoire épisodique chez l'humain***

Chez les humains, la mémoire à long terme n'est pas considérée comme une entité unique, mais plutôt comme plusieurs types de mémoire médiés par différents systèmes cérébraux (Squire, 2004; Squire et al., 1993). La mémoire à long terme peut être divisée entre la mémoire non-déclarative et la mémoire déclarative, qui inclut la mémoire épisodique.

La mémoire épisodique représente les événements passés personnellement vécus (Tulving, 1984; Tulving, 1985). Elle définit l'identité d'une personne, est considérée comme vraie et est associée avec l'idée de 'se remémorer'. Cette mémoire concerne un événement unique (ou épisode), avec un élément focal, dans un contexte spécifique (lieu et moment ; Tulving, 1984; Tulving, 1985).

La mémoire épisodique se développe tardivement, comme observé avec l'amnésie infantile, lorsque les souvenirs épisodiques sont inaccessibles jusqu'à trois ans (Squire et al., 1993). Les enfants développent les structures cognitives nécessaires autour de l'âge de quatre ans (Roberts, 2002; Suddendorf, 1994; Suddendorf and Corballis, 1997).

La mémoire épisodique est toujours associée avec une conscience de soi à travers le temps (Tulving, 1972). La conscience autoéotique est la conscience de sa propre existence et de son identité à travers le temps. La chronoesthésie est la conscience du temps subjectif dans lequel chacun vit et qui permet les voyages mentaux dans le temps (Tulving, 2002). La chronoesthésie est essentielle à la mémoire épisodique, car elle permet de se souvenir tout en sachant que l'événement ne se déroule pas maintenant, mais dans le passé (Schwartz and Evans, 2001).

Les composants temporels sont une part essentielle de la mémoire épisodique. La mémoire du temps peut être encodée de façon variée. Friedman (1993) a élaboré trois théories non-exclusives pour la mémoire du temps : basée sur la distance, sur la localisation ou sur le temps relatif d'occurrence. Les théories basées sur la distance correspondent à « il y a combien de temps » un événement s'est déroulé ; les théories basées sur la localisation correspondent à « quand » s'est

déroulé un évènement ; les théories basées sur le temps relatif d'occurrence correspondent à la perception de l'ordre des évènements, et la notion « d'avant-après ».

Les composants de la mémoire épisodique sont séparés et conservés individuellement. Quand ils sont remémorés, tous ces composants sont réassemblés ensemble pour recréer l'évènement. La mémoire est donc intrinsèquement reconstructive, comme expliqué par le cadre de la mémoire constructive (constructive memory framework ; Schacter and Addis, 2007b; Schacter et al., 1998; Schacter et al., 2012). La nature constructive de la mémoire épisodique est liée à son rôle d'imaginer des scénarios possibles, considérer les différentes options et simuler notre futur personnel (Schacter and Addis, 2007b; Schacter et al., 2012; Suddendorf and Corballis, 2007). Etant donné que les évènements futurs ne sont pas des répliques exacts du passé, un système constructif est nécessaire : il est l'outil flexible nécessaire pour extraire, recombinaison et réassembler les évènements en une forme différente (Schacter and Addis, 2007a). La nature constructive est aussi liée à une économie d'espace en compressant l'information pour éviter la surcharge (Schacter and Addis, 2007b).

La reconstruction de la mémoire épisodique est vérifiée par un processus de source monitoring (Johnson et al., 1993), qui récupère et évalue l'ensemble des composants contextuels d'un souvenir pour en déterminer les bases contextuelles (en d'autres mots, la source) et de distinguer ce souvenir des autres (Crystal et al., 2013; Johnson et al., 1993; Zaragoza et al., 2007a; Zaragoza et al., 2019a). Le source monitoring peut faire des erreurs, et dans ce cas il génère des mauvaises attributions de la source d'un souvenir à un autre souvenir (Loftus and Hoffman, 1989; Zaragoza et al., 2019a). L'effet de mésinformation est la mauvaise attribution d'une ou plusieurs caractéristiques d'un évènement trompeur au souvenir d'un évènement original, formant des faux-souvenirs (Loftus, 2005; Pickrell et al., 2017; Tousignant et al., 1986; Volz et al., 2017; Wade et al., 2007; Zaragoza et al., 2007a). Les faux-souvenirs sont définis comme des altérations de la mémoire épisodique, où les sujets se souviennent d'évènements ou de caractéristiques qu'ils n'ont pas vécu. Les faux souvenirs sont donc un indicateur des erreurs de source monitoring et constituent un moyen détourné d'étudier les processus d'encodage et de monitoring de la source à la racine de la mémoire constructive.

## ***2. Mémoire de type épisodique chez l'animal***

En l'absence de langage, la mémoire épisodique est étudiée chez les animaux non-humains à travers ses composants comportementaux. En absence d'indicateurs comportementaux de la conscience auto-néotique, cette mémoire est appelée de « type » épisodique (Griffiths et al., 1999). Les critères



comportementaux considérés pour la mémoire de type épisodique sont : 1) cette mémoire possède un contenu spécifique, 2) elle est structurée, et 3) elle est flexible (Clayton et al., 2003b).

Des études ont été réalisées en utilisant différentes méthodes. La mémoire du quoi-où-combien de temps auparavant a été étudiée chez le geai buissonnier (Clayton and Dickinson, 1998b; Clayton and Dickinson, 1999b; Clayton and Dickinson, 1999a; Clayton et al., 2001; Clayton et al., 2003a; Clayton et al., 2005; de Kort et al., 2005), la pie (Zinkivskay et al., 2009), la mésange à tête noire (Feeney et al., 2009), le colibri (González-Gómez et al., 2011), le campagnol des prés (Ferkin et al., 2008), le pigeon (Skov-Rackette et al., 2006), le macaque rhésus (Hoffman et al., 2009), les grands singes tels que le chimpanzé, l'orang-outan et le bonobo (Martin-Ordas et al., 2010) et la seiche (Jozet-Alves et al., 2013b; Schnell et al., 2021c). Une autre méthode, basée sur la mémoire du quoi-où-quand (localisation temporelle) a été étudiée chez le rat (Zhou and Crystal, 2009) et la mésange à tête noire (Feeney et al., 2011a). Le quoi-où-quel ordre a été étudié chez le rat (Ergorul and Eichenbaum, 2004; Panoz-Brown et al., 2016) et le chien (Lo and Roberts, 2019). D'autres chercheurs ont fait varier le contexte plutôt que le paramètre temporel, chez le rat (Eacott and Norman, 2004; Eacott et al., 2005; Panoz-Brown et al., 2016), le cochon (Kouwenberg et al., 2009) et le poisson zèbre (Hamilton et al., 2016). Enfin, d'autres chercheurs considèrent que la mémoire de type épisodique devrait être étudiée à travers des situations et des questions inattendues (Zentall, 2005). Des questions inattendues ont été posées à des pigeons (Zentall et al., 2001), des dauphins (Mercado et al., 1998), et des chimpanzés et orangs-outans (Martin-Ordas et al., 2013).

La mémoire de la source a été explorée chez le rat (Crystal and Alford, 2014; Crystal and Smith, 2014b; Crystal et al., 2013), chez le macaque rhésus (Basile and Hampton, 2017) et chez la seiche (Billard et al., 2020b), tandis que les faux-souvenirs ont été étudiés chez le pigeon (Garry and Harper, 2009; Harper and Garry, 2000), le bourdon (Hunt and Chittka, 2015) et le gorille (Schwartz et al., 2004).

### ***3. Planification du futur***

Les comportements orientés vers le futur peuvent être divisés en deux classes : les comportements sans conscience du futur, et les comportements avec une pensée orientée vers le futur, tels que la planification ou la mémoire prospective (Raby and Clayton, 2009). L'anticipation correspond à n'importe quel comportement qui prend son sens lorsque les événements le suivant sont pris en compte. Elle peut émerger sans le besoin d'une représentation future, à travers l'apprentissage, le conditionnement, des stéréotypes innés, des comportements inflexibles (tels que l'hibernation, la

migration) ou même par coïncidence (Suddendorf, 1994). À l'opposé, la planification du futur est définie comme une projection dans le futur pour pré-expérimenter un événement hypothétique qui implique soi-même et qui peut être utilisé de façon flexible pour planifier de futures actions (Atance and O'Neill, 2001; Eacott and Easton, 2012; Szpunar, 2010). La planification du futur implique que des besoins futurs soient anticipés indépendamment des besoins actuels (Clayton et al., 2003b).

L'hypothèse de Bischof-Köhler déclare que les animaux ne peuvent pas anticiper de futurs besoins ou états car les comportements des animaux sont liés à leur état actuel. Pour réfuter cette hypothèse, plusieurs critères ont été décidés pour explorer les représentations futures des animaux. Pour être qualifié de comportement de planification du futur, un animal doit pouvoir planifier un besoin futur indépendamment de ses besoins actuels. Le comportement ne doit pas être instigué par, ni satisfaire un besoin présent. Le comportement doit satisfaire un besoin qui fera partie de la réalité de l'animal dans le futur, donc une séparation spatiotemporelle claire entre l'action et sa conséquence doit être utilisée. L'exécution du comportement ne doit pas être déclenchée ou guidée par un stimulus de l'environnement (pas de comportement appris ou conditionnés), donc les essais uniques devraient être favorisés. Le comportement ne doit pas être inné, donc la flexibilité devrait être recherchée (Osvath and Osvath, 2008; Suddendorf and Corballis, 2010; Suddendorf, 1994; Suddendorf and Corballis, 2007; Tulving, 2005).

Des comportements de planification du futur ont été observés chez les bonobos et les orangs-outans (Bourjade et al., 2014; Osvath and Osvath, 2008), les singes saïmiris (Naqshbandi and Roberts, 2006), les corneilles (Kabadayi and Osvath, 2017), les geais buissonniers (Correia et al., 2007; Raby et al., 2007) et les geais des chênes (Cheke and Clayton, 2012).

## **B. Etude comparative des voyages mentaux dans le temps**

### ***1. Cognition comparée***

La cognition correspond aux processus par lesquels les informations de l'environnement sont perçues, traitées, retenues, récupérées et utilisées pour prendre des décisions et agir (Chittka et al., 2012; Neisser, 1967; Shettleworth, 1998; Shettleworth, 2000). Ces informations peuvent être manipulées, transformées, réduites, élaborées ou recombinaées pour générer de nouvelles informations (Bayne et al., 2019; Chittka et al., 2012; Neisser, 1967; Shettleworth, 1998). Ces processus sont flexibles et peuvent opérer même en l'absence des informations concernées (Neisser, 1967).

La recherche en cognition comparée a émergé de l'idée qu'il y aurait des processus cognitifs partagés par différentes espèces, notamment partagés par les humains et les animaux non-humains comme les grands singes (Beran et al., 2014; Bräuer et al., 2020; Wasserman et al., 2006). La cognition comparée explore deux questions : quels sont les processus cognitifs présents chez les animaux ; et comment la cognition évolue et quelles pressions de sélection façonnent la cognition (Clayton in Bayne et al., 2019; Chittka et al., 2012; Eaton et al., 2018).

La cognition comparée se focalise sur des domaines de recherche variés, comme la cognition sociale, la cognition spatiale, l'utilisation d'outils, les relations causales, la personnalité, la numérosité, les émotions ou encore les voyages mentaux dans le temps (Beran et al., 2014; Shettleworth, 2010). Elle montre que les capacités cognitives complexes ont émergé plusieurs fois indépendamment, à partir de substrats neuronaux variés. Trois hypothèses principales et non-exclusives essaient d'expliquer comment les capacités cognitives évoluent : l'hypothèse de l'intelligence sociale, l'hypothèse de l'intelligence écologique, et l'hypothèse de l'interaction prédateur-proie.

L'hypothèse de l'intelligence sociale a émergé de l'étude des gros cerveaux des primates, dont la taille est corrélée avec la complexité sociale de l'espèce. La complexité sociale est notamment visible à travers les stratégies « machiavéliennes » telles que la tromperie tactique, la manigance, le complot et la formation de coalition dans les combats pour la dominance (Barton and Dunbar, 1997; Barton and Dunbar, 1997; van der Bijl and Kolm, 2016). L'observation de cette compétition sociale a entraîné l'élaboration de l'hypothèse de l'intelligence machiavélienne (Barton and Dunbar, 1997; Dunbar, 1998). Cependant, la taille du cerveau et la complexité cognitive sont plutôt corrélées avec une autre type de complexité sociale : la taille du groupe, liée à la tendance aux comportements coopératifs, aux liens sociaux et à l'apprentissage social (Dunbar, 1998; van der Bijl and Kolm, 2016). Cela a mené à l'élaboration de l'hypothèse de l'intelligence sociale (Dunbar, 1998).

L'hypothèse de l'intelligence écologique considère que les gros cerveaux viennent du besoin de trouver et d'extraire de la nourriture dans un environnement irrégulier et imprédictible (Barton and Dunbar, 1997). Cette hypothèse suppose que les gros cerveaux se développent à cause du besoin de posséder une mémoire complexe et des cartes mentales pour se souvenir de la location spatiotemporelle de ressources disparates et éphémères, et la capacité d'extraire ces ressources (Barton and Dunbar, 1997; Dunbar, 1998). Cependant cette hypothèse n'a pas été confirmée chez les primates (Byrne and Bates, 2007).

L'hypothèse de l'interaction prédateur-proie suppose que la relation entre proies et prédateurs crée une course aux armements avec une forte sélection et un coût élevé pour la fitness. Cette course

aux armements impacte potentiellement les stratégies cognitives nécessaires pour éviter les prédateurs et trouver des proies (Byrne and Bates, 2007). La dynamique prédateur-proie peut être comparée à la dynamique entre les membres d'un groupe dans la compétition pour la dominance, puisque les deux dynamiques nécessitent des interactions avec d'autres individus à la recherche de gains personnels (Amodio et al., 2019). Cette hypothèse semble plausible car il y a une corrélation entre la taille des cerveaux des proies et de leur prédateurs (van der Bijl and Kolm, 2016), et également une corrélation entre la réponse face aux prédateurs et la taille du cerveaux chez les guppies (van der Bijl et al., 2015).

## ***2. Animaux étudiés***

La recherche comparative est souvent biaisée par un point de vue anthropocentrique (Beran et al., 2014; Bräuer et al., 2020; Wasserman et al., 2006), ce qui fait que la majorité des études comparatives sont focalisées sur les primates, et recherchent des capacités cognitives similaires aux humains. Cependant, d'autres espèces sont aussi régulièrement étudiées, telles que les rats, les pigeons et autres oiseaux, ainsi que les chiens, apportant de nouveaux points de vue en cognition comparée.

Le focus sur les mammifères et les oiseaux a amené à l'idée que l'émergence de cognition complexe viendrait d'un régime alimentaire omnivore, de challenges socio-écologiques avec une histoire de vie lente, une longue période développementale et une longévité importante (Bayne et al., 2019; Schnell et al., 2021a). Cependant, parmi les invertébrés, la cognition complexe a émergé chez des animaux possédant un régime alimentaire purement carnivore, une vie solitaire et une histoire de vie courte : les céphalopodes. Ces mollusques sont définis par un répertoire comportemental riche, complexe et flexible (Hanlon and Messenger, 2018). Ils chassent une grande variété de proies dispersées, donc la chair de certaines doit être extraite de sa coquille ou de sa carapace. Ils vivent sous de fortes pressions de prédation, et leurs interactions sociales sont principalement restreintes à la période de reproduction qui se déroule à la fin de leur vie d'un à deux ans pour la majorité des espèces. Les céphalopodes sont donc les candidats idéaux pour contester l'hypothèse de l'intelligence sociale et explorer les hypothèses d'intelligence écologique et d'interaction prédateur-proie, afin de mieux comprendre l'évolution de la cognition complexe (Schnell et al., 2021a).

# **Chapitre 1 : Mémoire spatio-temporelle chez les poulpes**

## ***Partie I : Exploration de la mémoire de type épisodique chez le poulpe (Article 1)***

Les seiches communes font preuve de capacités de mémoire de type épisodique en se remémorant ce qu'elles ont mangé, où et combien de temps auparavant (Jozet-Alves et al., 2013b; Schnell et al., 2021c). Pour explorer si ces capacités de mémoire de type épisodique sont communes à tous les céphalopodes ou si elles ont émergé spécifiquement chez la seiche, nous avons reproduit la même expérience avec des poulpes communs. Seul un individu a appris les taux de réapprovisionnement durant l'entraînement et ensuite montré des capacités de mémoire de type épisodique, tandis que les autres individus ont favorisé des stratégies de recherche de nourriture plus simples, montrant une grande variabilité entre individus. Nous avons fait l'hypothèse que les pressions environnementales puissent être moins contraignantes chez les poulpes que chez les seiches, ce qui pourrait expliquer pourquoi les poulpes ne se basent pas autant sur la mémoire de type épisodique que les seiches. Une autre hypothèse est que les poulpes possèdent peut-être des capacités de mémoire de type épisodique, mais qu'ils ne sont peut-être pas capables d'encoder le temps en termes de distance temporelle. Par conséquent, ils n'étaient peut-être pas capables de résoudre la tâche présentée de cette façon.

## ***Partie II : Exploration de la mémoire du temps chez le poulpe (Etude préliminaire 1)***

À la suite de l'étude sur la mémoire de type épisodique chez les poulpes, nous avons investigué leur capacité à encoder le temps pour explorer si leur incapacité à résoudre la tâche de mémoire de type épisodique venait de leur incapacité à encoder les distances temporelles. Nous avons par conséquent conduit une expérience pour explorer si les poulpes pouvaient se baser sur les temps relatifs d'occurrence, en d'autres termes l'ordre d'une séquence. Pour cela, une séquence d'images de coquillages était présentée aux poulpes, puis ils devaient choisir entre deux images laquelle était apparue le plus tôt dans la séquence. Les poulpes ont réussi cette tâche, indiquant qu'ils sont peut-être meilleurs pour encoder le temps en termes de temps relatifs d'occurrence plutôt qu'en termes de distances temporelles.

## Chapitre 1.I. Exploration de la mémoire de type épisodique chez le poulpe.

*Les poulpes turbulents sont de règle : Les poulpes *Octopus vulgaris* utilisent des stratégies multiples et individuellement variables dans une tâche de mémoire de type épisodique*

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### ***Abstract***

La mémoire de type épisodique a principalement été étudiée à travers des tâches expérimentales dans lesquelles les sujets devaient se souvenir de ce qu'ils ont mangé, où et quand ou dans quel contexte. Apparemment commune chez les mammifères et les corvidés, la capacité de mémoire de type épisodique a également été démontrée chez la seiche commune, un mollusque céphalopode. Pour explorer si cette capacité est commune à tous les céphalopodes ou si elle a émergé pour faire face à des contraintes écologiques spécifiques, nous avons conduit une tâche de mémoire de type épisodique avec sept poulpes *Octopus vulgaris*. Seul un individu a appris les taux de réapprovisionnement durant l'entraînement et ensuite montré une capacité de mémoire de type épisodique, tandis que les autres individus ont favorisé des stratégies de recherche de nourriture plus simples, comme l'évitement de la familiarité et de l'alternance, l'utilisation d'une stratégie win-stay (gagner-rester) et de sensibilité au risque. Une grande variabilité dans l'utilisation de ces stratégies a été observée entre les individus et au sein des essais d'un même individu durant l'entraînement. Puisque les poulpes semblent vivre sous des pressions environnementales moins contraignantes que les seiches, ils n'ont peut-être pas besoin de se baser autant sur la mémoire de type épisodique pour optimiser leur recherche de nourriture comme les seiches. Ces résultats mettent en lumière les différences d'utilisation des capacités de cognition complexe entre seiches et poulpes, qui sont peut-être dues aux différentes contraintes environnementales et de prédation.

### ***Mots-clés***

Poulpe, mémoire de type épisodique, stratégies de recherche de nourriture, variabilité individuelle

## Chapitre 1. II. Exploration de la mémoire du temps chez le poulpe

### *Mémoire de l'ordre temporel d'une séquence chez le poulpe*

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### ***Abstract***

Les informations temporelles peuvent être mémorisées de façon variée, sous forme de distance temporelle (« Il y a combien de temps ? »), de localisation temporelle (« Quand ? ») ou de temps relatifs d'occurrence (« Quel ordre ? »). Tandis que les humains peuvent se servir de façon équivalente de ces trois types d'encodage du temps, les autres espèces animales n'ont peut-être pas la même capacité. Une précédente expérience a montré que les poulpes ne semblent pas être capables de discriminer des délais écoulés, ils s'avèrent donc être incapables d'encoder le temps en termes de distance temporelle. Cependant, il est possible qu'ils puissent se baser sur un autre type d'encodage du temps, tel que les temps relatifs d'occurrence. Nous avons réalisé une expérience durant laquelle une séquence aléatoire de quatre images était présentée à des poulpes. Après un délai, ils devaient sélectionner entre deux images laquelle était apparue le plus tôt dans la séquence. Après entraînement, tous les poulpes testés ont réussi cette tâche, et certains ont même transféré leur apprentissage à de nouvelles images symboliques, démontrant ainsi que les poulpes peuvent mémoriser l'ordre des informations.

### ***Mots-clés***

Séquences, temps relatifs d'occurrence, poulpes, mémoire du temps

## **Chapitre 2 : Les faux souvenirs chez la seiche**

### ***Partie I : Pourquoi étudier les faux souvenirs ? (Revue 1)***

Les faux souvenirs sont des altérations de la mémoire épisodique qui reflètent les erreurs de reconstruction et de monitoring de la source. Ils sont largement étudiés chez les humains, mais très rarement chez les animaux. Pourtant, étudier les faux souvenirs chez les animaux pourrait permettre une meilleure compréhension des processus à la base de leur mémoire. La mise en place de critères clairs permettra de réaliser des études précieuses sur les faux souvenirs des animaux.

### ***Partie II. Faux souvenirs chez la seiche (Article 2)***

Les seiches sont connues pour se remémorer des événements spécifiques, autrement dit des souvenirs de type épisodique, mais les processus sous-tendant cette capacité sont inconnus. Nous avons élaboré un protocole favorisant la formation de faux-souvenirs chez la seiche, pour explorer les processus reconstructifs de leur mémoire. Les résultats obtenus suggèrent que les seiches forment des faux souvenirs visuels, et que cette susceptibilité est influencée par le niveau d'attention soutenue sur l'évènement trompeur, qui peut être modulée par des processus olfactifs. Ces erreurs de mémoire sont peut-être la première indication de la présence de processus reconstructifs dans la mémoire des céphalopodes.



## **Chapitre 1. I. Pourquoi étudier les faux souvenirs ?**

*Des erreurs pleines de sens : Etudier les faux souvenirs pour explorer la nature reconstructive de la mémoire*

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### ***Abstract***

Les faux souvenirs sont des altérations de la mémoire épisodique se produisant quand des individus se remémorent des événements ou des détails qu'ils n'ont pas vécu. Les faux souvenirs s'inscrivent dans le cadre de la mémoire constructive et de la mémoire de la source, qui stipule que les souvenirs sont constitués de multiples détails enregistrés séparément. Afin de se remémorer un souvenir, ces détails doivent être liés au moment de l'encodage pour être ensuite récupérés collectivement. Le souvenir ainsi reconstitué est évalué, à travers un processus de monitoring de la source, pour vérifier s'il a été correctement récupéré et si ce souvenir est plausible. Cependant, le monitoring de la source peut parfois échouer et attribuer erronément le détail d'un souvenir à un autre, créant ainsi un faux souvenir. Les faux souvenirs sont étudiés de façon extensive chez les humains, avec des études sur les faux souvenirs riches, avec les paradigmes d'effet de mésinformation, ou avec les illusions de mémoire associative de Deese-Roediger-McDermott. Tandis que les études sur les faux souvenirs chez les humains sont nombreuses, les études sur ce sujet sont particulièrement rares chez les animaux. Les études essayant d'explorer les faux souvenirs chez les animaux se sont plutôt focalisées sur des biais de reconnaissance ou sur la généralisation de la peur contextuelle, et les rares études qui ont utilisé un paradigme d'effet de mésinformation ont étudié très peu d'individus. Ce manque de recherche est regrettable, les faux souvenirs pouvant apporter des informations de valeur sur les processus de mémoire de type épisodique chez les animaux, ainsi que sur les processus reconstructifs et de monitoring de la source liés à elle. Nous proposons donc de mettre en place des critères pour définir les limites de ce nouveau domaine d'étude de la mémoire chez les animaux.

### ***Mots-clés***

Faux souvenirs, animaux, mémoire reconstructive, monitoring de la source

## Chapitre 2. II. Faux souvenirs chez la seiche

### *Faux souvenirs chez la seiche*

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### ***Abstract***

La mémoire épisodique est un processus reconstitutif *per se*, ce qui signifie que durant un évènement, les caractéristiques le composant sont encodées et mises en mémoire séparément dans le cerveau, puis reconstruites lorsque le souvenir de l'évènement est récupéré. Cependant, à cause de cette reconstruction, et même avec des processus contrôlant la fiabilité des souvenirs comme la mémoire de la source (par exemple, est-ce que je l'ai vu, senti ou entendu ?), certaines erreurs peuvent survenir. Ces erreurs mnémoriques ont particulièrement lieu quand différents évènements partagent plusieurs caractéristiques communes, produisant des superpositions difficiles à discriminer, menant à la création de faux souvenirs. La seiche commune (*Sepia officinalis*) est connue pour être capable de se souvenir d'évènements spécifiques, autrement dit des souvenirs de type épisodique. Afin d'étudier si cette mémoire est basée sur des processus reconstitutifs, nous avons élaboré un protocole favorisant la formation de faux souvenirs chez la seiche. Les résultats obtenus suggèrent que les seiches forment des faux souvenirs visuels, et que cette susceptibilité est influencée par le niveau d'attention soutenue sur l'évènement trompeur. Ces erreurs de mémoire sont peut-être la première indication de la présence de processus reconstitutifs dans la mémoire des céphalopodes.

### ***Mots-clés***

Mémoire, céphalopodes, faux souvenirs, processus reconstitutifs, processus attentionnels

### **Chapitre 3 : Planification du futur chez les coléoïdes.**

#### ***Partie I : Planification du futur chez la seiche et le poulpe (Article 3)***

Les voyages mentaux dans le temps présentent à la fois un côté rétrospectif, à travers la mémoire épisodique, et un côté prospectif, à travers la planification du futur. Ces deux capacités sont intimement liées, et la mémoire épisodique semble exister pour permettre la planification du futur. Puisque les céphalopodes font preuve de mémoire de type épisodique, nous avons décidé d'investiguer les capacités de planification du futur chez les seiches et les poulpes. Des seiches ont été soumises à une expérience où elles pouvaient planifier un futur besoin de nourriture à la place de suivre leur besoin actuel d'abri, tandis que les poulpes pouvaient planifier leurs futurs besoins de nourriture et d'abri. Ni les seiches ni les poulpes n'ont planifié leurs besoins futurs. Les céphalopodes ne possèdent donc peut-être pas de capacités de planification du futur, ou nos expériences n'ont pas pu mettre en lumière ces capacités.

#### ***Partie II : Planification du futur chez la seiche adulte (Etude préliminaire 2)***

Pour explorer l'influence de l'âge et du statut physiologique des seiches, nous avons reproduit l'expérience de planification du futur initialement conduite chez des seiches juvéniles avec des seiches adultes sexuellement matures. Ces seiches ont été soumises à la même expérience, où elles pouvaient planifier un besoin futur de nourriture à la place de suivre un besoin actuel d'abri. Certaines seiches ont planifié ce besoin futur, indiquant que les seiches possèdent peut-être des capacités de planification du futur, mais que le compromis entre nourriture et abri peut être influencé par de multiples paramètres qui ont conduit certains individus à favoriser l'abri plutôt que de planifier leur besoin de nourriture.

## Chapitre 3. I. Planification du futur chez la seiche et le poulpe

*Des voies évolutives différentes pour la mémoire de type épisodique et la planification du futur : un aperçu des capacités des céphalopodes*

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### ***Abstract***

La mémoire épisodique et la planification du futur sont généralement considérées comme deux volets du même système de voyages mentaux dans le temps. Il est possible que les caractéristiques neurobiologiques et développementales communes observées entre ces capacités chez les vertébrés soient le produit d'une évolution étroitement liée ou d'une phylogénie partagée. Les céphalopodes modernes, avec leurs origines évolutivement indépendantes et leurs capacités cognitives complexes, apparaissent comme des espèces prometteuses pour déterminer si ces capacités ont, ou non, des histoires évolutives séparées. Dans notre étude, nous avons testé les capacités de planification du futur chez deux espèces de céphalopodes, qui ont fait preuve – ou non – de capacités de mémoire de type épisodique : la seiche et le poulpe, respectivement. Les seiches communes ont été testées sur leur capacité à planifier un besoin futur de nourriture à la place de suivre leur besoin présent de se cacher. Pour explorer leur flexibilité dans un tel comportement, nous avons fait varier la valeur protective de l'abri. Les capacités de planification du futur des poulpes ont été examinées en leur permettant de déplacer de la nourriture et des abris à des endroits où ils en auraient besoin plus tard. Nos expériences ont montré que ni les seiches ni les poulpes ne faisaient preuve de planification du futur. Ces résultats peuvent être expliqués par les paramètres expérimentaux, mais ils peuvent aussi refléter la simple absence de capacités de planification du futur chez les céphalopodes. Puisque les seiches possèdent des capacités de mémoire de type épisodique, de tels résultats suggèrent que la mémoire épisodique et la planification du futur auraient des histoires évolutives séparées. Identifier les similarités et différences de cognition complexe chez les espèces vertébrées et les céphalopodes, et au sein des céphalopodes, sera d'une grande importance pour définir quelles pressions évolutives ont mené à l'émergence de capacités cognitives complexes.

### ***Mots-clés***

Céphalopodes, planification du futur, poulpe, seiche, voyages mentaux dans le temps, compromis

## Chapitre 3. II. Planification du futur chez la seiche adulte

*Premières indications de planification de besoins futurs chez la seiche commune adulte*

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### ***Abstract***

Les capacités de planification du futur sont souvent considérées comme une spécificité humaine, comme déclaré par l'hypothèse de Bischof-Köhler. Bien que cette hypothèse ait été contestée avec des études sur les mammifères et les oiseaux, une précédente expérience avec des céphalopodes n'a pas pu mettre en lumière des capacités de planification du futur chez la seiche et le poulpe. Cependant, nous avons fait l'hypothèse que l'âge ait pu influencer le comportement et l'état physiologique des animaux testés, ce qui les aurait empêchés d'exprimer des capacités de planification du futur. Pour étudier cette hypothèse, nous avons reproduit l'expérience de planification du futur, initialement réalisée avec des seiches juvéniles élevées en captivité, avec des seiches matures sexuellement. Ces seiches ont été soumises à une expérience où elles pouvaient planifier un besoin futur de manger plutôt que suivre leur besoin de se cacher. Contrairement aux individus plus jeunes, certaines seiches adultes ont planifié ce besoin futur, indiquant ainsi que les seiches pourraient en fait posséder des capacités de planification du futur. Cependant, la majorité des individus a continué de favoriser l'abri immédiat, indiquant que planifier le futur et faire un compromis entre un besoin présent pour un abri et un besoin futur pour de la nourriture semble être influencé par de multiples paramètres qui rendent les capacités de planification du futur difficile à explorer.

### ***Mots-clés***

Planification du futur, seiche, voyages mentaux dans le temps, compromis, différences liées à l'âge

## **Conclusion**

Pour conclure, cette thèse apporte de nouvelles données sur les voyages mentaux dans le temps chez les seiches et les poulpes. Les seiches semblent posséder des capacités reconstructives de mémoire de type épisodique et de potentielles capacités de planification du futur, montrant que cette espèce pourrait être capable de voyager mentalement dans le temps. Les poulpes, quant à eux, font difficilement preuve de capacités de mémoire de type épisodique et ne planifient pas leurs besoins futurs. Leur absence de capacités de mémoire de type épisodique vient peut-être du fait qu'ils encodent le temps en utilisant les temps relatifs d'occurrence plutôt que les distances temporelles. Des pressions environnementales différentes ont peut-être façonné les capacités cognitives de ces deux espèces. Se souvenir du passé et planifier le futur doivent probablement être nécessaires aux seiches pour gérer les contraintes sociales, écologiques, de recherche de nourriture et d'évitement de prédateurs, tandis que les poulpes semblent pouvoir dépendre de stratégies cognitivement moins exigeantes pour leur survie.

# **Annexes**

# **Annexes**

## **Annex 1: Exploration of Theory of Mind in the cuttlefish**

### **Theory of mind in cephalopods: Does one cuttlefish know what another does not know?**

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#### **Abstract**

Theory of Mind is the ability to understand the mental states of others, even when they differ from one's own. This ability is thought to have evolved to cope with social complexity, but it might also be linked with complex cognitive abilities such as Mental Time Travels. While still controversial in animals, Theory of Mind has been explored in various social mammals and birds, but never in solitary species. Cuttlefish, with their complex cognitive abilities but their partially solitary lifestyle, could be the ideal candidate to explore whether Theory of Mind can emerge only in the presence of social complexity. We here conducted an experiment where we explored whether a cuttlefish could act based on what another cuttlefish did not know. The tested cuttlefish could either select a prey which could not be seen by another cuttlefish or a prey which was visible by both cuttlefish. The behaviour of the tested cuttlefish indicated that it seems to know what information were available to the other cuttlefish, and it chose accordingly. This preliminary study is thus the first indication that a partially solitary invertebrate such as the cuttlefish might possess Theory of Mind.

#### **Key-words**

Theory of Mind, Cephalopods, Cuttlefish



## A. Introduction

Theory of mind (ToM) is the ability to infer and understand the mental states of others, such as desires and beliefs, and to understand they can differ from one's own (Krupenye and Call, 2019; Premack and Woodruff, 1978). This ability is considered to have evolved to solve complex social demands (Stone, 2006), but ToM could also be a by-product of the ability to form second order representations, which might have emerged along with complex cognitive abilities such as Mental Time Travels. ToM has been studied in various species (for a review, see Krupenye and Call, 2019), and several elements indicates that great apes (Premack and Woodruff, 1978; Krupenye et al., 2016; Karg et al., 2015; Schmelz et al., 2011), monkeys (Báez-Mendoza and Williams, 2020), lemurs (Shepherd and Platt, 2008), corvids (Dally et al., 2010; Ostojić et al., 2014), dogs (Maginnity and Grace, 2014) or bottlenose dolphins (Tomonaga and Uwano, 2010) possess a ToM. However, all these studies were conducted with animals living in social groups, thus evolving under heavy social selective pressures, rendering unclear whether ToM can emerge under lighter social constraints.

Common cuttlefish are known for their complex cognitive abilities, while presenting a partially solitary lifestyle, with younger individual and sexually mature adults gathering together (Drerup and Cooke, 2021; Hanlon and Messenger, 2018). Studying ToM abilities in this cephalopod might thus allow to explore the selective pressures favouring the emergence of the ToM. We conducted a preliminary study to explore the ability of a cuttlefish to imagine the knowledge, or its absence, of another individual. To do so, the tested cuttlefish could either select a prey which was visible for both cuttlefish, or a prey which could not be seen by another cuttlefish.

## B. Methods

### *1. Ethical statement*

The experiment was conducted in compliance with the French regulation for the protection and use of animals in research and the directive 2010/63/EU of the European parliament. The procedure was authorised (#22429 2019101417389263 v2) by the ethical committee of Normandy region (Comité d'Ethique de NORmandie en Matière d'EXpérimentation Animale, CENOMEXA; agreement number 54).

## **2. Subjects**

One subadult female cuttlefish (*Sepia officinalis*; nine months-old) was trained and tested in March and April 2022. Two other cuttlefish (*Sepia officinalis*; nine months-old, one male and one female) were used as demonstrators. Eggs were collected in the English Channel, cuttlefish hatched and were reared in group for two months at the SMEL (Synergie Mer et Littoral, Blainville-sur-Mer, France) before being transferred to the rearing facilities of the CREC (Centre de Recherches en Environnement Côtier, Luc-sur-Mer, France).

Cuttlefish were reared individually in circulating natural seawater at  $17 \pm 2^\circ\text{C}$ , under natural light conditions. At the beginning of the experiment, the tested cuttlefish and one demonstrator were placed in a white squared plastic tank (0.78x0.78m) divided by a transparent partition in two equally-sized compartments (0.78x0.39m), with one cuttlefish per compartment. The tank was enriched with pebbles and plastic algae. They were fed daily with live shrimps (*Crangon crangon* or *Palaemon serratus*) of suitable size.

## **3. Material**

During the experiments, partially opacified glass tubes (8 cm high x 4 cm in diameter) were used as targets. They were the same tubes as the ones used in the experiment by Poncet et al. (2023). The inside surface of the tube was almost entirely covered with an opaque laminated paper, with a vertical window (about 2 cm wide x 8 cm high) remaining transparent. The paper was printed with various black and white patterns identical on both sides (13 patterns were used; *i.e.* solid grey, black or white, grey and black checked, black and white striped...), and each tube presented a different pattern. By doing so, the cuttlefish could see the content of the tube by looking through the transparent window, and when the tube was rotated, the content could not be seen anymore. To prevent immediate access to the tubes, a transparent plexiglass panel was placed between the tubes and the cuttlefish, about ten centimetres away from the tubes.

## 4. Procedure

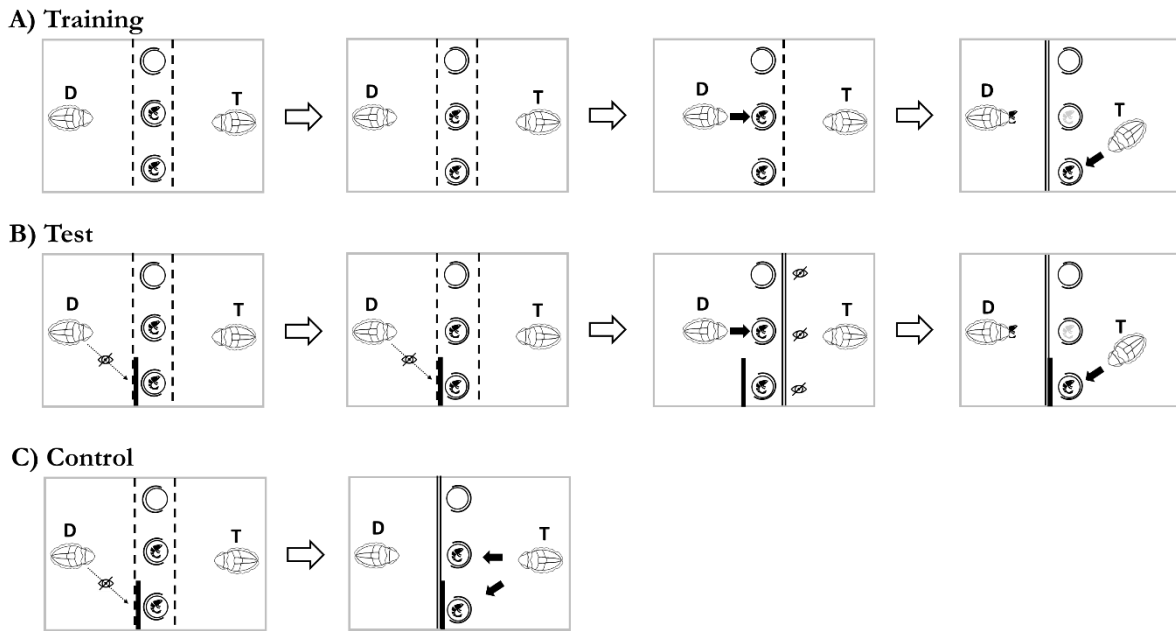


Figure 50: Representation of the procedure used during the experiment, during A) training trials, B) test trials, and C) control trials (See materials and methods for the detailed procedure).

D represents the demonstrator cuttlefish and T the test cuttlefish. Dotted lines represent transparent panels, double lines and thick black lines represent opaque panels.

### a. Training

Three tubes were placed between the two cuttlefish, with two tubes containing one shrimp and one empty tube (Figure 50A). Both cuttlefish were prevented to access the tubes by a transparent plexiglass panel one each sides of the tubes (dotted lines on Figure 50). At first, only the tested cuttlefish could see the content of the tubes. Then, the tubes were rotated and only the demonstrator cuttlefish could see the content of the tubes. The transparent partition was removed on the demonstrator side, and the demonstrator subsequently chose one tube while the tested cuttlefish witnessed the choice. The demonstrator virtually depleted the chosen tube and was rewarded with one shrimp, then an opaque partition (represented by a double line on Figure 50) was placed in front of the demonstrator. The transparent partition was removed on the tested cuttlefish side, and the cuttlefish could choose one tube, without seeing its content. The tested cuttlefish was rewarded with a shrimp only if it chose the tube containing the shrimp which was not depleted by the demonstrator.

### *b. Test*

The same apparatus as the training was used for testing. During testing, three tubes were placed in between two transparent partitions, between the two cuttlefish (Figure 50B). Two tubes contained a shrimp and one tube was empty. A small opaque plate (thick line on Figure 50) was placed on the demonstrator side to prevent the demonstrator to see one of the tubes containing a shrimp, while the test cuttlefish could see it. At first, the content of the three tubes was only visible by the tested cuttlefish. The tubes were rotated so the demonstrator could see the content of the tubes, except for the tube hidden behind the opaque plate. An opaque partition was then added so the tested cuttlefish could not see the tubes or the demonstrator anymore. The demonstrator was given a shrimp, then the opaque partition was moved from the tested cuttlefish side to the demonstrator side, and the test cuttlefish could choose one tube, without seeing its content. The tested cuttlefish was rewarded with a shrimp only if it chose the tube hidden by the small opaque plate, which was not depleted by the demonstrator.

### *c. Control*

For control trials, the organisation of the apparatus was the same as for the test trials (*i.e.* small opaque plate hiding one tube and the opaque partition; Figure 50C). After the tested cuttlefish saw the content of the tubes, the tubes were rotated and an opaque partition was added on the demonstrator side, and the tested cuttlefish could immediately choose one tube. Since none of the tubes had been depleted, the cuttlefish was rewarded for choosing either tube containing a shrimp. Test and control trials were randomly intermixed.

## **C. Results**

The tested cuttlefish was trained for nine trials and successfully chose the tube containing the non-depleted shrimp on seven out of nine trials (binomial test,  $p = 0.017$ ). She chose the same tube as the demonstrator on the two other trials.

The cuttlefish was subsequently tested for five test trials, and successfully chose the tube hidden from the demonstrator in all five trials (binomial test,  $p = 0.008$ ). The cuttlefish was also tested on five control trials, in which she chose twice the hidden tube, twice the other tube with shrimp and once the empty tube.

## D. Discussion

In this preliminary study, we explored the Theory of Mind in cuttlefish, by investigating the ability of one cuttlefish to know what another individual does not know. During training, the cuttlefish had to learn that if another individual chose a tube containing a shrimp, then this shrimp was not available anymore. Consequently, the cuttlefish had to choose the second tube with a shrimp which was not chosen by the other individual. The studied cuttlefish spontaneously selected the tube unselected by the other cuttlefish. In the Theory of Mind test, cuttlefish had to choose the tube hidden from the demonstrator individual to be rewarded, and the cuttlefish systematically and spontaneously chose this tube, while it randomly chose a tube during control trials.

This experiment thus indicates that the studied cuttlefish might have known that the demonstrator could not know that there was a shrimp in the hidden tube, and thus chose the tube according to this knowledge. The cuttlefish might have put herself in the place of the other cuttlefish to know their field of vision, and thus what they could see or not, and what they would choose. This behaviour corresponds to the Theory of Mind, since the cuttlefish seemed to understand the knowledge of the other cuttlefish, even if this knowledge differed from her own (*i.e.* the other individual cannot see what I see; Krupenye and Call, 2019; Premack and Woodruff, 1978).

The behaviour of the cuttlefish in the training is also interesting, since it shows that the cuttlefish did not rely on stimulus enhancement or social facilitation. Yet, octopuses show observational learning (Fiorito and Scotto, 1992), and while cuttlefish do not improve their hunting technique for crab when watching conspecifics (Boal et al., 2000b), they seem to choose a resting place depending on the behaviour of other individuals (Huang and Chiao, 2013) and hatchlings seem to be able to tune their hunting behaviour with which of other individuals (Sampaio et al., 2021). In our experiment, instead of observational learning, cuttlefish significantly favoured the tube not selected by the demonstrator. It seems the cuttlefish spontaneously knew that a tube that delivered a shrimp did not deliver another one, showing a fine understanding of the tube mechanics.

Finding indications of the Theory of Mind in cuttlefish can be surprising as this species is not known for its marked social behaviours. Cuttlefish are considered in between solitary and gregarious, as they are socially tolerant, juveniles can be found in group in the wild (Drerup and Cooke, 2021) and adults regroup during reproductive period. Even though this species is not considered as gregarious, the pressures during reproduction might be necessary to allow the emergence of Theory of Mind abilities, which might be necessary to compete with sexual competitors and optimise the chance of mating. Another hypothesis is that Theory of Mind might be useful in other field than the social domain, such as the Mental Time Travels abilities. Indeed,

some authors considers that Theory of Mind is necessary to mentally travel in time (Suddendorf, 1994; Suddendorf and Corballis, 1997), as someone who is unable to represent the mental state of another when it is different from their own present mental state will not be able to represent their own earlier or later mental state.

To conclude, this experiment shows the first indications that cuttlefish might possess Theory of Mind abilities, but further studies including more individuals are now needed to confirm this finding.

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# Etude comparative des voyages mentaux dans le temps chez les céphalopodes

## Résumé

Les voyages mentaux dans le temps sont la capacité à voyager mentalement dans son propre passé, connue sous le nom de mémoire épisodique, et dans son propre futur, connue sous le nom de planification du futur. Pour comprendre quelles pressions évolutives façonnent l'émergence de ces capacités cognitives, il est utile d'étudier des espèces présentant une histoire évolutive indépendante des vertébrés communément étudiés, telle que les céphalopodes. Deux espèces de céphalopodes ont été étudiées dans cette thèse : la seiche commune et le poulpe commun. Ces deux espèces possèdent des capacités cognitives complexes mais présentent chacune une façon unique de répondre à leurs contraintes environnementales. De précédentes expériences ont montré que la seiche possède des capacités de mémoire de type épisodique, se remémorant ce qu'elle a mangé, où et combien de temps auparavant. Dans une première expérience, nous avons reproduit ces études avec des poulpes pour explorer leur capacité à utiliser la mémoire de type épisodique. Seul un individu a réussi cette tâche, tandis que les autres poulpes ont eu recours à d'autres stratégies. Nous avons alors émis l'hypothèse que les poulpes aient échoué à cette tâche car ils ne pouvaient peut-être pas encoder le temps en termes de distance temporelle (*i.e.* « il y a combien de temps »), mais plutôt encoder l'ordre des événements. Des poulpes ont donc été testés sur leur capacité à se souvenir de l'ordre des images dans une séquence, et ils ont réussi la tâche. Dans une autre expérience, les processus de mémoire reconstructive chez la seiche ont été mis en lumière en utilisant des faux souvenirs, qui se sont révélés être un outil utile pour explorer les systèmes constructifs et de monitoring à la base de la mémoire de type épisodique. Enfin, une expérience sur les capacités de planification du futur des seiches et des poulpes subadultes a montré qu'ils ne planifiaient pas leurs futurs besoins de nourriture et/ou d'abri. Cependant, certaines seiches adultes se sont montrées capables de planifier leur futur besoin de nourriture, bien que la majorité des individus ne l'ait pas fait. Ensemble, ces résultats montrent que les seiches semblent posséder des capacités de voyages mentaux dans le temps alors que les poulpes ne semblent pas en présenter, indiquant comment les pressions écologiques peuvent façonner l'émergence de telles capacités.

**Mots-clés :** Voyages mentaux dans le temps, Mémoire de type épisodique, Planification du futur, Cognition comparée, seiche, poulpe

## Comparative study of Mental Time Travels in cephalopods

### Abstract

Mental Time Travels are the ability to travel mentally into one's personal past, also known as episodic memory, and into one's personal future, also known as future planning. To understand which evolutive pressures shape the emergence of these cognitive abilities, it is valuable to study species presenting an independent evolutionary history from the commonly studied vertebrates, such as the cephalopods. Two species of cephalopods were studied in this thesis: the common octopus and the common cuttlefish. Both share complex cognitive abilities while presenting each a unique way to handle their environmental constraints. Previous experiments showed that cuttlefish possess episodic-like memory abilities, remembering what they ate, where and how long ago. In a first experiment, we reproduced these studies with octopuses to explore their ability to use episodic-like memory. Only one individual succeeded in the task, while the others relied on variable strategies. We emitted the hypothesis that octopuses failed the task because they might not encode time in temporal distance (*i.e.* "how long ago") but rather use the order of events. Octopuses were thus tested on their ability to remember the order of images in a sequence, and succeeded in the task. In another experiment, cuttlefish reconstructive memory processes were revealed using false memories, which proved to be a useful tool to explore the constructive and monitoring systems at the basis of episodic-like memory. At last, an experiment on the future planning abilities of subadult cuttlefish and octopuses showed that they did not plan for their future needs for food and/or shelter. However, some adult cuttlefish were able to plan for their future need for food, even though the majority of individuals did not. Altogether, these results indicate that cuttlefish might possess Mental Time Travels abilities while octopuses might not, hinting how ecological pressures shape the emergence of such abilities.

**Keys-words:** Mental Time Travels, Episodic-like memory, Future planning, Comparative cognition, cuttlefish, octopus